

Cremnophilous succulents of southern Africa: diversity, structure and adaptations

by

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Othonna cremnophila [88], from south-facing cliffs of the Rosyntjieberg, Richtersveld, Northern Cape. Artist: Jeanette Loedolff.



DECLARATION

I, Ernst Jacobus van Jaarsveld, declare that the thesis that I hereby submit for the degree Philosophiae Doctor at the University of Pretoria, is my own work and has not previously been submitted by me for a degree at this or any other tertiary institution.

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ABSTRACT

Cremnophilous succulents of southern Africa: diversity, structure and adaptations

Ernst Jacobus van Jaarsveld

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The vertical cliff-face habitat is renowned for many specifically adapted plant species that exhibit a high degree of local endemism. Over a period of nine years the succulents and bulbous succulents on cliff faces in South Africa and Namibia were systematically surveyed and documented. Distinction was made between succulents growing on cliffs as part of a wider habitat and those found only on cliffs (obligate cremnophytes). Most major cliff-face habitats in the study area were visited and all plants were documented. A check list and descriptions (including adaptive traits) of the 220 obligate cremnophilous taxa are provided.

During the study some 45 new cremnophilous succulent taxa were discovered and named, representing almost 20% of the total and proving that cliff habitats are some of the least studied environments, not only in southern Africa but globally. Among the newly described cremnophilous taxa is the genus *Dewinteria* (Pedaliaceae).

Using stem length, three basic cliff-face growth forms are identified—compact or cluster-forming ‘cliff huggers’, cliff shrublets or ‘cliff squatters’ and pendent ‘cliff hangers’. Compact growth (often tight clusters or mats) is mainly associated with the winter-rainfall

Succulent Karoo and Thicket regions, especially Namaqualand. However, further north the same compact growth forms are associated with an increase in altitude such as the Drakensberg Escarpment and other northern mountains. Most pendent growth forms are associated with the eastern and southeastern summer-rainfall regions; a number of smaller pendent shrublets occur on the high quartzitic sandstone mountains of the Western Cape. The degree of specialisation varies from highly adapted (smaller percentage) to less specialised (often eco-forms), and some taxa have no obvious adaptations.

This study revealed a general increase in succulence in most obligate cremnophilous succulent species (compared to closely related species in other habitats), a reflection of their xeric habitat, and plants tend to be more compact. Also, there is a shift in reproductive output, including an increase in vegetative reproduction (backup), wind-dispersed seed and enriched flowering associated with certain species. Most obligate cremnophilous succulent plants in the study area have cliff-adapted features, ensuring long-term survival.

Keywords: adaptations, biogeography, cliff-adapted features, cliff face, cremnophytes, ecology, evolution, flora, specialisation, succulent plants.

CHAPTER 1

INTRODUCTION

1.1 Objectives, key questions and hypotheses

The flora of cliffs is one of the least studied biotic assemblages in the world. Most of these plants are uniquely adapted to this type of habitat and are known as cremnophytes (from the Greek, *kremnos* = cliff + *phyton* = plant). In southern Africa, here defined as South Africa and Namibia, these vertical rock faces are the habitat of many succulent plants. This study is the first in the world to focus only on these obligate cremnophytes, and in particular those that are essentially succulents and bulbous succulents.

The principal aims of this study were to:

- Describe and document all the obligate or near-obligate succulent plants (and their bulbous component) growing on cliff faces throughout South Africa and Namibia.
- Describe and interpret the morphological adaptations of succulent cremnophytes to the cliff-face habitat, both vegetatively and in terms of sexual reproduction.

The key questions to be asked, included:

- How many obligate or near-obligate succulent cremnophytes occur in southern Africa and what are their identities?
- What are the adaptive traits of succulent cremnophytes distinguishing them from related plants from non-cliff habitats?
- What is the influence of geology and climate on the geographical distribution of succulent cremnophytes?
- What is the conservation status of succulent cremnophytes?

Obligate cremnophilous succulent plant species grow in the absence of larger herbivores. The vertical habitat furthermore demands a shift in strategy with regard to plant morphology and reproductive behaviour. How do cremnophytes survive in a hyper-arid terrain (high water run-off) and in the absence of larger herbivores? This study focuses on the macro-morphological and reproductive adaptations of obligate cremnophilous succulents that enable their self-sustaining long-term survival on the cliffs.

The only constant environmental feature of cliffs is the vertical aspect of the habitat. All other features of the habitat (e.g. rainfall, geology, aspect, altitude, solar radiation, growth space) vary. North-facing cliffs (southern hemisphere) result in high exposure to the sun, while south-facing cliffs experience extended shade and hold moisture for longer periods. Altitude influences variables such as temperature and rainfall. Therefore, just how do the various succulent and succulent bulbous cremnophytes adapt and adjust to the vertical orientation of the cliff when exposed to gravity as well as to all these other environmental variables?

Apart from documenting the diversity of succulent cremnophytes in the study area, the main hypotheses tested in the study are:

- Obligate succulent cremnophytes show many specialised adaptations in morphology and behaviour that enable them to survive in their cliff habitat.
- Obligate cremnophytes that show an increase in succulence and other cliff-adapted features, at the same time show a decrease in armour. Cliff plants are therefore expected to be less thorny (mechanical defence) and less bitter (chemical defence) than their plain-dwelling relatives, not as well camouflaged and with adjusted growth and reproduction behaviour.

1.2 Succulent riches of South Africa and Namibia

The succulent richness of South Africa and Namibia is well documented (Van Jaarsveld 1988a; Smith *et al.* 1997; Van Wyk & Smith 2001). Some 3 500 species and infraspecific taxa of succulents occur throughout South Africa and Namibia. In southern Africa, succulent plants reach their greatest abundance and diversity in the semi-arid, winter-rainfall (summer-dry) climate of the southern and western parts of South Africa where they often are the dominant life form. They occupy almost all habitats, especially those that dry out rapidly, and

these are especially common in dry river valleys and on rocky outcrops where there is little competition from other non-succulents.

Evolutionary adaptations of plant life forms are diverse and those in plants from especially arid and semi-arid habitats are often most remarkable (Jürgens 1986). Southern Africa is exceptionally rich in xerophytes, many of which display intriguing structural and physiological adaptations to extreme habitats such as fog deserts, cliff faces and quartz pebble fields, and to fire, grazing pressure and other animal disturbances. A high proportion of these specialised xerophytes are local endemics (Schmiedel & Jürgens 1999; Van Wyk & Smith 2001).

The preponderance of xerophytes in southern Africa can be ascribed to the long history of aridity in parts of the region, terrain diversity, as well as to local habitat isolation and the evolutionary propensity and plasticity of some of the plant taxa (Van Jaarsveld 2000a). Examples include xerophytes such as the gymnosperm *Welwitschia mirabilis* (Bornman 1978), members of the angiospermous family Mesembryanthemaceae, for example *Lithops*, *Gibbaeum*, *Conophytum* and *Pleiospilos* and many other succulent plant taxa in families such as Crassulaceae, Asclepiadaceae and Euphorbiaceae (Marloth 1908; Van Jaarsveld & Struck 1995).

In the present study particular attention has been given to the structural and reproductive behavioural adaptations of obligate cremnophytes, their geographical distribution patterns, habitats (terrain, geology and aspect) and to the way in which they differ from taxonomically related members of the particular group growing on adjacent accessible terrain. The similar growth forms displayed by cliff-face succulents and bulbs throughout the world are due to similar selective environmental pressures. Information gathered during the study will also be used in a future publication on southern African cliff-face succulents in which the species and their adaptations will be illustrated by various botanical artists.

1.3 Cliffs and cremnophytes

Cliff faces are well represented all over South Africa and Namibia and a particular habitat of many cliff-adapted and opportunistic biota (termed cremnobiota). These biota vary from miniature life forms (lichens and algae), various higher plant species, lizards and smaller mammals to larger animals such as baboons (primates). This study focuses on the obligate succulent cremnophytes and their cliff-face habitat.

For this study, a cliff is defined as a vertical or near vertical rock face or precipice of various geological formations. Cliff characters depend on the composition of the rock (geology), evolutionary time scale and the impact of various other environmental factors (e.g. aspect, wind, rainfall and temperature).

Cliffs in southern Africa are found along the coast and associated incised river valleys, inland escarpments, inselbergs and other mountainous parts. Cliff sizes vary and, following Larson *et al.* (2000), a formation higher than 4 m is regarded as a cliff. Terminology has been adopted from Larson *et al.* (2000). According to them, three elements are present on cliff faces: the cliff top which consists of a plateau or sloping ridge, the cliff foot or cliff pediment at the cliff base, and the cliff face. The cliff face varies among localities and is occupied by ledges, cracks and crevices, the more specific habitats occupied by succulent cremnophytes. The cliff foot often has a scree slope (due to weathering and rock falls).

The only relatively constant feature of a cliff is its vertical profile; all other features (altitude, climate, geology, aspect) vary. However, even the vertical profile is variable. Larson *et al.* (2000) write: ‘The critical distinction between a cliff and a slope may be that objects falling from cliffs usually fall through the air before they hit solid ground, whereas objects falling down slopes normally maintain at least sporadic and probably painful contact with the ground. The point here is that it is impossible to define a critical angle that separates cliffs from other structures. Furthermore, from a scientific perspective, we gain little by trying to make such strict definitions. What we can do is recognize that slope angles from 180° (the underside of an overhang) to 90° are all strictly “cliff”, whereas slope angles less than 90° are less so.’ It is the long-term effect of this vertical habitat that has moulded plants morphologically and physiologically.

Definitions of succulent plants are given in detail in Chapter 2. For the purposes of this study a succulent is defined as a plant that is adapted to grow in a dry habitat (ground water at times depleted) and that stores sufficient quantities of water in its leaves, stems or roots, thus enabling it to survive dry periods. The adopted definition includes leaf, stem and/or root succulence. Only succulent plants and bulbous succulent plants have been considered in this study. The two semisucculent genera, *Dewinteria* and *Stemodiopsis*, have been used as ‘out-groups’ showing that without some storage of moisture (succulence), other additional backup strategies are necessary to ensure sustained life on the cliff face.

1.4 Cremnophilous succulent plants

In southern Africa at least 220 cremnophilous taxa have made cliffs their permanent habitat (true cremnophytes). One of the challenges was to determine what an obligate cremnophilous succulent plant is, as some succulents simply grow opportunistically on cliffs, whereas many others (species, varieties and ecotypes) have developed special adaptations enabling them to grow only in this type of habitat. In the case of the latter taxa, cliffs are their sole habitat and refuge. There are many borderline cases of succulent plants that have their main habitat on the cliff, but are occasionally found on non-cliff habitats as well. Many succulent plants are commonly associated with cliffs but have distributions that extend to non-cliff habitats. Some of them are *Crassula cultrata*, *C. nudicaulis* var. *nudicaulis*, *C. perforata*, *C. rupestris* subsp. *rupestris*, *Haemanthus albiflos* [10] and *Portulacaria afra*.

Obligate cremnophilous succulent and succulent bulbous plants have made the cliff face their exclusive habitat. It is this very inaccessibility and human and animal fear of cliffs that provide a safe haven for these cremnophytes. The plants are thus protected by the precipice itself. The absence of large animal disturbances enables the plant to relax on defences and focus its genetic resources on other adaptive aspects such as coping with aridity, the vertical nature of the habitat and reproduction on the rock face. Owing to the vertical orientation of cliffs, water run-off is extreme, resulting in mostly an edaphically very dry habitat and with succulents often a conspicuous feature.

Cliffs are commonly encountered throughout the mountainous regions of South Africa, from the coast to the high Drakensberg Escarpment at 3000 m. Cliffs are represented in all the various biomes of South Africa and Namibia (Mucina & Rutherford 2006), including Desert along the west coast (Werger 1983) and the subtropical Indian Ocean Coastal Belt along the east coast.

1.5 Shaped by the cliff

What makes cliff plants so special or peculiar? As shown above, in most conventional habitats plants are moulded into their various shapes by evolution and natural forces such as competition, fire and herbivory. On the cliff, however, among the primary moulding forces is the vertical habitat with its extreme water run-off, lack of soil, ever-present gravity and exposure to light from a more or less 90° plane, while disturbances such as herbivory and fire are lacking or greatly reduced. Because of the widespread incidence of cliffs throughout

southern Africa, several environmental variables, for example geology, aspect, altitude and latitude, have contributed significantly to the diversity of cliff plants.

Cliff plants also have to survive potential damage from events such as rock falls, falling debris and animals that have adapted to be partially at home on the cliffs, for example rock dassies (*Procavia capensis*) and chacma baboons (*Papio ursinus*). Fortunately weathering of most southern African rock faces is extremely slow, allowing stability of the substrate and therefore sufficient time for cliff plants to evolve adaptive surviving strategies. In southern Africa there is also a marked increase in succulence and succulent plant diversity associated with terrain diversity such as mountainous regions and dry river valleys.

1.6 Historical review

Hitherto cliff vegetation has been grossly neglected in studies worldwide (Larson *et al.* 2000). Past studies were mainly opportunistic (part of floras) or short essays on reproductive adaptation of plants in the Mediterranean (Snogerup 1971; Thompson 2005). Oetli (1903) and Wetter (1918), however, did pioneering work on chasmophytes, especially those of limestone cliffs in Europe. In 1987, Peter Bapst (University of Cape Town), under the supervision of Prof. Eugene Moll, studied the cliff-face communities of Table Mountain. This study was unfortunately never published due to his tragic death, but a summary of this work appeared in *Veld & Flora* some years ago (Moll & Van Jaarsveld 2007).

On a more global scale, Douglas Larson and his team at the University of Guelph, Canada, formed an interdisciplinary research group in 1985, focusing mainly on the function and structure of cliff ecosystems with the emphasis in the northern hemisphere. In 2000, Douglas Larson, Uta Matthes and Peter Kelly co-authored the first scientific book on cliff faces: *Cliff ecology: patterns and process in cliff ecosystems*. They realised the significance of and the need for understanding cliffs as neglected habitats, and I quote them (Larson *et al.* 2000: 301): ‘While attempts have already been made to answer some of the many questions posed about the structure and function of other habitats, this is not the case with cliffs. The study of cliffs is still in its infancy and every question resolved produces an array of new questions that demand resolution. It is an exciting time to be exploring the ecological complexities of a previously ignored ‘place.’ I cannot agree more with these authors, and the many new cremnophilous species recently discovered and named in the study region reveal a need for further research, especially in the subtropics and tropics.

1.7 Layout of thesis

The various disciplines investigated in this thesis are here represented and addressed as 12 chapters that can be divided into six main parts: an introduction to cremnophytes and their cliff-face habitat (Chapters 1–3), structural adaptations and reproduction (Chapters 4 & 5), phytogeography, evolution and conservation (Chapters 6–8), an overview of cremnophilous growth forms and a summarising check list of obligate and near-obligate cremnophilous taxa (Chapters 9 & 10), findings, general discussion and conclusions (Chapter 11) and the species treatments representing the bulk of the thesis (Chapter 12), followed by Appendices 1, 2 and 3.

Chapter 1 commences with a general overview of succulent cremnophytes. The study area is then defined, highlighting the occurrence of cliff faces in South Africa and Namibia (Chapter 2). Chapter 3 deals with the cliff-face habitat, its vertical orientation and the diverseness of other features such as geology and climate, influenced by factors such as latitude, aspect and situation. Chapter 4 (the main focus of this study) addresses the various structural adaptations of obligate succulent and bulbous succulent cremnophytes, for example an increase in cliff-adapted features such as an increase in succulence and the three main growth forms associated with cliffs—cliff hangers, cliff huggers and cliff squatters. Reproduction on the cliff demands specialist reproductive strategies such as a vegetative propagation backup (vegetative propagules, rooting at nodes) and seed dispersal that is mainly by wind, all treated in Chapter 5. Chapter 6 explains how representation and diversity of cremnophytes vary according to geology, climate and situation. Historical evolutionary driving forces are discussed in Chapter 7, for example the long history of aridity and inland uplift, explaining present distributions in the light of historical models. Owing to their relatively stable nature, cliffs act as refugia for cremnophilous and other succulents and should therefore be conserved (Chapter 8). Chapter 9 consists of a diagram of the cremnophilous growth forms. It depicts the adaptive pathways of the 220 cremnophytes identified in this study. Chapter 10 is a detailed check list in table format of the main features of the 220 identified cremnophytes. General discussion and conclusions follow in Chapter 11. All 220 species and their adaptations to the cliff face are individually treated in Chapter 12. Each treatment includes a brief description, an account of the distribution, and dispersal strategies. Most taxa are illustrated by means of photographs, some also by colour plates. The many publications that have emanated from this study are listed in Appendix 3.

CHAPTER 2

METHODS AND DEFINITIONS

2.1 Study area

Since 2001 I have investigated the prominent cliff faces of most of the important mountain ranges, the Great Escarpment, inselbergs and river valleys in the study area, which includes South Africa, Namibia and the Kingdoms of Swaziland and Lesotho. This was done by vehicle, on foot or by other means (Van Jaarsveld 1991b) and in the field I was always assisted by supportive colleagues and students. Parts of the major inaccessible river valleys in South Africa and Namibia such as the Orange, Mzimvubu and Thukela Rivers were explored in canoes.

2.2 Methods

Plants were obtained by rock-climbing, occasionally using a catapult or aluminium tubing with a hook at the tip. After storms, plants or portions of plants were gathered at the base of cliffs. Living plants or vegetative material were collected, assembled and grown on at Kirstenbosch National Botanical Garden where their growth and reproductive behaviour could be investigated and the plants photographed or illustrated by botanical artists (Tamlin Blake, Gillian Condy, Gillian Forster, Cora Jardine, Elbie Joubert, Eric Judd, Jeanette Loedolff, Gerhard Marx, Lisa Strachan and Vicki Thomas).

Observations presented here have benefited from the author's 36 years experience of botanical exploration in southern Africa. In addition, major works and field guides on southern African plants, especially bulbous ones and succulents, were consulted for possible cremnophytes (e.g. Reynolds 1950; Toelken 1985; Hilliard & Burt 1987; Hammer 1993; Van Jaarsveld 1991b, 1994a,b; Retief & Herman 1997; Goldblatt & Manning 2000; Egli 2001, 2002, 2003; Hartmann 2001a,b; Albers & Meve 2002; Pooley 2003). Other important check lists consulted include Germishuizen & Meyer (2003) and Germishuizen *et al.* (2006).

Topographic maps of southern Africa were obtained from the Chief Director of Surveys, Mowbray, and regions with potential cliff environments were identified and subsequently visited. This mainly included inspecting the maps for drainage lines of all major river systems as well as for cliffs along the coast and the inland Great Escarpment. The excellent satellite photographs available on Google Earth on the internet were also a handy tool. A geological map of the Council

for Geoscience (Keyser 1997) and the latest vegetation map of South Africa (Mucina *et al.* 2005) were also consulted for establishing specific features of the various cliff faces.

Cliffs are hazardous places and were always approached with safety in mind. Binoculars were often used for spotting plants on cliff faces. Once potential cremnophytes had been located, the base of the cliff was inspected and the safest possible routes to the plants were planned. The plants were then examined and documented (notes, photographs and herbarium specimens). In some cases a catapult was used to shoot down vegetative parts with a stone. When all other means to obtain plant material failed, standard rock-climbing techniques such as abseiling were used (Fyffe & Peter 1990) as a last resort. Digital and conventional cameras were used to photograph plants *in situ* and localities were recorded with a GPS.

Plants grown at Kirstenbosch from material collected in the field were used for additional observations on behaviour (e.g. vegetative reproduction, growth rate and flowering times) and for preparing more herbarium specimens. Fully grown adult plants were also weighed and plants of each species recorded when fully turgid. The cultivated plants were illustrated by various botanical artists for a future book on the cliff-dwelling succulent and bulbous plants of southern Africa.

To test their chemical defence mechanisms, leaves of the various cremnophilous members of *Aloe* and their close non-cremnophilous relatives were cut and the taste of the leaf sap was recorded.

2.3 Definitions

In this section certain terms frequently used in the thesis, are defined.

Succulent plants are commonly found in the study area as an adaptation to a dry environment (Van Jaarsveld 1988a). Von Willert *et al.* (1992) showed the importance of succulence (as part of a plant tissue) as an adaptive feature to a dry environment. In spite of the semi-arid or arid environment, most succulents nevertheless do require a fairly regular moisture supply. The term 'succulent plant' is a widely used concept and the degree of succulence varies, with many borderline cases. For practical reasons, the definition of Von Willert *et al.* (1992) was used.

Succulent (Von Willert *et al.* 1992): ‘A succulent (or succophyte) is a plant possessing at least one succulent tissue. A succulent tissue is a living tissue that, besides possible other tasks, serves and guarantees an at least temporary storage of utilizable water, which makes the plant temporarily independent from external water supply, when soil water conditions have deteriorated such that the root is no longer able to provide the necessary water from the soil.’

The moisture that succulent plants carry (in leaves, stems and roots), taxes the plant and consequently succulent plants need a strong support system (Von Willert *et al.* 1992). This is especially true of ascending succulent growth forms. Dicotyledons such as arborescent mesembs (*Stoeberia arborea* and *Euphorbia* spp.) have secondary growth (and woody xylem). Monocotyledons do not have normal secondary growth, but often have a secondary peripheral cambium consisting of vascular bundles providing a strong fibrous skeleton, a feature prominently displayed in dead remains of *Aloe dichotoma*. Smaller succulent plants solve their weight support system by a compact growth form of which Von Willert *et al.* (1992) distinguish three types:

- i) Compact leaves in an acaulescent rosette where the outer leaves touch the substrate (e.g. *Crassula hemisphaerica*, *Gasteria* spp., *Haworthia* spp.).
- ii) Compact growth, leaves closely packed, touching each other, thus forming a support (e.g. *Crassula columnaris*).
- iii) Prostrate growth as in *Jordaaniella* spp. and *Senecio radicans*.

Obligate succulent plants on cliffs demand a shift in growth form adaptation as well as in the structure of the reproductive parts. Sometimes this is drastic, other times one sees only subtle differences.

Chasmophyte: A plant growing on rocks, rooted in detritus and debris in crevices and fissures (Lincoln *et al.* 1982). Many succulent plants are chasmophytes but not all chasmophytes are succulent.

Crempnophyte: A plants growing on cliff faces (vertical to near vertical rock face) in rock crevices, cracks or on rocky ledges, in a mainly vertically or near vertically orientated environment (Jackson 1971). Most crempnophytes can also be classified as chasmophytes, but not all chasmophytes are crempnophytes (cliff-dwelling). Obligate succulent crempnophytes are succulent plants of which at least 90% of the main population grow only on cliffs. These

succulent plants have made cliffs their permanent habitat. They are fully equipped (morphologically, structurally and reproductively) for long-term survival on cliffs. The term *Kremnophyte* is used by Usher (1970). The etymology of the term is in fact from Greek, *kremnos* a cliff, and *phyton* a plant. In this theses the term ‘cremnophyte (s)’ are used throughout, as referring to a plant or plants growing on cliffs. Three types of cremnophytes are recognised:

Cliff squatter: A cremnophyte that grows as a solitary main stem, usually exhibiting a squat or compact, but non-pendent, ascending growth (e.g. *Othonna cremnophila* [88], *O. triplinervia* [89] and *Delosperma laxipetalum* [198]).

Cliff hanger: A cremnophyte with pendent stems (e.g. *Huernia pendula* [81], *Aloe challisii* [15], *A. meyeri* [22]). The leaves can also be hanging (*A. hardyi* [20]) or are sometimes recurved (*A. dabenorisana* [17]). Some cliff hangers exhibit epinastic growth, the leaves and stems growing towards gravity (*A. corallina* [16]).

Cliff hugger: A cremnophyte that grows in tight clusters against the cliff face. This includes many succulent plants that proliferate from the base or increase in size by division of the stems (e.g. *Crassula cymbiformis* [117], *Gasteria glomerata* [46], *Plectranthus ernstii* [168], *Tylecodon longipes* [156]). Some cliff huggers have pendent leaves (**leaf hangers**), for example *Albuca cremnophila* [64] and *A. thermarum* [68].

Epinasty: A geotropically positive response due to unequal growth (resulting from different auxin levels) of a leaf or stem. It is often the result of gravitropism (Wareing & Nasr 1961). The downward curvature is a response to the faster growth of the upper surface of a leaf or stem, compared to the lower surface. Of the 220 obligate cremnophilous taxa occurring on cliffs in the study area, 29 (13%) display epinasty and as a result have a pendent growth. Plants grown in containers at Kirstenbosch retained this pendent growth mode as so clearly seen in *Albuca thermarum* [68], *A. cremnophila* [64], *Aloe challisii* [15], *A. hardyi* [20], *A. corallina* [16], *Bulbine cremnophila* [31], *B. latifolia* var. *curvata* [32] and *Gasteria rawlinsonii* [48].

Amphicarp: The term amphicarp was reviewed by Barker (2005). ‘Amphi’ is a prefix pertaining to two types, systems or sides. According to Cheplick (1987), amphicarp is a term used for the phenomenon where a plant produces two types of seed, for example above and below ground. It therefore also implies flowers of two kinds—arboreal and buried flowers (geoflorous). Amphicarpic plants produce only a portion of their seed below ground

(geocarpy) while the rest is conventionally dispersed. This phenomenon usually occurs in plants of arid regions and, according to Barker (2005), it is associated with cleistogamy, where flowers are formed below ground, and consequently with heterodiaspory so clearly seen in the short-lived semisucculent *Dewinteria petrophila* [221]. Also see Table 2.1.

Growth form: Characteristic appearance of a plant under a particular circumstance (Lincoln *et al.* 1982), in this study usually a cliff face.

Life form: Structural features and method of perennation, and the result of the interactions of all life processes (phenotypic and genotypic) (Lincoln *et al.* 1982). The appearance of plants as trees, shrubs or herbs as a result of their adaptation to their environment.

Raunkiaerian life forms: Raunkiaer (1934) classified all plants by growth forms based on the type and position of renewal buds with regard to ground level. In this study, growth forms pertain to the position of renewal buds with regard to growth space on the cliff.

Phanerophyte: Tall arborescent plant.

Chamaephyte: Plant with growing buds at or just above ground level (or ledge or crevice of a cliff).

Cryptophyte: Plant with renewal buds below ground (hidden in a crevice or ledge of a cliff).

Hemicryptophyte: Plant with renewal buds at ground level (or from crevice or ground level of a cliff ledge).

Therophyte: An annual (renewal buds above ground) that completes its life cycle within the rainy season.

Although most of these life forms can be found on cliffs, most obligate cremnophytes fit into the chamaephyte (stem hangers, cliff huggers and cliff squatters) or hemicryptophyte (leaf hangers) life form category; therophytes are rare.

Lithophyte; epiphyte: Lithophytes are plants that grow on rocks. Epiphytes grow on other plants for anchorage and support and are usually found on tree branches (non-parasitic). Lichens and species of moss are regularly encountered on cliff faces (lithophytic) in the study area. These two groups are poikilohydric, drying out in between wet periods. *Parmelia* spp. (lichens) especially are important pioneers on solid rock faces, creating a suitable habitat for cremnophilous succulents such as *Conophytum* spp. and small *Crassula* spp. Dense stands of

Parmelia form a perfect habitat where detritus can accumulate, ideal for providing a foothold where fine Crassulaceae (seed dust diaspores carried by wind) and *Conophytum* seed (locally dispersed by water action) can establish. *Parmelia* spp. present on a cliff are also an indicator of regular moisture such as fog or dew.

A few ‘lithophytic’ succulent orchids are encountered on cliff faces in the northeastern part of the Eastern Cape and in southern KwaZulu-Natal. These plants also occur on boulders and accessible rocky sites and are not necessarily obligate lithophytes as they also occur as epiphytes on trees. There are three such orchids—*Tridactyle bicaudata* subsp. *rupestris*, *Rangaeris muscicola* and *Polystachya pubescens*. Occasionally other species, usually epiphytic on trees, are also encountered on cliffs (including *Ansellia africana*, Africa’s largest epiphytic orchid).

Therophytes: Plants that complete their life cycle in a single season, e.g. *Aeollanthus namibensis*, a dwarf annual chasmophytic succulent. Although not an obligate cremnophyte, it also grows on cliffs and was collected on cliffs near Ruacana in savanna where it is locally abundant. It has spreading branches and divided leaves, with local seed dispersal. *Dewinteria petrophila* [221] is a weak perennial semisucculent cremnophilous herb (cremno-therophyte) from the northern Kaokoveld that deposits its seed deep in crevices by means of specialist negatively phototropic basal branches. It is an obligate cremnophyte.

Plagiotropism: Many plants on level ground exhibit plagiotropic or procumbent growth. Plagiotropic plants can afford to lengthen and do not have to cope with gravity as they are supported by the horizontal terrain. On a cliff, plagiotropic plants will exhibit distinctly pendent growth. Examples include species of genera such as *Delosperma* and *Plectranthus*.

TABLE 2.1—Terminology relating to amphicarp and geocarp in plants growing on cliff faces adapted from Barker (2005)

Terminology	Type	Subtype	Species
Active cremnocarp	subterranean (crevice) fruiting from aerial flowers	aerial flowering and subsequent burial in cliff crevice by active growth	<i>Colpias mollis</i> , <i>Stemodiopsis rivae</i> [222]
Cremno-amphicarp	two different floral and fruiting modes (crevice cleistogamy and aerial chasmogamy)	flowers and fruits produced above and in cliff crevices	<i>Dewinteria petrophila</i> [221]

CHAPTER 3

THE CLIFF-FACE HABITAT

The cliff as habitat is well described by Larson *et al.* (2000). Cliff size, morphology, age and location are important as it determines the various cremnobiota, their diversity, distribution and population size. It is therefore necessary to consider various cliff formations, their characteristics and origin in the study area and elsewhere.

Cliffs occur throughout earth, are part of the lithosphere and are the product of a particular vertical scar weathering pattern. Plants occupy most habitats on earth. Cliffs are part of the geomorphology (of various geological formations) and the study of their biota has largely been neglected in the past (Larson *et al.* 2000). The outer ‘skin’ (upper mantle) is covered by the lithosphere (visible outer part), hydrosphere (oceans or lakes) and the atmosphere. Interactions between these three spheres with the biosphere (living organisms) give rise to the pedosphere (soil). Drainage lines expose evidence of various historical geological events in the form of different layers. It is the sun that is the main driving force of most of the outer erosion (via water action, heating and cooling, wind and gravity) caused by recycling of moisture (via the atmosphere) from the hydrosphere (rainwater). The lithosphere is not stable and is driven by internal forces in the lower and upper mantle (plate tectonics) of the earth, often causing uplift (mountain-building), volcanoes, etc. The difference in rock composition and continual erosion (drainage lines such as rivers, etc.) shape the landscape. Nothing on earth is static and the surface texture reflects historical geological processes and other events such as crater impacts; mountain-building and erosion are thus continual processes. Gravity and erosion ensure the recycling of material to lower aspects and eventually the depositing of material in the hydrosphere (oceans). This process, although continual, is more intense where the rainfall is higher, and erosion much more rapid. Existing cliffs, although often more static owing to the solid formations, will therefore eventually also be weathered down and new formations formed.

3.1 Formation of cliffs in southern Africa

The subcontinent is geologically diverse and cliffs are present from the sedimentary coastal and other sea cliffs to the highest, basalt-capped mountain tops in Lesotho (3000 m a.s.l.). Cliffs are commonly found along the inland escarpment, along incised river valleys, on other mountains as well as on inselbergs. The Egosia Fault along the southeast coast has resulted in spectacular

sea-facing sedimentary (sandstone) cliffs with waterfalls that plunge directly into the sea. Cliffs usually consist of exposed vertical bedrock of various geological formations, and the nature of the cliff face varies according to the rock type, rock strength and historical erosion events.

Apart from water action resulting in cliffs along drainage lines, cliffs can also be shaped by wave action along the coast or by sinkholes caused by chemical weathering as in dolomite (Lake Otjikoto and Lake Guinas in Namibia). Cliffs vary from small to very large and from solid to very unstable. The present properties of any particular cliff face reflect the geology, rock texture, strength, past seismic activities and rate of erosion. Each cliff face has its unique characteristics, usually consistent with a particular geological formation.

3.1.1 Cliff bedrock strength

Cliffs vary greatly in their outer morphology, a result of the weathering and erosion process, and are dependent on the strength and consistency of the bedrock formation. Rock strength is also influenced by, among other things, historical tectonic movement and differences and inconsistency in pressure. The outer morphology of each cliff face is a unique ‘fingerprint’ reflecting the past and is continuously shaped by ever-changing weather patterns. Some cliffs are stable (very hard geological formations) and some are soft and less stable (softer formations). Variability of the strata also leads to distinct erosion patterns, the softer material being removed at a faster rate than the harder, more weatherproof formations. Sunamura (1992) investigated the inherent mineral strength of unweathered rock formations. He found Mesozoic-Palaeozoic sedimentary rocks with a strength value of, for example, 2 000–3 000 kg cm². Igneous rocks had values ranging from 500–3 000 kg cm² and tertiary sedimentary rocks 300–1 600 kg cm². Lavas have a much lower value, namely 200–400 kg cm².

3.1.2 Ledges, fissures and cracks

Ledges, fissures and cracks are the result of geological heterogeneities exposed to the weathering process. Inconsistencies within a formation result in a distinct weathering pattern for each rock type. This pattern is the result of, among other things, past sedimentation and seismic activity and the removal of the softer, less resistant material and, as a consequence, the remaining cliff face (or abrupt vertical rock margin). Each geological formation results in a set of particular outer cliff-face characteristics and patterns. Stable cliffs of a strong texture (usually without a distinct scree below) carry a greater diversity of obligate cremnobiota than unstable cliffs (the latter with a distinct scree or talus deposit at the base).

3.2 Geology

3.2.1 Sedimentary rocks

3.2.1.1 Sandstone and quartzitic sandstone

In the study area, most obligate cremnophilous succulents (175; or 80%) are confined to these rock types, especially to rocks of the Cape Fold Belt (Cape Supergroup) centred in the southern and southwestern part of South Africa, with an isolated outlier, the Msikaba Formation, in the northeastern part of the Eastern Cape and southern KwaZulu-Natal (Thamm & Johnson 2006). The Cape Supergroup includes the Bokkeveld, Table Mountain and Witteberg Groups (Johnson *et al.* 2006: 443–460). Although variable in texture, most of the rock faces are stable, especially the considerably harder metamorphic quartzitic rocks. Rocky screes at the pediment often reveal the stability of the cliff. Sandstone of the Cape Supergroup is acidic and poor in mineral content, all additional challenges for plants adapted to this rock type. The rock faces are rich in horizontal and vertical crevices, ledges and fissures and are usually well vegetated. The colour of sandstone (mainly quartz arenite) varies, but it is usually (Cape Supergroup) whitish to pale reddish. This pale colour reflects the sunlight and sandstone is therefore considerably cooler during the hours of sunshine than darker formations. The low-mineral, dystrophic, rocky soils result in a higher species frequency of usually longer-lived (and slow-growing) cremnophytes such as *Crassula rupestris* subsp. *marnieriana* [135], *Gasteria rawlinsonii* [48], *G. glomerata* [46], *G. glauca* [45] and *Plectranthus ernstii* [168].

In Limpopo Province a number of cremnophytes are confined to sandstone of the Soutpansberg and Waterberg Groups (*Delosperma zoutpansbergense* [205], *D. waterbergense* [204], *Aloe soutpansbergensis* [29]). They are of the Kheisian (Palaeoproterozoic) age (Barker *et al.* 2006). These rough-textured coarse-grained rocks range in colour from purplish to whitish grey. Weathering patterns are similar to those of the Cape Supergroup, with horizontally and vertically cracked blocks allowing sufficient growth space. These rocks also give rise to sandy, mineral-poor, acidic soil. The Wolkberg sandstone (*Aloe thompsoniae* [30], *Cyrtanthus junodii* [7]) is coarse-grained and light-coloured, with spectacular cliffs on the eastern margin (Wolkberg Group, Langkrans Formation, Transvaal Supergroup) (Eriksson *et al.* 2006).

3.2.1.2 Conglomerate

Conglomerate cliffs are best developed in the Eastern and Western Cape (Uitenhage Group). They represent Jurassic and Cretaceous deposits in the south and east (Shone 2006). The colour of this type of substrate, especially the Enon Group, varies from reddish to whitish. The rock consists of spherical quartz pebble rocks embedded in a reddish, mineral-poor, sandy, limonitic cement (Shone 2006). These loose-standing mountains/hills are a conspicuous feature of the landscape around Oudtshoorn. This type of rock does not lend itself to fissures and large fractures, and consists mainly of dwarf pockets and ledges. The reddish conglomerate hills around Oudtshoorn and at Enon and Hankey have some cliff faces, and have only two obligate cremnophilous species (1%), *Machairophyllum brevifolium* [213] near Oudtshoorn (Western Cape) and the obligate cliff form of *Haworthia attenuata* [51] near Enon (Eastern Cape).

3.2.1.3 Shale and mudstone

Owing to greater water permeability (because of dimensional change) these cliffs are less stable (owing to rapid weathering) than the quartzitic sandstone-derived cliffs described above, and usually have a prominent scree face below. Shale and mudstone cliffs in the southeastern part of South Africa (Karoo Supergroup, especially the Beaufort Group), harbour a rich cliff-face flora. The rock has sufficient fractures, crevices and ledges and the gives rise to neutral loam and clay loam, mineral-rich soils. The colour of the rocks varies but it is usually brownish to dark brown (Johnson *et al.* 2006). There are 38 taxa (17%) confined to cliffs of this rock type.

3.2.1.4 Dolomite

Dolomite cliffs are usually hard and stable, especially in semi-arid regions. This rock type has many natural fractures, fissures and ledges, providing excellent habitat for cremnophytes. Dolomite, compared to the other sedimentary rocks, is not well represented in the study area. However, in spite of being less frequent, it has quite a number of cliff endemics (11 taxa, 5% of total). The obligate cremnophilous succulents endemic to dolomite are located mainly in the north (*Aloe hardyi* [20]; Olifants River Valley, Mpumalanga), southern Namibia and Kaokoveld (Kunene River) in the northwest of Namibia (*A. corallina* [16], *Lavrana haagnerae* [82]). In Namibia these cliffs consist of Proterozoic Namibian dolomite (Otavi Group, Damara sequence) (Mendelsohn *et al.* 2002). In the Limpopo Province and Mpumalanga it is represented by the older and rough-textured Chuniespoort Formation (Malmani Subgroup, Transvaal Supergroup; Eriksson *et al.* 2006). In both cases it is dark and rough in texture, with many fissures and

crevices. Dolomite rock is grey-black to brown and readily absorbs heat from the sun. Most cremnophytes are confined to shady southern or east-facing cliffs.

3.2.2 Igneous or magmatic rocks

3.2.2.1 Granite and gneiss

Granite cliffs are best represented in Namaqualand and Namibia and are less common elsewhere. They include Paarlberg, the lower slopes of Lion's Head (Western Cape) and Ploegberg (Richtersveld, Cape Granite Suite) (Scheepers & Schoch 2006), Brandberg and Spitskoppe (Namibia), and Otjihipa (Kaokoveld). These fairly homogeneous formations were often formed in a single event and have few fissures and cracks. Compared to sedimentary rocks, the texture of the rock face does not allow much foothold for succulent cremnophytes (Porembski *et al.* 1994). Nevertheless, there are a few dwarf succulent cremnophytes in the southern and northwestern parts (9; 3%). In the north, *Aeollanthus haumannii* [165], *Pelargonium vanderwaltii* [163] and *Tetradenia kaokoensis* [173] have been found at Otjihipa (Kaokoveld, Namibia). *Adromischus schuldianus* subsp. *brandbergensis* [103] is confined to south-facing cliffs of the Brandberg (Namibia). In the south, *Conophytum carpianum* [177] is confined to the Ploegberg (Richtersveld), growing on upper east-facing cliffs. *Conophytum danielii* [178] and *C. hanae* [182] grow in Namaqualand. The colour of this formation varies from mottled grey to light and dark grey.

3.2.2.2 Basalt, dolerite and rhyolite

Basalt cliffs are prominent along the central Drakensberg Escarpment (Drakensberg Group of the Karoo Igneous Province, Duncan & Marsh 2006). Although the most pronounced and best represented cliffs in southern Africa, these rock types are poor in endemic succulent cremnophytes. The structure of the rock allows for sufficient crevices, ledges and fractures for plant establishment. Only two obligate cremnophytes are confined to basalt rock types, namely *Delosperma nubigenum* [199] and *Cyrtanthus flanagani* [4] (less than 1% of the obligate cremnophytes). Basalt, dolerite and rhyolite rocks give rise to fertile soils that vary from slightly alkaline to neutral. Dolerite intrusions occur scattered throughout South Africa, but without any endemic cremnophytes. The same is true of the Lebombo rhyolite cliffs. A few obligate cremnophytes found here, but they are not endemic to this formation. *Gasteria batesiana* var. *batesiana* [41] grows on rhyolite cliffs and *Drimia loedolffiae* [71] on dolerite cliffs.

3.3 Cliff weathering and erosion

Weathering is the initial stage of denudation. It is the ‘digestion’ (or ‘decomposition’) of rock via physical processes (*in situ* movement action), chemical processes (mainly driven by climate) as well as biological processes (tree roots, bacteria, lichens, etc.). The cliff face is subject to continual weathering and erosion. Erosion involves the physical movement of the ‘digested’ part of the rock via gravity, water and wind to lower-lying regions. The pattern of weathering (rate of weathering and cliff character) is directly related to the rock type (hardness), climate and positioning.

Weathering is thus caused by physical (mechanical), chemical and to a lesser extent biological processes, and results in erosion due to gravity, water and wind action.

3.3.1 Cliff weathering

Physical weathering occurs as a result of a number of factors such as temperature fluctuations, dimensional changes (swelling and retracting due to water absorption) and biological processes such as plant root action (physical and chemical).

Thermal stress on rocks is well known, especially in the warmer, dry parts of the world. Weathering of this type occurs mainly on the outer surfaces of rocks (e.g. ‘onion skin’ weathering of granite).

Freezing and frost action play an important role in colder parts (above 2000 m) such as in the Drakensberg Mountains and in colder climates. Frost action causes plate-like fractures in a number of rocks (Ritter 1978). According to Matsukura (1990), the creation of overhangs and notch formation in colder climates is a direct result of freeze-thaw at the cliff pediment. This type of weathering process is confined to colder temperate climates of the world.

Mudstone and shale rocks are water-permeable, becoming swollen with water when wet, and shrinking during dry periods (dimensional change). Moisture fluctuation in this rock type has a direct influence on the weathering process (Matsukura & Yatsu 1982).

Biological processes also have an influence. Weathering of rock formations by rock-splitting figs is common throughout the warmer parts of the study area (where frost is not too severe). In Namaqualand, *Ficus cordata* and *F. ilicina* are commonly found on cliffs.

Seedlings (from seed germinating in crevices) initially have a succulent tap root and through secondary thickening of the stem, the rocks are moved. In the eastern and northern parts other species such as *F. burkei*, *F. burtt-davyi*, *F. glumosa*, *F. ingens* var. *ingens*, *F. salicifolia* and *F. tettensis* cause damage to rocks. These species can also cause extensive damage to artificial man-made structures such as vertical building walls.

Fire also has an influence on cliff weathering in the higher-rainfall parts of South Africa. Cliffs above Kirstenbosch (Cape Peninsula, Western Cape) below Maclear's Beacon are well vegetated and the author observed rock falls during a fire (and directly after). This was caused by the burning of dry tree stumps embedded among rocks on the sheer cliffs. This was also observed on Chapman's Peak between Hout Bay and Noordhoek (Cape Peninsula).

Chemical weathering is mainly the result of precipitation and the action of various dissolved substances on particular rock formations. The weathering rate depends on the mineral type, annual rainfall, temperature and cliff situation. Chemical weathering is slow in arid climates but more rapid in higher-rainfall regions. Weathering processes in quartzite and sandstone cliffs (silicate rocks) are slow because of the low ion-exchange capacity, and these are among the most stable cliffs globally. The Cape Fold Belt mountains are an example, consisting of hard quartzitic sandstone, poor in nutrients. Small wonder these cliffs carry the largest diversity of obligate succulent cremnoophytes of any rock type in the study area. Sandstone cliffs therefore usually have smaller scree slopes below compared to other formations in southern Africa.

In carbonate rocks such as dolomite, weathering is relatively fast. Calcium carbonate dissolves in water, resulting in a particular weathering pattern. Dolomite cliffs in South Africa and Namibia have a rich and distinctive cliff-face flora. The most stable cliffs are situated in dry savanna, grassland or desert (Peltier 1950; Whittaker 1975).

3.3.2 Cliff erosion

Erosion is the mechanical denudation process involving the force of gravity, water and, to a lesser extent, wind. The latter becomes more important in desert climates and often together with water acts as a combined force. The mechanical action of flowing water has resulted in most of the cliff faces related to river valleys in southern Africa. This includes the various river systems below the Great Escarpment, to the east, west and south. Waterfalls also have an

influence on the shaping of cliffs. Sea currents and wave action have a major influence on sea-facing cliffs (Caris *et al.* 1989). Weathering rates along sea-facing cliffs are high, especially in the case of mudstone and shale cliffs. A weathering rate of 300 mm per annum has been recorded in New Zealand (Healy & Kirk 1982) and as high as 3 000 mm in Japan (Sunamura 1992).

Cliff faces are also known for their rock falls, which can occur on a small to large scale. On a larger scale it includes the removal of sections of the rock face and can be the result of three types of mass movement (Trenhaile 1987). This includes a rock fall, topple or slide. Rock falls often occur as a result of underlying weaker rocks that are gradually weathered away, resulting in the collapse of the cliff edge. Topples are loose vertical rock towers (vertically inclined at the joints), especially sedimentary rocks. The rock towers gradually become detached and topple under the force of gravity. Cliff slides are rare in southern Africa and are usually the result of slope failure due to a weaker portion of the underlying strata.

3.3.3 Obligate cremnophilous succulents: adaptation to rock type

Obligate succulent plant endemism to a specific rock type is high and geology is therefore an important factor to take into consideration. Adaptations to mineral-poor soils have been well documented in the winter-rainfall fynbos flora of South Africa (Day 1983; Groves *et al.* 1983; Cowling 1992). The highest diversity of obligate succulent cremnophytes is found on mineral-poor quartzitic sandstone soil of the Cape Supergroup in the southeastern Cape, which receives rainfall at any time of the year. Obligate succulent cremnophytes endemic to mineral-poor quartzitic sandstone soil are generally slow-growing, with long-lived functional leaves. Some of them are *Aloe haemanthifolia* [19], *Crassula badspoortense* [113], *Gasteria rawlinsonii* [48], *G. glauca* [45] and *G. glomerata* [46].

3.4 Cliff moisture-holding capacity (hydrology)

The water-holding capacity of formations is important as it directly relates to cliff vegetation. Most obligate succulent cremnophytes have a relatively shallow root system and occur on cliffs that dry out rapidly. Water-holding capacity and availability of water are dependent on rainfall, temperature, aspect and rock type. South-facing cliffs remain moist for longer periods than exposed north-facing ones. Cliffs in winter-rainfall regions remain moist for longer periods owing to a lower rate of evaporation.

Water accumulation in bedrock crevices is primarily dependent on rainfall. Water is firstly accumulated in soil adjacent to or above cliffs and then discharged in adjacent lower-lying areas. According to Larson *et al.* (2000), the hydraulic pressure on level ground will be more or less symmetrical. However, on cliffs it will result in water moving towards the cliff face (except the upper cliff edge owing to less percolating water access). The various fissures thus have a continual supply of water, the amount depending on the rainfall. According to Larson *et al.* (2000), scree slopes should also have a higher water release. Water-holding capacity is furthermore directly related to rock type. Solid igneous or magmatic rocks on domes with few crevices have a much lower water-holding capacity than cliffs of a more fractured nature. Richer clayey soils in pockets would also hold water for longer periods than sandstone.

3.5 Cliff-face habitat and environment

One of the main objectives of this work is to document the adaptation of obligate succulent and bulbous cremnophytes to a vertical or near vertical habitat. This vertical environment and its effect on succulents form the main topic of the study. It is therefore necessary to consider this habitat type in more detail. The only constant feature that obligate cliff biota have to deal with, is the vertical nature of the habitat. All other physical environmental components such as sun radiation, temperature, wind, moisture availability, latitude, altitude, geology and growth space, are variables. We firstly investigate vertical orientation and gravity.

3.5.1 Physiography

The environmental features of vertical orientation have been well covered by Larson *et al.* (2000) and are summarised here and placed in a southern African context. Larson *et al.* (2000) related various components that are affected by vertical orientation and that make it so drastically different from surrounding level ground. The vertical terrain affects sun radiation (aspect, seasonality, altitude and latitude), temperature (sun radiation and absorption of heat from the rock face) and wind. It also affects precipitation. Energy absorption levels of rock types also differ according to the geological formation (dark-coloured dolomite absorbs heat more rapidly than light-coloured quartzitic rock types).

3.5.1.1 How the cliff-face habitat differs from level-ground habitats (conditions obligate cremnophytes have to face on vertical cliffs)

- i Vertical orientation (influences growth direction, the growth habitat now vertically orientated).

- ii Little or no soil profile, exposure to rock. Various geological formations ranging from mineral-poor, quartzitic sandstone to mineral-rich shale, mudstone and igneous rocks such as dolerite and granite.
- iii Modified sun exposure (the aspect determines sun exposure, north-, south-, east- or west-facing).
- iv Rainfall becomes less effective (in spite of little or high precipitation, a constant high run-off, and the moisture availability period also related to aspect). On south-facing aspects (southern hemisphere), moisture will remain for longer periods owing to less evaporation.
- v Temperature regimes influenced by the bare rock face (rock type and influenced by the aspect, altitude and latitude, and also by wind and moisture).
- vi Wind is directly affected (wind related to temperature and climate).
- vii There is an absence of disturbances and grazing from larger mammals and other larger animals.

3.5.2 Vertical orientation of the cliff habitat and gravity

All biota are victims of the omnipresent gravitation force and adapted likewise. Strong bones, powerful muscles or woody growth are adaptations enabling some animals or plants to cope with gravity. Succulent tissue, because of increased weight, taxes a plant and larger succulents generally have a woody supportive system (Von Willert *et al.* 1992). For most plants, a permanent vertical habitat demands an adjusted lifestyle and it affects their morphology and reproduction. Obligate cremnohytes have to adapt, both in morphology and reproduction, to deal with a vertically orientated habitat.

According to Larson *et al.* (2000) ‘the force of gravity is perpendicular to the surface and acting to stabilize it.’ The steeper the slope, especially in the case of cliffs, the more destabilising the effect of gravity. Any loose material (soil, rock and organic matter) becoming detached will fall to lower ground (or ledges) where it is stabilised. Characteristic screes and plant debris at cliff bases are well known. Resources for normal growth (growth space, soil, moisture) are thus limited.

It is clear that, in spite of the vertical orientation, some plants have made cliffs their habitat. The diversity is, however, limited to a few specially adapted cremnophilous individuals. Cremnophilous succulent and bulbous plants (obligate and facultative cremnohytes) adapt genetically and phenotypically to their particular cliff-face habitat.

3.5.2.1 Vertical orientation, gravity and its influence on plant growth

I shall first consider at the effect of a cliff habitat on facultative cremnophytes such as trees and then look at the effect on obligate cremnophytes when planted on level ground. Most plants are very adaptable (phenotypic plasticity). Larson *et al.* (2000) have clearly shown the stunted (dwarfing) effect on trees on cliffs with limited growth space in temperate regions. The shepherd's tree (*Boscia albitrunca*) is a subtropical African savanna tree species that usually grows on level ground. Near Griekwastad, a shepherd's tree on a south-facing banded-ironstone cliff face became pendent. Pendent growth forms have also been observed on south-facing cliffs in the Vandersterberg (Richtersveld). A cliff habitat has the same effect on *Portulacaria afra* and *Euphorbia evansii* in the savanna region in eastern South Africa. When growing under normal circumstances these two species become small, distinctly ascending trees. Why do the plants become pendent? Plants usually grow towards a light stimulus or source, and on a vertical surface or plane the tendency is to grow away from the cliff towards the light source, especially in the case of shady south-facing cliffs. The vertical growth axis taxes the plant considerably and gravity soon takes its toll. Vertical orientation can therefore affect growth direction. In these examples plants had sufficient growth space. However, space on cliffs is most often very limited and this will also influence plants, as is clearly shown by Larson *et al.* (2000).

Trees are often dwarfed on cliffs and in southern Africa there are many examples of especially wild fig trees (*Ficus* spp.) that are naturally dwarfed owing to limited space. The dwarfing effect also solves the gravitation issue. Cliffs (gravity and light direction) together with limitation of growth space can thus alter the growth of plants and as a result they then become either pendent or compact and stunted. This is even more so in succulents as the succulent tissue is a burden on the plant (Von Willert *et al.* 1992). When plants of obligate cremnophilous *Aloe hardyi* [20] (growth of branches and leaves pendent on cliffs) are planted in a container or level ground (in absence of herbivores), the plants grow horizontally or become pendent when in a pot. The leaves bend down and show epinastic growth. Their growth behaviour is therefore determined genetically. Smaller, compact, cluster-forming obligate cremnophilous species show very little change when planted on level ground. This study revealed several of these genetically determined growth forms—the cliff hangers (either hanging leaves or hanging stems or both) and the cliff squatters, which include compact growth forms hugging the cliff face. Von Willert *et al.* (1992) have also shown how the mechanical problems of succulents can be overcome by a compact habit (packing of leaves in

rosettes; reduction of internodes; columnar stems). There is also a tendency in succulent plant life forms on cliffs to be smaller and more compact than their counterparts of more conventional habitats, thus adopting a habit that is less taxing on the plants (see Table 11.5).

3.5.3 Precipitation

Cliffs receive precipitation from rainfall, dew and fog. The vertical orientation of cliffs has an effect on both the amount of direct rainfall as well as the water-holding capacity of the rock face. The amount of available moisture depends on the amount, annual distribution and intensity of rainfall, nature of the rock (permeability) as well as on the aspect and temperature. These factors are important in understanding the distribution of succulents on cliff faces. Larson *et al.* (2000) have shown that availability of moisture on cliffs is misunderstood and often underrated. Vertically orientated bare rock (high run-off) and its limited growth space suggest that cliffs are more arid than surrounding level ground. In spite of the high run-off on cliffs, Larson *et al.* (2000) have shown that availability of moisture on cliffs varies according to the rainfall, rock type and weathering patterns.

Two thirds of southern Africa is semi-arid and well known for its succulent richness (Van Jaarsveld 1988a), especially the Succulent Karoo region. In South Africa rainfall varies considerably in both amount and seasonal distribution. Summer rainfall is mainly experienced in the north and east, winter rainfall mainly in the west and southwest, with an intermediate zone between the two where rainfall can be experienced at any time of the year. Although succulents are well adapted to limited water supply, the seasonal distribution of rainfall becomes important.

Rainfall during the cool winter season (less evaporation due to lower temperatures, shorter day lengths) can be used more effectively—the reason why succulents are often dominant in semi-arid parts of the winter-rainfall region. The cool south-facing aspects of cliffs have a much greater succulent plant diversity (winter and summer rainfall), and even in subtropical summer-rainfall regions, moisture on the cooler south-facing aspects is subject to less evaporation. Intensity of a rain shower is also important. Rainfall in the winter-rainfall region is less intense and coincides with cold fronts. The gentle hills of the Succulent Karoo corroborate this. The summer-rainfall region often experiences convectional rainfall (thunder showers), and of a much higher intensity and for shorter periods. The sharper topography (due to erosion) also reflects flash flooding (Jürgens 1986).

Succulents (obligate and facultative cremnophytes) are usually commonly associated with cliffs throughout southern Africa (and more so than surrounding, level ground in higher rainfall regions), suggesting a xeric habitat, which, in spite of drying out rapidly, provides an efficient moisture supply for their cliff existence. In the study area, obligate succulent cremnophytes are found from regions along the west coast with rainfall of around 25 mm to regions along the Drakensberg Escarpment with more than 2 000 mm per annum. Although succulents (globally) can withstand periods of drought, they need a fairly regular supply of water (Ellenberg 1981; Von Willert *et al.* 1992). Most succulents have shallow roots, and the limited soil on cliffs is subject to rapid evaporation. In spite of their dependence on annual rainfall, especially in the semi-arid and arid parts, precipitation from other sources such as dew or fog becomes more important.

3.5.3.1 Cliffs and the rain shadow effect

Rainfall on cliffs is limited due to the rain shadow effect of the vertical surface. The area covered by direct rainfall on a vertical surface is therefore less than on a horizontal surface (Lundqvist 1968). However, wind will cause deviation (more or less), depending on its direction. On steep slopes, below a cliff, direct precipitation increases as the slope angle decreases, steeper angles thus receiving less rain than level ground. Rain on cliffs runs off rapidly but will accumulate in crevices and ledges. On horizontal ground, rainfall accumulates and has time to penetrate. Overhangs also clearly create places where even less moisture is available. There are always exceptions as occasional penetration of moisture via the rock matrix can nourish cremnophytes from the horizontal roof of an overhang.

3.5.3.2 Water-holding capacity on the cliff

The water-holding capacity of the various rock formations and ledges differs. Some formations lend themselves to crevice formation (especially sedimentary rocks) whereas other magmatic rocky types such as granite, are more solid and have a lesser water-holding capacity. Water-holding capacity of bare rock itself is very limited and of less consequence to succulent cremnophytes. The water-storage capacity of rock types also varies greatly. Well-weathered rocks such as granite will hold greater amounts of water as their porosity increases. The water content of rocks also varies; 0.05% of dry weight for chert, 0.09–0.28% for limestone, 0.18% for basalt and 0.13–1.2% for different granite types (Rejmanek 1971). However, fractures, hairline cracks (depending on the weathering pattern) will hold water that

would be available to plants, thus playing an important part in availability of moisture. Moss and ferns often germinate on artificial man-made cliffs such as vertical concrete and brick work, especially on shady south-facing aspects (southern hemisphere). According to Lewis & Burgy (1964), sandy soil holds 25% of water by volume and clay soils as much as 60%. In spite of the low water-holding capacity of the rock, the matrix potential (water tension) of rock is much lower than that of soil, and moisture is therefore more easily available to plants such as chasmophytes.

3.5.3.3 Dew and fog

Fog is associated with cold oceans and is prevalent along the southwest coast of Africa, Chile and Baja, California. The distribution of many succulent and other xerophytic plants clearly follows the fog belt. The Namaqualand coast and coastal Namibia are subject to regular fog and some obligate cremnophytes are distinctly associated with this moisture providing low cloud. This foggy cloud provides moisture in the form of condensed droplets. Von Willert *et al.* (1992) recorded 0.7 mm of precipitation on a flat horizontal plate over a period of six hours of fog. The surface architecture (e.g. hairy surface) of many plants is clearly designed fog traps.

Precipitation from dew on cliffs can be clearly seen in the occurrence of dense stands of lichens such as *Parmelia* spp., especially on cooler south-facing aspects. Lichen fields on cliffs are therefore excellent indicators of dew and fog deposits and associated cremnophilous succulents. Dew deposits also vary, even within a small area. Patterns of lichen establishment reflect this clearly. The seasonal distribution of rainfall is also important. Most obligate cremnophytes in our study are confined to areas where rainfall is fairly evenly distributed throughout the year as well as to regions experiencing rainfall mostly in winter. In spite of summer-dry conditions experienced within the winter-rainfall region, the mountain tops are often covered by moist clouds that provide additional precipitation.

The limited water-storage capacity of cliffs thus clearly favours the establishment of succulents as well as poikilohydric plants such as lichens, and some ferns and mosses. From the above it is clear the moisture-holding capacity of the various cliff faces varies greatly, both at the macro- and micro-scale. Plants will seek out microhabitats that receive sufficient moisture for their survival, whether direct rain, dew, fog or seepage.

3.5.3.4 Cremnophytes adapting to a limited water supply

Rapid drainage on a cliff demands an efficient water-storage facility in succulent cremnophytes. Water is stored in both leaves and stems or both or, in some cases, in the roots of the plant.

3.5.3.4.1 Increase in succulence

Obligate cremnophilous succulents generally show an increase in succulent storage tissue and related features. In these plants, leaves can become almost subterete when fully turgid, and the internodes are shorter (often tightly arranged into a subcylindrical leafy stem, etc.) when compared to level-ground relatives. This genotypic adaptation is clearly a response to the stress of the cliff habitat (lack of moisture and efficient moisture storage). Examples include *Aloe meyeri* [22], *Gasteria rawlinsonii* [48], *Crassula rupestris* subsp. *marnieriana* [135], *C. perforata* subsp. *kougaensis* [131] and *Plectranthus purpuratus* subsp. *purpuratus* [171] (see Tables 11.6, 11.11).

3.5.3.4.2 Dependence on fog

Precipitation in the form dew and fog is an important source of moisture. Many cremnophytes are clearly dependent on fog as part of their moisture-gathering and their distribution follows cliffs in the fog belt region (*Conophytum stephanii* [190], *C. ricardianum* [189], *Jensenobotrya lossowiana* [211] and *Tylecodon singularis* [158]). Along the west coast, rainfall is very scanty (25–70 mm in parts). Adaptations include hairy leaves (small to large) with fog-trapping abilities. Examples include *Anacampteros scopata* [220] (densely hairy stems), *Conophytum stephanii* [190], *C. ernstii* [179], *T. cordiformis* [153], *T. ellaphieae* [155] and *T. singularis* (hairy leaves). *Tylecodon singularis* is remarkable for having a bowl-like hairy leaf up to 150 mm across as well as a channelled petiole at the base of the leaf, clearly an aid in utilising fog.

3.5.3.5 Cremnophytes adapting to seasonality of rainfall

In regions where rainfall occurs in a specific season, succulent cremnophytes are accordingly adapted. In the study area there are 51 (23%) obligate succulent cremnophytes that become deciduous (such as *Tylecodon*) or aestivate (*Conophytum* species) during the dry summer season. However, most (167 or 77%) are evergreen.

3.5.3.5.1 Summer-deciduous

Cremnophilous succulents from the winter-rainfall region (Succulent Karoo and Fynbos) (73 taxa) have a larger portion of species becoming leafless during the long, dry summers. In fact, 42 (58% of winter-rainfall cremnosucculents) plants have been identified as summer-deciduous (19% of total succulent cremnophytes). This includes members of the genus *Tylecodon* and the summer-deciduous members of *Othonna* that have succulent leaves and stems. The leaves become deciduous in late spring. Most of these taxa, however, have additional photosynthetically active bark. *Crassula nemorosa* [127] is a summer-deciduous succulent geophyte.

3.5.3.5.2 Aestivation (summer dormancy)

Members of *Conophytum* become dormant in the dry summer and are not deciduous in the true sense. Although their leaves are annually replaced, moisture is recycled and a new leaf pair develops in late spring, the older pair withering and forming a dry protective cover (tightly covering the young leaf pair). This cover is shed every autumn when the new leaf pair emerges.

3.5.3.5.3 Winter-deciduous

Only nine obligate succulent or bulbous succulent cremnophilous taxa have been identified as winter-deciduous. Some of them are the succulent bulbous cremnophytes *Cyrtanthus falcatus* [2], *C. flanaganii* [4] and *C. junodii* [7]. *Tetradenia kaokoensis* [173] from the Kaokoveld in northern Namibia becomes deciduous in the dry winter months. It does not have photosynthetically active bark but tuberous (storage) roots.

3.5.3.6 Shallow root system

Cremnophytes often have to deal with limited growing space and their roots are often restricted to narrow crevices. Water is only temporarily or periodically available, and succulents store water in their succulent tissue. Von Willert *et al.* (1992) mention succulent roots with extensive lateral development, sometimes 10–20 m away from the plant, and roots often growing underneath rocks. These humid conditions below rocks are often exploited by various succulents, with intense root competition. The narrow crevices would therefore be well exploited by obligate cremnophytes.

3.6 Radiation

The sun is the primary source of light energy for plants. Radiation varies on a daily and seasonal basis. The rays of the sun (power of $1\ 370\ \text{Wm}^{-2}$) reach the upper atmosphere where a portion is firstly deflected, a further part is scattered and another portion, called direct solar radiation,

penetrates directly (Larson *et al.* 2000). Radiation that penetrates the earth's atmosphere therefore has two components, diffuse radiation and direct radiation. The sum total of the diffuse and direct radiation is termed global radiation and has a wavelength range of about 300–2 500 nm.

The light received on the south side of a shady cliff is diffuse radiation (southern hemisphere). Light radiation received on the shady southern aspects of cliffs has been described as open shade (Stoutjesdijk 1974). According to Larson *et al.* (2000) photosynthetically active wavelengths in open shade are present at higher proportions than light received from under a tree canopy. This open shade, also called blue shade (open blue sky in absence of direct sun), is therefore more beneficial to plants than light under a leaf canopy.

The amount of radiation incidence on a plant is determined by the angle of the rays of the sun on the plant's surface—the closer the angle to the perpendicular, the greater the light radiance. Diffuse radiation is not influenced as much by the angle of incidence as direct rays. The angle of the rays is controlled by three factors, aspect, slope and the sun's position in the sky (position determined by latitude, date and time). The radiant flux density on a horizontal surface can be predicted by using these three parameters (Monteith & Unsworth 1990).

Cliffs are vertically orientated and here the angle of incidence is affected by the vertical habitat and aspect (Garnier & Ohmura 1968). A combination of factors (aspect, vertical orientation, latitude, date and time of day) interact to determine the amount of radiation a cliff receives. Generally there is a decrease of light energy received on a cliff compared to that of a horizontal surface. A north-facing cliff in the southern hemisphere would receive slightly less light than level ground (angle of the sun towards the cliff face). Many succulents from the Succulent Karoo have narrow ascending leaves, thus minimising the amount of surface exposed to the sun. East- and west-facing cliffs would receive about only half as much direct sunlight and a south-facing cliff would receive no direct radiation at all and would be in shade for most of the day (plants dependent on diffuse radiation). However, in winter, the peak value for north-facing cliffs (southern hemisphere) is slightly higher on cliffs than on level ground. Generally cliffs therefore receive less light than horizontal surfaces. Latitude determines the sun's angle of radiation incidence and there is an increase in radiation with a latitudinal increase (north- and south-facing cliffs). Variation of light on cliffs therefore varies considerably according to aspect and latitude.

3.6.1 Effects of sun radiation

Sun radiation on cliffs varies according to the aspect. This has a major effect on the distribution of cremnophytes on cliffs.

3.6.1.1 South-facing cliffs

Although cremnophilous succulents are found on all aspects, most taxa have a clear preference for shady south-facing slopes. In fact, very few are found only on exposed northern aspects. Of the 220 obligate taxa identified, more or less 185 taxa (84%) have been recorded from south-facing cliffs, of which 124 (56%) are obligate south-face cremnophytes. Within this greater group there is also variation such as occurrence on a wider aspect range (south-, east- and southwest-facing). South-facing cliffs in southern Africa remain shady and cool for most of the winter months and have a greater diversity of obligate cremnophytes than north-facing cliffs. This microclimate remains moist for longer periods (together with lower temperatures) and receive quality light, beneficial to many succulent and bulbous plants. Plants growing on south-facing cliffs are modified (leaf morphology and presentation), enabling them to cope with the low light intensity. Modifications relate to leaf orientation, size and translucence, among other things.

3.6.1.2 Leaf presentation and orientation

The leaves of *Aloe dabenorisana* [17] (Northern Cape) and *Haworthia angustifolia* var. *baylissii* [50] (Eastern Cape), both obligate cremnophytes, are in rosettes that re-curve so as to maximise leaf surface exposed to open-light 'blue light'. Close relatives growing on exposed, sunny, north-facing cliffs differ in their leaf orientation. *Aloe perfoliata* and *A. meyeri* [22] have ascending leaves that do not re-curve but draw together (mitriform) during the hot, dry season, protecting the inner leaf surface from excessive exposure to the sun. *Haworthia angustifolia* var. *angustifolia* from sun-exposed regions also has narrow, ascending leaves that do not re-curve.

Members of *Tylecodon* are closely related to *Cotyledon*, differing by their leaves which are spirally arranged and which become deciduous during the long, dry summer period, a state that is less taxing on the plant. The smaller cremnophilous *Crassula* species growing on cliffs also have rosettes exposing a greater surface to the light source. For example, the leaves of *Crassula cymbiformis* [117], *C. intermedia* [123], *C. cremnophila* [116] and *C. orbicularis* [128] are in an open rosette. When these genetically shade-adapted cremnophytes are grown in full sun, they are rapidly scorched and then succumb.

3.6.1.3 Windows

Windows are found in the leaves of some succulents such as members of the Mesembryanthemaceae and succulent species of *Senecio*; they are especially well known in stone plants in genera such as *Lithops* and *Fenestraria*. The plants grow with the greater part of their leaves below the soil surface, the windows thus allowing deep penetration of light.

Multiple windows in the Mesembryanthemaceae can clearly be seen as small translucent dots in thick leaves of *Pleiospilos* (hence the name). The lenses (dots) act as light wells enabling light to reach the deep inner tissue (Schanderl 1935). They consist of groups of translucent cells directly below the epidermis.

In this study, 46 (20%) cremnophilous taxa were identified with windows varying from prominent to not so prominent. These cells are without pigment and well developed, especially in many cremnophilous members of *Haworthia*, *Senecio* and *Conophytum*. Several of the smaller *Haworthia* spp. growing on shady south-facing cliffs have leaves in an open rosette. Their leaves bear distinctive translucent windows, allowing deep penetration of light into the inner succulent leaf tissue, thus maximising light intake on shady cliffs. This includes *Haworthia cymbiformis* var. *setulifera* [53], *H. gracilis* var. *picturata* [55] and *H. mirabilis* var. *consanguinea* [58] (Marloth 1909). Cremnophilous *Conophytum* species also have leaves with achlorophyllous dots acting as lenses. *Senecio pondoensis* [92] has linear leaves bearing a distinct translucent linear window on the adaxial surface. *Adromischus schuldtianus* subsp. *brandbergensis* [103] has a broad window on its adaxial leaf surface, a unique feature among the Crassulaceae. It grows on south-facing cliffs of the Brandberg in northwestern Namibia.

3.6.1.4 Anthocyanin production on the abaxial leaf surface

Many shade plants (sciophytes) have a characteristic reddish purple anthocyanin layer on their abaxial (under-) surface (Lee *et al.* 1979; Middleton 1998). Anthocyanin production is usually very common in succulents, especially when the plants are subject to sunny, exposed, dry situations. This phenomenon is particularly prominent during the dry season. It is associated with excessively high exposure to ultraviolet light, especially in the absence of moisture. Examples include *Aloe spicata*, *Crassula capitella* subsp. *thyrsiflora* [115] and *Kalanchoe luciae*. Anthocyanin production in this case may well hold the advantage of protecting the leaves from excessive sunlight, thus acting to reflect the sunlight.

Why should anthocyanins be produced by so many shade plants? Lee *et al.* (1979) found that in shade-adapted plants, the thin cyanic layer on the lower surface acts to reflect light, thus maximising the trapping of light. *Tylecodon petrophilus* [157] has large spatulate to suborbicular leaves in a dense leaf canopy completely covering the stems. The leaves are purplish on the abaxial (lower) surface owing to anthocyanin production. The leaves are much larger than those of *Tylecodon* species growing in semi-exposed or full-sun regions. The plants can afford to grow larger leaves to compensate for the lower light intensity and the red layer reflects the light, thus adding in optimal photosynthesis.

3.6.1.5 North-facing cliffs

The moisture regime of exposed north-facing cliffs is much reduced owing to direct sunlight and higher temperatures. Consequently the diversity of obligate cremnophytes on north-facing cliffs is much reduced. In this study, 34 (15%) obligate cremnophytes have been identified as growing on north-facing slopes, only five (2%) of them restricted to exposed northern faces. Rocks absorb energy of the sun and heat is also reflected onto plants. In subtropical and tropical parts at low altitudes (below 800 m) exposure to direct sunlight and additional exposure to heat from the rock face itself are more than most succulent cremnophytes can handle. If the temperature of the leaves is too high, together with a lack of sufficient root moisture, growth would certainly be impossible, resulting in death. Taxa that easily succumb under such conditions include most of the smaller leaf succulents (e.g. *Crassula*, *Haworthia*, *Conophytum*, etc.).

Aloes, on the other hand (and *Lavrانيا* below), are among the few succulents that can tolerate exposed north-facing cliffs at lower altitude. These aloes are well adapted to extreme heat and aridity, their succulent leaves orientated in tight rosettes (leaves becoming erectly spreading during the moist season), which become mitriform (drawn into a point) during the dry season. The inner crown is thus well protected from direct exposure and heat from the sun. Additionally, the thickened leaf epidermis is grey-green (epidermis often also covered in a waxy powdery bloom). The grey-green is believed to reflect radiation of the sun and the waxy epidermis possibly limit transpiration. Examples include *Aloe corallina* [16], *A. dewinteri* [18], *A. omavandae* [25] and *Aloe hardyi* [20].

Lavrania haagnerae [82] (Asclepiadaceae) is a stem succulent occurring on cliffs in the tropics (Sesfontein, west- and north-facing dolomite cliffs). It has cylindrical succulent stems growing in branched clusters and is distinctly grey-green. The cylindrical succulent stems cope better with heat than leaf succulents do, as shown by Jürgens (1986).

3.7 Wind

Generally cliffs experience more wind than horizontal ground (Hetu 1992) and this is exploited by various cliff-dwelling animals such as birds. It also aids dispersal of airborne seed. Most cremnophytes are dependent on wind for seed dispersal. Wind patterns on cliffs vary greatly, depending on the situation, from heavy coastal winds to light wind on sheltered cliffs. Coastal cliffs at Cape Point Nature Reserve experience heavy southeasterly trade winds for most of the year. Wind behaviour has been well studied (Arya 1988).

Air movement from behind a cliff and away from it will cause turbulence. The updraft of the turbulence ensures the uplift and transport of airborne seed to higher ground. Air movement towards a cliff will compress the air, with wind velocity increasing at the cliff edge and the updraft ensuring the uplift of wind-dispersed seed.

The drying and cooling effects of wind are well known. Cliffs (north-facing, southern hemisphere) also trap heat from the sun. Wind speed affects the microclimate (Larson *et al.* 2000). It has a drying and cooling effect on damp cliffs and, in contrast, condensing water on cliffs when the surface temperature is below the dew point. Wind can also cause damage, and after heavy storms fragments of cremnophytes can be picked up from the base of cliffs.

3.7.1 Wind and succulent cremnophytes

Most obligate succulent cremnophytes have wind-dispersed seed. Members of the Mesembryanthemaceae have capsules that are hygrochastic and the seeds are dispersed by rain. *Drosanthemum anemophilum* [206] is a cremnophyte with hygroscopic capsules, but once open, they remain open. The seeds are flattish and clearly wind-dispersed. The small capsules in members of *Conophytum* are light and wind can play a role in dispersal as well. *Oxalis pocockiae* [219], a summer-deciduous cremnophilous geophyte, produces small winged bulbils dispersed by wind. This is the only case of wind dispersal of vegetative propagules found in this study.

3.8 Temperature

The distribution of succulents is not only limited to arid habitats (but with predictable regular rain) but also to regions with extremes of temperature. In regions with severe frost (during growing season) succulents also become rare. Kaemmer (1974) has shown a clear decrease in succulents at Teno (Canary Islands) with an increase in altitude, especially above the cloud line where severe frost is experienced. Temperature is therefore an important factor, and each species requires a temperature range for optimal growth performance.

Winter-rainfall succulents require cool temperatures for growth and aestivate during hot summers while summer-rainfall species show very little growth during cooler winter weather. Temperature is directly related to the amount of sun energy radiated from the sun and this is affected the greatest by latitude and altitude. Temperature on the cliff therefore varies according to aspect, season and time of day. It is also influenced by moisture and wind.

On cliffs, succulents grow in close proximity of rocks. Radiation energy from the sun is absorbed by the rock surfaces to various degrees (depending on the geology) and will also influence the immediate area. Dark-coloured rock types such as dolomite are less reflective and reach higher temperatures, while the paler coloured quartzitic sandstone warms up more slowly owing to the reflective properties of this rock type. The amount of energy radiation absorbed therefore varies depending on the geology.

In warm, semi-arid climates such as the Knersvlakte (Western Cape) many dwarf succulents are strictly confined to white quartz gravel flats. Plants that germinate in adjacent dark-coloured gravel soon succumb because of the extreme temperatures (Schmiedel & Jürgens 1999). Exposed north-facing cliffs of dark-coloured formations such as dolerite, mudstone or dark-coloured shale sustain a lower diversity of cremnophytes.

3.8.1 Temperature and latitude

South Africa falls partially within the tropics but the southern portion experiences a warm temperate climate. Succulent cremnophytes clearly reach their greatest diversity in the warm temperate climatic zone (mild winter and summer temperatures), which favours leaf succulent life forms (Jürgens 1986). In the tropical northern parts the diversity of succulent cremnophytes on exposed north-facing cliffs at lower altitudes is greatly reduced. Temperature extremes (north face and close to a rock face) combined with aridity will rapidly kill off smaller succulent

plant growth forms, especially leaf succulents. There are a few exceptions such as members of *Aloe* (with their tight central rosettes) that are extremely hardy, and a few taxa can survive north-facing cliffs at lower latitudes and altitudes in the tropics.

3.8.2 Temperature and altitude

Temperature decreases with a rise in altitude, and plant-associated communities are clearly related to this altitudinal gradient. The same with succulent cremnophytes and this is the reason why many dwarf succulents (associated with higher latitudes) can survive on cliffs in the tropics. In the northern parts of southern Africa (especially north of the Tropic of Capricorn), these succulents occur at altitudes at least 800 m and higher above sea level. Examples include many of the cremnophilous grass aloes (*Aloe nubigena* [24], *A. thompsoniae* [30], *A. challisii* [15] and *Crassula* spp.).

In the Kaokoveld (latitude 17–19° S), the obligate cremnophilous succulent diversity on cliffs is mainly concentrated from about 800 m. The smaller cluster-forming cremnophilous growth forms in the latter area are similar to those occurring below the tropics at lower altitude (but higher latitude). However, succulents do not lend themselves well to freezing and this is the reason why there are very few cremnophilous succulents at altitudes above 2000 m. They include mainly dwarf rosulate species of *Crassula* and *Delosperma nubigenum* [199], a mesemb with a procumbent to pendent growth along the KwaZulu-Natal Drakensberg Escarpment. Werger (1983) has shown that succulents become scarce in regions where temperatures drop below 4–5°C.

3.8.3 Temperature and the coast

The oceans have a moderating influence on average temperatures along the coast, especially the west coast of South Africa and Namibia. The upwelling of cold deeper-lying water along the west coast ensures a cool climate for most of the year (Du Pont *et al.* 2005). Consequently evaporation is less, with a marked influence on the cremnophytes of the region.

The cool climate along the western Namaqualand and Namibian coast ensures a dwarfing effect on many succulents. It is similar to the cool conditions on mountain tops (alpine effect), and here succulents are often mat- and cluster-forming and prone to the selection of dwarf forms. *Aloe ramosissima* is a non-cremnophilous example closely related to *A. dichotoma*. The same dwarfing effect can be seen in the dwarf small-leaved cremnophilous *Gasteria pillansii* var. *hallii*

and *G. pillansii* var. *ernesti-ruschii* [47] compared to the larger *G. pillansii* var. *pillansii* growing away from the coast. The warm south-flowing Indian Ocean along the southeast coast of South Africa ensures a moderate, warm, subtropical climate with mild, frost-free conditions.

3.8.4 Temperature and its influence on succulent plant life forms

Jürgens (1986) has shown the influence of temperature on the various succulent growth forms in southern Africa. In a study of South African succulents, he related life form composition to climate and temperature. He identified a leaf succulent zone (leaf succulent chamaephytes) associated with cooler winter-growing conditions and a stem succulent zone (arborescent succulents) associated with warmer subtropical conditions. In between these regions both life forms can be found. The short growing season of the leaf succulent zone in winter also promotes the dwarf ‘alpine growth’ form of many succulents (Van Jaarsveld 2000a). The small, compact succulent growth form (ground huggers) can make the most of the energy of the sun trapped by the ground in winter.

During the dry summers most winter-growing succulents aestivate and various adaptations enable the plants to cope with summer temperatures. There is therefore a selection towards the smaller cluster-forming succulents so characteristic of the winter-rainfall zone.

The northern tropical summer-rainfall succulents are much larger, arborescent types bearing cylindrical stems so characteristic of hot deserts. The dwarfing (lilliputian) effect of succulents (growing under cool conditions in the south) also allows for greater species diversity. Consequently, together with terrain diversity, this is probably one of the main reasons for the great diversity of succulents in the winter-rainfall region of South Africa. The lilliputian world allows for greater species numbers.

3.8.5 Temperature and growth forms on local cliffs

In spite of the various vegetation zones discussed under 6.6, most of the 220 more or less obligate cremnophyte succulents fall under the umbrella of leaf succulents. There are only four stem succulents (Asclepiadaceae) and a few intermediate growth forms (stem and leaf succulence) such as some members of *Tylecodon* and *Othonna* and a few other individuals with dwarf thickset stems and succulent leaves. The few stapeliads (Asclepiadaceae) consist mostly of pencil-thick, pendent stems—*Huernia pendula* [81] and *Tromotriche baylissii* [83]. The stems of *Lavrana haagnerae* [82] are thicker and the plant is cluster-forming.

3.9 Disturbances on the cliff face

Cliffs are remarkably free from the kind of disturbances normally found on level ground (Larson 2000). Disturbances on cliffs in southern Africa include rock falls, nesting birds, the activities of some mammals and the odd fire.

3.9.1 Rock falls

Rock falls depend on the stability of the cliff face. Large screes, or talus slopes below cliffs, usually indicate unstable cliffs. Most local cliffs in southern Africa are remarkably stable in particular geological formations such as sedimentary quartzitic sandstone and dolomite. Shale and mudstone cliffs are less stable, but still have many cremophilous succulents.

3.9.2 Fire

The effect of fire on vegetation has been well documented (Groves *et al.* 1983; Van Wilgen *et al.* 1992). Adaptations include strategies such as corky bark (insulating), sprouting from a lignotuber after a fire or reseedling (Van Jaarsveld 1994a). Fire is absent from most cliffs. However, in densely vegetated and higher-rainfall areas, ledges carrying fynbos vegetation will occasionally burn. The semi-arid parts, however, are free from fire. Fire therefore plays a minor role in shaping local cliff vegetation.

3.9.3 Disturbances by animals

Herbivory is important in shaping vegetation, especially in semi-arid (non-cliff) environments (Everard 1987; Midgley 1991; Stuart-Hill 1992; Kerley *et al.* 1999; Van Jaarsveld 2001). This results in various adaptive plant strategies such as mechanical defence (e.g. spines), chemical defence (latex in Euphorbiaceae) and camouflage (blending into vegetation, e.g. *Gasteria bicolor*, or resembling stones as in *Lithops* spp.). Cliffs, on the other hand, are a remarkably stable habitat, free from disturbances by megaherbivores. However, there are a few animals in southern Africa that can indeed reach parts of cliffs that are generally inaccessible to most others. They include rock rabbits or dassies (*Procavia capensis*), klipspringer (*Oreotragus oreotragus*), the smaller Namaqua rock rat or dassierot (*Aethomys namaquensis*), the namtap (*Graphiurus cedarbergensis*) and chacma baboons (*Papio ursinus* subsp. *ursinus*).

Obligate cremnophytes that sometimes germinate on accessible ledges, show clear signs of grazing by some of the animals mentioned above. *Conophytum taylorianum* subsp. *ernianum* [192] on the Hunsberg cliffs has been observed partially grazed by rock rabbits and *Aloe haemanthifolia* [19] by klipspringer. Although most cliff faces show little disturbance by mammals, chacma baboons are primates that favour cliffs for sleeping. Here they find safety from predators such as leopard (*Panthera pardus*) and spotted hyaena (*Crocuta crocuta*). Chacma baboons are clearly the best adapted cliff-dwelling mammals in Africa. They are associated with cliff faces throughout the continent and show remarkable agility to negotiate vertical cliffs. They are natural cliff dwellers and can reach many obligate cremnophytes.

Although most obligate succulent cremnophytes grow on sites inaccessible to baboons, many germinate on ledges that are accessible to these animals. *Gasteria rawlinsonii* [48] is a larger, pendent, shrubby, obligate succulent cremnophyte. In contrast to a drop in defensive strategies observed in most cremnophytes, some forms of *G. rawlinsonii* (Geelhoutboskloof) have clearly visible prickles on the leaves, especially on the leaf tips. This may well to be a baboon deterrent and one of the few defence strategies noted in obligate succulent cremnophytes. *Gasteria rawlinsonii* is endemic to the Baviaanskloof in the southeastern Cape and baboons are very common here (hence the name Baviaanskloof!). The plants grow on sheer cliffs inaccessible to humans and most mammals, in well-wooded, narrow kloofs and gulleys. The strong leafy branches of *G. rawlinsonii* can grow to 1 m or longer and could support the weight of a baboon. The extended branches are also strong and fibrous in contrast to those of other species of *Gasteria*. The sharp, blackish prickles at the leaf tips are a clear deterrent to grabbing baboon fingers. *Gasteria rawlinsonii* is variable and most forms (distichously leaved types) are without prickles and at the same time grow in sites clearly inaccessible to baboons. The Geelhoutboskloof region of Baviaanskloof is well wooded, sometimes with tall *Podocarpus* trees (hence the name Geelhoutboskloof) that provide access to parts of the cliff.

3.9.4 Relaxation of defence

The lack of herbivory on most local cliffs has clearly resulted in plants that show a relaxation of armament and camouflage properties so commonly seen on horizontal surfaces (Van Jaarsveld 2000a). Larson *et al.* (2000: 224) also state: ‘No report has been published to show that plants on cliffs have conspicuous defence mechanisms of any type that work against the pressures of competition or herbivory.’

Obligate cremnophilous aloes (a group closely related to *Gasteria*) are excellent examples and in most such taxa the leaf margin either lacks teeth or, if teeth are present, they are much reduced in comparison to related species on level ground. Examples include *Aloe corallina* [16], *A. mendesii* and *A. nubigena* [24]. The obligate cremnophilous species of *Conophytum* have soft, fragile leaves (*C. carpianum* [177], *C. ricardianum* subsp. *ricardianum* [189], *C. tantillum* subsp. *amicorum* [191]) compared to the firm leaves of their counterparts on level ground (see Table 11.14). The leaves of *Gasteria glauca* [45], *G. glomerata* [46] and *G. rawlinsonii* [48] also are without the camouflage so clearly present in most level-ground members of *Gasteria*. This clearly suggests a relaxation in cremnophilous defence strategies.

3.10 Climate in South Africa and Namibia

Climate (rainfall, temperature, wind) is chiefly determined by three factors: latitude, the relation to the coast, and altitude. These factors are important in determining the type and distribution of succulent cremnophytes in the study area. On the micro-scale, aspect is important, especially cliffs, as it will determine the amount of light and the temperature. These factors result in adjustment in growth in most succulent cremnophytes (see below).

On the macro-scale, Koppen & Geiger (1930) established a simple working system of the world's main climatic regions. Their system is based mainly on temperature and precipitation and they zoned the world into six major climatic zones: A (tropics), B (dry climates), C (temperate, mild winters), D (temperate summers, cold winters), E and H. Three of these zones are represented in our region: C, Mediterranean climate in the south (mainly Western Cape and the western part of the Eastern Cape); the climate is warm-temperate with cool winters. C, the Highveld region in Gauteng and the Free State; the climate is temperate with mild winters but with frost at night. B, dry climates of the semi-arid karoo and desert regions along the west coast and western interior.

3.10.1 Latitude

Latitude determines the amount of daily sun radiation, which in turn influences daily temperatures, especially in winter. South Africa and Namibia lie between 35 and 17° S (Limpopo Province, 22° S). The coolest month is July and the hottest January. There are two main climatic regions to which plants are adapted—the northern mainly summer-rainfall parts (areas north of the Tropic of Capricorn falling well within the tropics), with vegetation mainly

belonging to the Palaeotropical Floristic Kingdom, and in the south the very species-rich Cape Floristic Kingdom. The southern part lies within a Mediterranean climate regime (Dalman 1998), as found in parts with similar latitude and landmass (Western Australia, parts of Chile, California and the Mediterranean). The summer-rainfall regions above the escarpment have a warm temperate climate that is more severe and with frost (heavy to light). The Mediterranean climate type represents a mild climate with long, hot, dry summers and short, wet winters. Cremonophytes are well represented in both the summer- and winter-rainfall parts of the study area but are much more diverse in the regions influenced by winter rainfall (all-year rainfall).

Obligate cremonophytes north of the Tropic of Capricorn are mainly confined to higher ground with cooler temperatures. Summer temperatures here, especially in desert regions such as the Namib, are extreme and succulents are often confined to a limited niche such as above 800 m altitude or in a zone subject to regular fog from the Atlantic Ocean. At lower altitude in these parts, temperatures on the exposed northern cliff faces are too high to sustain most perennial cremonophytes. *Aloe corallina* [16] is perhaps the most hardy exception, occurring on lower slopes along the Kunene River, where it is often confined to cooler south-facing slopes.

3.10.2 High pressure system

Between the tropics and the temperate zone of the world there exists a prevailing high pressure system. It is caused by two large cells of circulating air (Hadley Cell) on both sides of the equator and driven by convection. Hot air rising over the equator moves north and south respectively. As the air moves southwards, it loses most of its moisture and descends over a broad area between Durban and Springbok. This results in the characteristic semipermanent high pressure system that prevents cloud formation over the central parts of South Africa and Namibia. It also results in the south Atlantic high pressure system along the west coast and in the southeast trade winds so characteristic of the summer months along the Cape coast. These strong winds have an important influence on the north-flowing Benguela Current.

The south Indian high pressure system causes the moisture-bearing northeasterly winds to enter over the escarpment as the high pressure belt weakens over the interior in summer, resulting in thunder showers and convective rain typical of the escarpment and interior. In winter, the high pressure cell over the interior intensifies, and moisture-bearing winds cannot penetrate, resulting in winter aridity. Rainfall of the eastern interior varies from about 400 to more than 2 000 mm per annum along the eastern Great Escarpment.

3.10.3 Winter rainfall in the west and south (Ferrel westerlies)

These prevailing winds have an influence between the northern Hadley Cell and the Polar Cell in the south. Strong winds spiral eastwards around the globe and result in the characteristic low pressure systems that induce the cyclonic winter rainfall and cold fronts on which the winter-rainfall flora depends. The winter rainfall in the south varies from about 200 mm (rain shadows) to more than 2 000 mm on the higher sea-facing slopes.

3.10.4 Coastal and semicoastal parts

The ocean has a moderating influence on the adjacent land so characteristic along the west coast of southern Africa. Along the west coast, the cold north-flowing Benguela Current is responsible for the regular formation of fog (as far as southern Angola), a source of precipitation vital to especially many succulents along the west coast. The warm south-flowing Agulhas Current of the Indian Ocean ensures regular moisture in summer, nourishing the subtropical coastal parts in the east and southeast.

Most South African and Namibian succulent cremnophytes are found below the Great Escarpment in milder coastal or semicoastal parts where frost is absent or light.

3.10.5 Benguela Current (cold ocean and the formation of fog)

The Benguela Current flows northwards along the west coast of southern Africa. Strong prevailing southeast trade winds caused by the south Atlantic high pressure cell result in the upwelling of very nutrient-rich, deep-lying cold water along the shores of the west coast. It has an influence along the west coast as far as southern Angola. This cold ocean (8–14°C) cools the air and prevents the uptake of moisture in sufficient quantities; instead it brings to the region regular fog and heavy dew. Most obligate cremnophytes of the lower Orange River such as *Anacampseros scopata* [220], *Tylecodon singularis* [158], *T. bruynsii* [151] and *Conophytum stephanii* subsp. *stephanii* [190] have ‘fog trapping’ hairs and are therefore dependent on regular fog as a supplement to precipitation.

3.10.6 Altitude (temperature and rainfall)

Altitude is important for it determines temperature and rainfall. Altitudinal differences are caused by the uneven terrain of the land mass. Mountains form barriers and characteristically cause either rain shadows or orographic rain (due to the rising and cooling moist air so typical

in many parts of South Africa). Generally there is a decrease of 5°C for every 1000 m rise in altitude. The south- and east-facing mountains have a much higher rainfall.

3.10.7 Inner escarpment and other mountains

As moist air from the Indian Ocean rises along the high eastern Drakensberg Escarpment, moisture is deposited, making this the region in South Africa with the highest rainfall (800 mm to above 2 000 mm per annum). The Cape Fold Belt mountains running parallel to the south and west coast form a natural barrier (1000–2000 m) causing aridity to the north and east. This barrier results in, among other things, the dry climate of the Little Karoo and Tanqua Karoo, the latter receiving less than 25 mm per annum in parts. The Langeberg and Riviersonderend Mountains in the south form a natural barrier to the moist winter-rainfall clouds, resulting in a semi-arid climate north of the Langeberg. The Bokkeveld and Roggeveld Mountains also form a barrier, blocking off winter rainfall and resulting in the desert climate experienced in the Tanqua Karoo.

3.10.8 Temperature

The general temperature of the study area can be described as mild, the coastal parts along the east coast with warm temperatures (subtropical climate) and frost a rarity. The higher-lying inland parts above 1000 m altitude are prone to frost and occasional snow. This is, however, short-lived, with temperatures warming up during the day. Most succulents are sensitive to temperatures below freezing and there are a limited number of succulent plants occurring above the Great Escarpment. Some of them are well adapted to lower temperatures and are cold-tolerant. Cliffs at higher altitudes in the Drakensberg harbour few succulents and succulent bulbous endemics, mainly members of the genera *Aloe*, *Crassula*, *Delosperma* and *Cyrtanthus*, all of which are cold-adapted.

3.10.9 Rainfall

Two thirds of southern Africa has an arid to semi-arid climate, with rainfall of less than 500 mm per annum. South Africa and Namibia lie between two diverse climatic zones, the tropics to the north and the temperate zone to the south. Rainfall is often unpredictable; the Ferrel westerly winds extend to the southern Cape, fighting off the south Atlantic high pressure system and forcing it to the north. In summer, the south Atlantic and south Indian winds counter by deflecting the cold fronts to the south.

CHAPTER 4

STRUCTURAL ADAPTATIONS OF SUCCULENT AND BULBOUS CREMNOPHYTES TO THE CLIFF HABITAT

4.1 Introduction

The diverse succulent cremnophilous flora in South Africa and Namibia and its adaptations reflect a long history of aridity (Van Jaarsveld 1988a). Obligate succulent cremnophytes in the study area (South Africa and Namibia) differ from related plants growing on level ground in several ways (subtly to markedly different). The vertical cliff habitat is relatively stable, and cremnophytes grow in absence of the disturbances from megaherbivores, a challenge that plants on level ground constantly have to face.

Growth space on a cliff is also limited, and water run-off rapid. Consequently this vertical habitat or environment effects growth behaviour of obligate cremnophytes, both structurally and reproductively. Apart from the vertical orientation, all other environmental factors vary, as discussed in Chapter 3. This chapter aims to describe or explain the various adaptive traits on the cliff, including the growth modification behaviour (genotypic and phenotypic) of the more or less 220 obligate cremnophytes identified in the study area. How are obligate succulent cremnophytes adapted for life on a vertical environment?

I will first look at adaptive features such as succulence and adjusted growth (leaves, stems) to cope with this particular environment. This chapter has two parts, the first (4.1–4.5.1) deals with succulence and succulent plant morphology on the cliffs (including growth rate). The second part (4.5.2–4.8.3) deals with the various growth forms of succulent cremnophytes according to their stem length and other diagnostic features. These growth forms are schematically depicted in a dendrogram in Diagram 9.1 in 9.1.1, with the text following this diagram.

The various cremnophytes are well adapted to their cliff habitat. Their particular cliff-adapted growth form and behaviour is a response to a combination of factors. The main selective driving forces in the evolution of cremnophytes are the vertical orientation of their habitat and the absence of disturbances by larger herbivores. It was shown earlier (Chapter 3) that the mineral resources, availability of moisture (time of availability), light radiation,

temperature, altitude and growth space also have an effect on the size and growth form of these plants. Cremonophytes orient their leaves, stems and roots to optimally access the available physical resources on the cliff. These resources include sun radiation, growth space as well as moisture and minerals, which they access through their roots. Consequently leaves and stems are adjusted according to the availability of light (orientation and lengthening of stems) in response to the cliff environment. Roots are always in balance with the above-ground parts and they are interdependent. The extreme water run-off demands sufficient succulence (moisture storage) as discussed above. Succulence burdens the plant, and when it grows perpendicular to the cliff, gravity will take its toll unless the plant shows special adaptations to counter this force.

4.2 Gravity and its effect on growth form and size

Gravity is an omnipresent force that we tend to overlook. It was considered in more detail in Chapter 3. All life forms on earth are adapted to cope with gravitation, which is always constant in direction. Plants are victims of their habitat and have to make optimal use of their space by orientation of their growth to maximise the intake of light. Most plants resist gravity and grow in the opposite direction (auxin displacement on the lower side resulting in opposite geotropic response). Consequently most arboreal plants have sturdy ascending woody growth that supports them and keeps them in an erect position. Owing to their moisture-storage capacity, succulent plants have to carry this weight. Non-succulent cremonophytes usually have sturdy, woody stems that are well equipped to carry the weight (e.g. *Aloe barberae*, also members of *Adansonia*, *Euphorbia*). Some smaller mesembs also have woody stems.

4.2.1 Reduction in size: cliff squatters, cliff hangers and cliff huggers

The size of cremonophytes is important (see Table 11.5). Small plants can easily resist gravity owing to their size and close proximity to the cliff (by analogy, small geckos can easily negotiate a ceiling, but larger and heavier ones will rapidly fall to the ground when trying to do the same). Although succulent cremonophytes vary in size, there is also a direct relationship between plant size (weight) and growth form. Compared to their level-ground relatives, there is a general reduction in plant size.

Apart from a general reduction in size, there are three basic growth forms encountered on cliffs. Cliff hangers (often the heavier growth forms as in *Aloe* and *Gasteria*) have a distinct pendent growth. Cliff squatters are smaller shrublets with solitary, ascending growth. Cliff huggers (usually light weight) consist of dwarf cluster-forming growth forms hugging the cliff face.

However, *Aloe pavelkae* [26], the largest southern African cremnophyte so far encountered, is an exception. *Jensenobotrya lossowiana* [211] is another amazing cliff hanger from the Namib coast north of Lüderitz with pendent bunches of densely arranged, grape-like, club-shaped leaves. Larger plants have stems up to 1 m long and certainly weigh several kilograms. It has, however, a strong woody support in the form of a main branch as thick as a man's arm.

The obligate cliffs squatters are arborescent succulents that remain ascending (occasionally some branches becoming pendent). They are the smallest in number of the three groups. Compared to close relatives on non-cliff sites, there is a reduction in size and increase in succulence. *Drosanthemum anemophilum* [206] is a paradox—it has erect, sturdy branches up to 2.5 m tall where it grows on cliffs and at the base of cliffs at Rooinek Pass south of Laingsburg.

The largest group of cremnophytes are the smaller (often dwarf) cluster forms (cliff huggers) as found in *Crassula* and *Haworthia*. *Drimia uniflora* [73] is the world's smallest succulent bulbous species, a few mm in diameter, commonly found on cliffs in South Africa, especially in the winter-rainfall region.

South Africa is extremely rich in dwarf succulent plants (Ihlenfeldt 1994; Milton *et al.* 1997; Schmiedel & Jürgens 1999), with some 600 dwarf species predominantly confined to the winter-rainfall region. Outside the winter-rainfall region, dwarf succulents are usually confined to higher altitudes. The dwarf cremnophytes are all confined to shady south- and east-facing aspects (lower temperatures) where moisture is retained for longer and direct sun radiation has little influence.

Because of smaller body size, more plants can fit into the cliff habitat and smaller sized plants most probably respond better to smaller precipitation events (Cohan 1998). Smaller body size demands proportionally more water than larger body size, and the south-facing cliffs (retaining moisture longer) are therefore ideal for exploitation by dwarf succulent plants (Cohan 1998). Relative to their volume, the smaller body size (proportionally larger surface area) enables the plant to heat up rapidly during warm weather and hugging their substrate enables them to benefit from thermal heat of the cliff surface. This is also one of the possible reasons why many alpine plants have a compact habit embracing their substrate (Van

Jaarsveld 2000a). Compact dwarf succulents are rarely found in hot deserts, and large succulent plants are not often encountered in cold deserts.

4.3 Succulence and modification of growth form on the cliff

Adaptations to the cliff face not only require efficient moisture-storage abilities, but also modification of growth form and both will be considered. For the present study, the epigeous or semi-epigeous bulbous plants growing on cliffs have also been included since they comply with the definition of a succulent plant (see Chapter 2). The water-storage tissue function is expressed in the various succulent obligate cremnophilous growth forms.

4.3.1 Increase in succulence

Although there is a general decrease in plant size on a cliff, there is an increase in succulence of obligate succulent cremnophytes, when compared to related species on level ground. Succulent plants grow in habitats with little competition from mesophytic plants. The latter, which are non-succulent, are without significant moisture-storage ability, and therefore cannot compete when dry conditions set in. Succulent plants on cliffs can be solitary or sometimes grow in association with other cremnophytes.

Discussed below, is an account of the main moisture-storage organs as a function of drought tolerance on the cliff. Von Willert *et al.* (1992) distinguished two types of radically different water-storage tissues in succulent plants. The first includes irreversible water-storage tissue (all-cell succulent leaves, mainly rapid growing annual or short-lived succulent plants or short-lived deciduous leaves). The second type includes succulents with reversible water-storage tissue (partially succulent leaf type and long-lived plants). Most succulent cremnophytes have water-storage tissue that is reversible. The partially succulent leaf type displays differentiation of functions, such as parenchyma cells for water storage. The degree of succulence thus varies among the various tissues of succulent plants. The degree of succulence is determined from the water content at saturation point.

4.4 Roots

Roots are vital organs responsible not only for both moisture and nutrient uptake, but also for providing anchorage. Most succulent plants have shallow root systems that can rapidly take up moisture (Von Willert *et al.* 1992). They occur in habitats that regularly become dry and, in the case of cremnophytes, in limited or restricted growth space. Most have adjustable roots.

They can grow new roots rapidly when needed, thus exploiting a good rainy season (Hammer 1993). Growth space on cliffs varies from broad ledges to, more often, narrow crevices. Roots have to be adaptable to these conditions.

Roots of the 220 species of obligate cremnophytes recorded in this study were investigated, but no marked macro-morphological differences from their level-ground counterparts were found. The roots of most are mainly fibrous or semisucculent in the case of monocotyledons. However, there is a marked increase in root succulence in the succulent Lamiaceae. Of the nine obligate cremnophilous Lamiaceae identified, three have tuberous roots (Van Jaarsveld 2006a), all from the summer-rainfall eastern and northern parts of South Africa and Namibia. This includes two species of *Plectranthus*, namely *P. dolomiticus* [167] and *P. mzimvubuensis* [170], and *Tetradenia kaokoensis* [173]. The formation of root tubers in these taxa is retained in cultivation and they are clearly a water-storage facility. In the case of *P. dolomiticus* and *Tetradenia*, the roots become fleshy or swollen, while *P. mzimvubuensis* has distinctly fleshy, globose tubers up to 60 mm in diameter.

Lithophytic orchids (facultative) on cliffs have a characteristic velamen identical to their epiphytic tree-dwelling relatives (Harrison 1972). Lithophytic *Ficus* species (facultative cremnophytes) have wandering roots. The seedling root, however, is distinctly succulent. This is a case of temporary succulence enabling the seedling to get a foothold on the dry cliff, while the wandering roots search for better ground (Van Jaarsveld 1983). Most cremnophytes have a strong rootstock occupying crevices and providing sufficient anchorage.

4.5 Stems

The stem characteristics (length of internodes, branching and growing points) determine the life form. Congested stems give rise to plants with compact leaves and growth forms as in bulbs and cluster-forming plants (genotypic). An extension of internodes, on the other hand, results in arborescent growth forms. Stems can remain simple or can become much branched, forming clusters or shrubs and trees. Stems are also adjustable—lengthening in a dark crevice and growing towards the light (phenotypic variation). Stems and the length of the internodes are therefore very important, especially on a cliff, determining the three main types of growth form. When internodes become extended, a strong support base is required to resist gravitation (except in creepers and climbers, which either sprawl on the ground, lean on other plants or have tendrils).

4.5.1 Direction of stem growth on the cliff

Before considering the various adaptations of succulent plants, it is important to take into consideration the direction of growth on a cliff. The orientation of the cliff is vertical. Plants have to make the most of the available light and consequently their leaves and stems grow laterally or outward, away from the cliff towards the source of radiation. However, supporting horizontal or ascending growth of succulent branches places a weight burden on the plants. Solving this problem, two distinct growth form patterns emerge—pendent growth and shortened or compact growth. In nature there are no rigid barriers and some in-betweens also exist. In the case of a compact growth form (short internodes), the leaves can become long, extended and pendent (hangers) or remain short and compact (huggers). The disadvantage of being short and compact is a smaller surface for photosynthesis and for transpiration. The advantage is not having to deal with the constant force of gravity and effectively increase succulence.

In stem succulents the stems also act as a moisture-storage organ. Stem functions in obligate cremnophytes vary considerably. They can be succulent or woody and in some cases they are leafless, then becoming the main assimilating organ.

4.5.2 Stem length and cliff growth forms

Of the 220 cremnophytes recorded in this study, 91 (42%) taxa have extended (elongated) stems, including both the pendent succulent cliff hangers and ascending succulent- to woody-stemmed succulent shrublets (cliff squatters). The second group comprises plants with a markedly abbreviated stem growth (123 cliff huggers, 56%). Compared to succulent plants on non-cliff habitats, there is a general increase in stem succulence, compensating for the hyper-arid terrain. Growth patterns in cremnophytes that differ from those of their non-cremnophilous relatives are discussed below. The stems of the woody type are usually thin and not photosynthetic (evergreen leaves) while the succulent-stemmed species are often deciduous but with photosynthetically active stems. *Jensenobotrya lossowiana* [211] is an exception as the base of the woody stems can become as thick as a man's arm (Spencer Bay, Namib coast) (Van Jaarsveld 2008).

4.5.2.1 Extended stems

The two groups (cliff squatters and cliff hangers) are discussed below. They are not only cremnophytes, but also chamaephytes. The cliff hangers have pendent stems and the cliff squatters usually have ascending stems but can also become partially pendent.

4.5.2.1.1 Cliff squatters

This group includes arborescent shrubby plants but with abbreviated growth, often with a swollen base and thickset stems, resulting in short shrublets. The habit is due to genotypic factors and is not simply a case of stunted growth.

4.5.2.1.1.1 Stems succulent

A distinct form of *Othonna triplinervia* [89] confined to cliffs in the Eastern Cape differs markedly from its shrubby level-ground relatives in having a much shorter, reduced growth of up to 300 mm tall. The cliff form has a thickset succulent stem base (caudex), whereas the stems are abbreviated, flaccid and can become pendent when growing in a cliff situation. The conventional (non-cremnophilous) forms of *O. triplinervia* consist of erect growth (shrubs up to 2.5 m tall, with sturdy woody stems). *Othonna dentata* is an ascending succulent shrublet about 300–400 mm tall on coastal cliffs from the Cape Peninsula to Still Bay (Western Cape). Its close relative, *O. osteospermoides* from non-cliff habitats in the Swartberg (Western Cape) is an ascending shrub 1–2 m tall.

Othonna cremnophila [88] (Richtersveld, Northern Cape) is a short, thickset, ascending shrublet with markedly abbreviated succulent stems, covered in a powdery bloom. The related *O. cyclophylla* (Richtersveld, Northern Cape) is an erect shrub bearing slender, erect branches without powdery bloom.

Plectranthus ernstii [168] (section *Plectranthus*) has markedly swollen, abbreviated stems, articulated at the base. These cylindrical swollen stems serve as water-storage organs. The swollen stems are a unique apomorphy in the genus *Plectranthus* (especially in the usually forest-dwelling section *Plectranthus*) and a clear adaptation to the xeric cliff habitat (Van Jaarsveld 2006a). It occurs on cliff ledges in gorges from Oribi Gorge in the north to the Msikaba River Gorge in the south. Close relatives of *P. ernstii* (*P. strigosus*, *P. verticillatus*, *P. stylesii*) growing in rocky terrain away from the cliff face, lack the succulent stems.

Pelargonium mutans [162] from KwaZulu-Natal also has articulated succulent stems and slightly fleshy leaves, which can become deciduous in the dry winter season.

Kleinia articulata has mottled green articulated stems. Although not an obligate cremnophyte, the species is often associated with cliffs in the Little Karoo. When growing on cliffs, it can become pendent or scandent. *Kleinia galpinii* [85] has a succulent stem base and also subterranean stolons anchoring the plant and providing additional vegetative backup should the base succumb to fire. This reduction in stem size associated with cliff faces is a clear adaptation to this cliff habitat with its limited space and stresses related to gravity.

There is therefore a clear tendency towards reduced growth in obligate cremnophytes but at the same time an increase in succulence.

4.5.2.1.1.2 Stems woody

All cremnophilous mesemb species (especially the ascending taxa) have woody stems and do not differ markedly from their level-ground relatives. They include *Lampranthus affinis* [212], *Drosanthemum anemophilum* [206] and *Ruschia knysnana* [215].

Erepsia heteropetala [209] is a small shrublet (up to 200 mm tall) on cliffs in the Hottentots Holland Mountains. It has abbreviated stems (becoming woody) that may become pendent on south-facing cliffs. The closely related *E. lacera*, a short-lived (re-seeding after fire) perennial, grows on the adjacent Paarl Mountain and has an erect, woody growth up to 500 mm.

Jensenobotrya lossowiana [211] (Namib region), *Oscularia cremnophila* [214] (Western Cape coast) and the genus *Scopelogenia* (three species) are obligate cremnophilous mesembs, all becoming woody with age.

Tetradenia kaokoensis [173] (Kaokoveld, Namibia) has ascending, sparsely branched, woody stems with extended phyllopodia. The stems are not photosynthetically active. It has large fleshy leaves that become deciduous in the dry winters.

4.5.2.1.2 Cliff hangers

Many cliff-hanger plants display epinastic growth (a drooping, geotropically positive growth form), thus differing from their level-ground relatives. In many obligate cliff species this trait is genetically fixed.

Some opportunistic cliff plants may take on a pendent form (remaining woody), but will change to an erect habit when grown under level-ground conditions (phenotypic plasticity). Examples of succulent and non-succulent plants in the latter category include *Portulacaria afra*, *Euphorbia evansii* and *Boscia albitrunca*.

Pendent growth due to genetic modification (epinastic growth) is the distinguishing factor that separates cliff hangers from non-cremnophytes. All obligate cliff hangers have flexible stems compared to those of their non-cremnophilous relatives, a feature that appears to be an adaptation to the cliff habitat. The flaccid, flexible stems do not have to resist gravity and are consequently cost-effective compared to woodiness. Some of the larger branched cliff-hanger aloes such as *Aloe pavelkae* [26] (southern Namibia) reach a considerable size. Increase is mainly from division and the main stem (trunk) can grow to more than 3 m, bearing up to 25 rosulate heads.

Most non-cremnophilous aloes exhibit an ascending to erect growth. They include plants such as *Aloe arborescens*, *A. barberae* and *A. dichotoma*. Woody plants (dicotyledons) usually have secondary growth responsible for increase in stem girth, thus providing support. Succulent monocotyledons lack pronounced woody growth (owing to the lack of conventional secondary growth), but vascular bundles are sometimes added to the stem by a secondary peripheral cambium. This secondary tissue is rich in fibres and result in a sponge-like skeleton so characteristic of *Aloe dichotoma*, a sturdy framework supporting the heavy rosettes and stems (Von Willert *et al.* 1992).

4.5.2.1.2.1 Stems pendent; foliated

Gasteria rawlinsonii [48] and *Aloe meyeri* [22] have long, flexible stems with extended internodes that remain leafy. These leaves are perennial, therefore long-lived. This is an adaptation enabling the plants to conserve moisture. The leafy stem growth habit is not solely confined to cliff faces. The related *A. arenicola* from the sandy Namaqualand coast and *A. pearsonii* from the central Richtersveld Mountains also have a leafy stem and are well

adapted to their arid environment. Retaining leaves for longer periods and slow growth, as in many fynbos plants, are often associated with soils low in mineral content. It is economically more viable (in nutrient-poor soil) to invest in long-term leaves than to replace them annually.

Leafy stems are also found in species such as *Crassula badspootense* [113], *C. rupestris* subsp. *rupestris* [136] and *C. rupestris* subsp. *marnierana* [135] (columnar body), *Plectranthus purpuratus* [171] and *Cotyledon pendens* [108]. *Othonna capensis* [87], *Senecio muiirii* [91] and many species of *Delosperma* have leafy stems hanging down the cliff-face like a curtain and rooting where stems touch the substrate. *Jensenobotrya lossowiana* [211] is another cremnophyte with leafy stems at first, the basal part of the stem becoming leafless with age.

Crassula rupestris [135, 136] and *C. perforata* [131, 132] are morphologically very variable, and both have a wide distribution, mainly associated with Succulent Karoo on flats and mountains (see Table 11.6). In both species there are an increase in succulence and decrease in size of obligate cliff-face forms (dry river valleys of the Transkei, Eastern Cape). These differences are genetically fixed as they persist in cultivation. In some cliff-face forms, internodes are very short and consequently the fused leaf pairs are closely adpressed, forming a cylindrical stem-like structure. This is well pronounced in *C. rupestris* subsp. *marnierana* [135] and *C. perforata* subsp. *kougaensis* [131] at the Kouga Dam. The standard widespread Succulent Karoo form (which occurs in the same region as the cremnophilous form) has (non-flexible) woody stems, becomes much larger and the nodes are much further apart.

Crassula perforata [131, 132] from Enon Formation cliffs (Eastern Cape) and shale cliffs (Western Cape) has markedly swollen obovate leaves (when fully turgid) that have lost their dorsiventrally compressed shape. This is never the case in the larger non-cremnophilous forms of *C. perforata*—therefore a clear increase in xeromorphic features among the cremnophilous forms of these two species.

4.5.2.1.2.2 Stems pendent; aphyllous, cylindrical and succulent

Many cremnophytes have cylindrical succulent stems devoid of leaves of which most are pendent. *Tromotriche*, *Huernia pendula* [81] and *Rhipsalis* (Eastern Cape) have elongated, flaccid, pendent, pencil-thick succulent stems (terete to square, with reduced or short-lived leaves) functioning as the main assimilating organ. In *Tromotriche* the stems can grow up to 1 m or longer. The stems branch from the base, forming loose hanging clusters. *Lavrانيا*

haagnerae [82] (dolomite cliffs, northern Namibia) has thicker, firmer, shorter, decumbent stems up to 30 mm in diameter.

Huernia pendula [81], *Tromotriche choanantha* [84], *T. baylissii* [83] and *T. longii* (pendent microchamaephytes) have pencil-like pendent stems that display epinastic growth. *Rhipsalis baccifera* subsp. *mauritiana* [95] is another example of this growth form. *Huernia procumbens*, *Orbea hardyi* and *O. conjuncta* are near-obligate cremnophytes with similar lengthened stems. The stems are terete in *Rhipsalis* and *H. pendula*, but obtusely square or angled in the others. Bruyns (1989) reported six habitually cremnophilous stapeliad taxa confined to Africa; of these, only *H. leachii* (Mozambique) and *H. similis* (Angola) occur in neighbouring countries.

4.5.2.2 Stems abbreviated, resulting in reduced growth

Stems of this group are greatly abbreviated, resulting in growth hugging the rock face. This includes the various cremnophilous bulbous plants as well as many other dwarf succulent species. The leaves of many of these hugging plants are in tight rosettes. Rarely some grow in tight clusters, but with long drooping leaves.

4.5.2.2.1 Cliff huggers

Stems of this group are short owing to the abbreviated internodes that result in a compact growth. Bulbs have congested stems (remaining acaulescent). However, on cliffs, bulbous plants often grow in dense clusters, some rarely remaining solitary. Reducing the size of the plant body is an effective way of coping with gravity on a vertical plane. General growth forms in this category include low-growing globose clusters (rarely solitary) and plants growing as dense mats in crevices, thus adpressed to the cliff face (less weight tax compared to long-stemmed plants). The distinction between the abbreviated and extended growth categories is not always clear-cut, and there are intermediate growth forms. *Drimia uniflora* [73] is perhaps the smallest of the cremnophilous bulbous plants. It forms dense clusters of bulbs (each only a few mm in diameter) and is one of the smallest flowering plants in the world.

Apart from being able to cover a larger surface area, cliff huggers can also heat up more readily than succulents with large bodies. The disadvantage is that these plants are more prone to desiccation and destruction under conditions of extreme temperatures, hence many are found mainly on south-facing aspects in warm-temperate winter-rainfall (e.g. Cape

mountains) or summer-rainfall (e.g. Drakensberg) regions. Cremonophytes with abbreviated stems comprise the largest group of cliff dwellers (126; 57%), with the monocotyledons slightly more (65 taxa) than the dicotyledons (60 taxa).

4.5.2.2.1.1 Stems abbreviated; congested, bulbous cremonophytes

Bulbous plants are known for their abbreviated, congested stems and modified fleshy leaf bases (bulb scales). These plants are usually cluster-forming, with the bulbs exposed (epigeous). Their leaves vary in orientation; when elongated and long, they become pendent, but when shorter and compact, they can be spreading to ascending. The exposed bulbs are often photosynthetically active. This group includes species such as *Albuca batteniana* [63], *Cyrtanthus montanus* [9], *C. labiatus* [8], *Ornithogalum longibracteatum* [78], *O. juncifolium* var. *emsii* [77], *Schizobasis intricata* [80] and *Haemanthus albiflos* [10].

There is a reduction in the size in *Ornithogalum longibracteatum* (cliff-face form) from cliffs along the Bashee River (Eastern Cape). *Drimia uniflora* [73] is the species with the smallest bulbs and is probably the most widely distributed cremonophyte in the study area. The bulbs of *Albuca shawii* [67] are often hypogeous or partly exposed. Its elongated leaves become drooping on cliffs. Related species from non-cliff habitats usually have hypogeous bulbs. *Cyrtanthus herrei* [5] grows in large robust clusters, the bulbs always epigeous and covered with dried bulb scales, and the sturdy leathery strap-shaped leaves remaining ascending.

4.5.2.2.1.2 Stems abbreviated; compact, globose to mat-forming clusters

Mat-forming growths are commonly encountered in *Crassula socialis* [144], *C. capitella* subsp. *thyrsiflora* [115] (Kouga cliff-face form), *C. cymbiformis* [117], *Tylecodon decipiens* [154], *T. torulosus* [160] and *Plectranthus ernstii* [168]. In these taxa, plants fill up crevices and small ledges, tightly clinging to the rock face. The plants spread by vegetative means, the stems rooting where they touch the soil. These plants sometimes share the crevice with other succulents or become so dense that they dominate a particular spot. Members of *Tylecodon* are adapted to winter-rainfall conditions and lose their leaves in the hot, dry summers.

Many cremonophytes from the warm-temperate southern parts of South Africa form small, rounded clusters of many tightly packed stems, bulbs (epigeous) or leaf rosettes. These compact rosettes or bulbs can be solitary, as in *Crassula cremonophila* [116], or multi-headed as in *C. pseudohemisphaerica* [133] or *C. montana* subsp. *montana* [125]. Other examples

include *Haworthia cymbiformis* [52, 53], *Gasteria glomerata* [46], *Conophytum taylorianum* [192, 193], *Crassula montana* subsp. *quadrangularis* [126], *C. setulosa* [139–141], *Drimia uniflora* [73], *Ornithogalum longibracteatum* [78] and *Ornithogalum juncifolium*. Relatives of these taxa from more accessible habitats also form clusters, sometimes similar to those of cremnophytes, but others often sunken into the ground and the plants well camouflaged.

All cremnophilous *Conophytum* species form rounded compact clusters and the leaves are apically fused (although evergreen, young leaves covered in remains of old leaves during summer aestivation). The stems are short, not succulent (covered in remains of the old leaves). *Tylecodon* (summer-deciduous), on the other hand, has photosynthetically active succulent stems, often sprouting from a thickset base. The stems can be orthotropous, but are mainly plagiotropous and will root where they touch the soil. The short stems can become drooping. *Tylecodon decipiens* [154], *T. longipes* [156] and *T. torulosus* [160] have short, compact growth and the leaves become deciduous in summer. *Tylecodon ellaphieae* [155] has pointed phyllopodia, which are possibly aiding the plant in trapping fog. *Tylecodon buchholzianus* var. *fasciculatus* [152] from cliffs on the Oograbies Mountains (Vyftienmyl se Berge) near Port Nolloth occurs on east- and south-facing cliffs in the coastal fog belt. It has many branched succulent assimilating stems that remain leafless (occasionally they do grow a few leaves). *Tylecodon buchholzianus* var. *buchholzianus* is widespread in northern Namaqualand (rocky slopes), is much larger (less branched) and produces leaves in winter.

Othonna armiana [86] has a short, compact, caudiciform stem covered in phyllopodia. *Othonna herrei* is similar (non-cremnophilous). However, it is a small, erect shrublet with longer stems and without the basal swollen caudex. The genus *Othonna* is mostly confined to the winter-rainfall region and is often summer-deciduous. Most cluster-forming cremnophilous members of *Aloe*, *Gasteria* and *Haworthia* are evergreen, proliferating from the base and with compact growth. Their stems are short and hidden by the dense rosulate growth.

4.5.3 Stem succulence on the cliff

Many cremnophilous succulents have succulent stems or a combination of both stem and leaf succulence. Owing to the moisture baggage (weight), cremnophytes with ascending stems need an efficient woody support system. Dicotyledonous succulent species, such as *Othonna cremnophila* [88] and *Aeollanthus haumannii* [165], have secondary growth, the strong xylem skeleton providing an effective support. The pendent species do not need investment in a

woody support system for keeping stems in an ascending position, but the stems must be strong enough to support the weight of the plants.

Monocotyledons usually do not have conventional secondary growth. They have, however, additional, interconnected fibrous vascular bundles that are added to the stem by a secondary peripheral cambium (Von Willert *et al.* 1992). These stems can become woody in ascending aloes for instance but most cremnophytes only need a strong fibrous support system to cope with gravity. The smaller *Tylecodon* species have thick, short, intertwined succulent stems (e.g. *T. longipes* [156], *T. torulosus* [160] and *T. decipiens* [154]). These plants have a compact habit (often plagiotropous) against the rock face, enabling them to deal with gravity.

4.5.3.1 Stem and leaf succulence

Members of *Tylecodon* (Crassulaceae) have both succulent stems and leaves. In summer the leaves are deciduous, but the stems remain photosynthetically active. *Tylecodon buchholzianus* var. *fasciculatus* [152] (Richtersveld) produces very few leaves and relies more on the function of the terete succulent branches for photosynthesis. *Tylecodon buchholzianus* var. *buchholzianus* from non-cliff habitats (Richtersveld and Namaqualand) produces the normal annual winter foliage, becoming deciduous in late spring. *Othonna cremnophila* [88] is a summer-deciduous stem succulent (south-facing cliffs, Rosyntjieberg, Richtersveld). The cylindrical stems are covered with a dense, white, woolly layer of trichomes and a powdery bloom which help to prevent moisture loss in the dry cliff-face habitat (Lovegrove 1993).

4.5.3.2 Succulent internodes and phyllopodia

Aeollanthus haumannii [165] (Otjihipa cliffs, Namibia) has fleshy phyllopodia (internodes swollen). Plants become deciduous in winter, but are occasionally evergreen. Some cremnophilous members of *Tylecodon* also have fleshy phyllopodia, but not as markedly succulent as in *A. haumannii*. The branches of *T. ellaphieae* [155] (Rosyntjieberg, Richtersveld) and *T. petrophilus* [157] (Skaaprivier Poort, Namaqualand) are densely covered in phyllopodia. These vary from pointed to truncate. The habitat of these plants coincide with regular fog and dew fall and the increase in stem surface could perhaps be regarded as assisting with trapping of fog. Both the latter species occur in a semi-arid winter-rainfall region (Namaqualand).

4.5.3.3 Caudex

A caudex can be defined as a combined succulent root and stem (Jackson 1971), as found in *Anacampseros scopata* [220], a dwarf species from east-facing cliffs in the Richtersveld. The plants grow in horizontal quartz cracks and ledges (Oograbies Mountains, coastal Richtersveld).

4.5.3.4 Stem and fog-trapping hairs

Anacampseros scopata [220] from Oograbiesberg (near Port Nolloth, close to the Atlantic Ocean and with a cool climate) grows in horizontal quartz crevice layers in a region subject to regular coastal fog. These dwarf tuberous-rooted plants (tuber about 12 mm long) have 1–35 stems, each truncate at the apex. Its stems and small obovate succulent leaves (2–3 mm long) are covered in a dense tangled mass of white hairs, the latter functioning in trapping of fog (Williamson 1994). Water is stored in the succulent stems and tuberous roots. The plants occur mostly in shade or partially shaded positions together with other cremnophytes with fog-trapping abilities such as *Conophytum stephanii* [190] (hairy leaves) (Hammer 1993, 2002).

4.6 Leaves

Leaves are vital assimilating organs for most cremnophytes and variously adapted to their specialised arid habitat. Leaves vary among the various cliff-adapted growth forms (also in colour and texture), from short- to long-lived, dorsiventrally flattened, terete, globose, some fused, mostly highly succulent or sometimes non-succulent. Their shape is directly related to the phyllotaxy, which differs from decussate to a dense spiral arrangement in tight rosettes. The globose leaf shape is the ultimate moisture-storage configuration (minimum surface to volume rating). In a few cases leaves are reduced to minute scales, the stems then taking over the assimilating processes (cremnophilous Asclepiadaceae). Bulbous plants have two leaf types: the persistent modified bulb scales and the normal leaves. The leaves of the cliff bulb *Schizobasis intricata* [80] are rudimentary, soon withering. The inflorescence and exposed bulb are the main assimilating organs.

Leaves can be persistent and long-lived (*Gasteria rawlinsonii* [48]) or deciduous and annually replaced (*Tylecodon*). In succulent bulbous taxa the basal portion of the leaves is reduced to fleshy scales. Most succulent leaves, especially in plants with extended internodes and ascending leaves, are a burden to the plant owing to their voluminous nature and consequent weight tax. Plants solve the problem by having a cuneate leaf base instead of a

strong petiole (Von Willert *et al.* 1992). Plants with abbreviated stems and leaves in a tight rosette do not have this problem.

4.6.1 Leaf succulence on the cliff

Leaves of cremnophytes play a vital role and there is much variation in general morphology, succulence and duration. Leaves vary from short and compact to long and pendent. Bulb scales are modified leaves and have been added below.

4.6.1.1 Long-lived perennial leaves

Perennial succulent leaves have a function of water uptake and storage (becoming turgid) when it rains and losing water during dry periods (desiccation). The leaves therefore have a long-term function of water storage, they are the assimilating organs and are not annually replaced. The repeated filling (turgidity) and emptying (desiccation) also demands efficient anatomical adjustments to allow for such drastic changes. Von Willert *et al.* (1992) have shown that anatomical provision allows for shrinkage without damage to tissue in triangular and circular (in cross-section) leaves. Shrinkage and swelling are made possible by special folding structures. Examples include most members of *Gasteria*, *Aloe*, *Haworthia*, *Crassula* and *Cotyledon*. Dorsiventrally flattened leaves that have become turgid and inflated, simply become flattened again during drought. Examples include *G. rawlinsonii* [48], *G. batesiana* var. *dolomitica* [42], *A. meyeri* [22] and *Cotyledon pendens* [108]. The leaves can inflate to such a degree that they almost become subterete. *Crassula pubescens* subsp. *rattrayi* [134] from cliffs near Graaff-Reinet has obovate to oblanceolate, dorsiventrally flattened leaves which, when fully turgid, are almost club-shaped. On south-facing cliffs with only a limited supply of light, some leaves have further adjustments such as windows that allow for deep penetration of light to reach the chloroplast-containing tissue.

4.6.1.2 Succulent leaves annually replaced

Some succulents remain evergreen (have perennial long-lived leaves) while a group from the dry Western and Northern Cape become deciduous and are annually replaced.

4.6.1.2.1 Deciduous leaves

In *Tylecodon*, *Othonna cremnophila* [88] and *Tetradenia kaokoensis* [173], the leaves become deciduous during the dormant season. The stems of *Tylecodon* and *O. cremnophila* remain photosynthetically active. Storage of water in the leaves is therefore temporary.

4.6.1.2.2 Summer-aestivating leaves

In members of *Conophytum* leaf pairs are characteristically fused into an apically truncate, obconical body. The fused leaf pairs are annually replaced and the moisture of the current leaf pair is recycled, the current leaf pair becoming a protective sheath for the developing leaf pair (during the dry summer months). *Conophytum* spp. shed their sheaths with the first rains in autumn (Hammer 1993, 2002). Many other mesembs have thin stems and short-lived leaves that are annually replaced. *Conophytum* spp. occur on cliffs throughout Namaqualand (Northern Cape) and are winter growers, often associated with the fog belt of the Atlantic Ocean. *Conophytum* spp. are found on cliff and non-cliff habitats. Those that are cremnophytes form small, rounded clusters.

4.6.1.3 Leaf shape as an adaptation to the cliff

Leaf shape is related to the growth form of the plant and function of the leaves. Shape is very variable (linear, terete, dorsiventrally flattened to short and club-shaped) and reflects the various taxonomic groups, their habitats and in each case is the product of specialisation.

There are three basic leaf types among cremnophytes and they are related to stem length. The first type is found in plants with acaulescent rosettes of long, linear, drooping leaves as in *Bulbine latifolia* var. *curvata* [32]. The second type refers to densely packed, usually shorter leaves, in acaulescent rosettes as in *Haworthia turgida* [60]. The third type relates to shorter leaves evenly spread along elongated stems as in *Crassula badspootense* [113]. Some (e.g. *Aloe hardyi* [20]) have extended stems with drooping rosettes of densely packed leaves. Leaf shape varies among plants with elongated stems and extended internodes. This includes dorsiventrally flattened, terete, cuneate, obovate or orbicular leaves. Dorsiventrally flattened succulent leaves tend to be broader on shady cliffs, compensating for the lower light intensity. *Tylecodon petrophilus* [157] from cliffs in northern Namaqualand (Skaaprivierspoort) has unusually large, orbicular to obovate leaves for such a relatively small plant. Compact bulbous plants have either shorter ascending to spreading or elongated leaves that become pendent. The leaves of non-bulbous rosulate plants also vary; they are usually short and numerous or rarely elongated and pendent. Plants with elongated stems usually have evenly spread, short, variously shaped leaves. They are often tightly packed in a pseudostem. The leaves of *Crassula perforata* [131, 132], *C. badspootense* [113] and *C. rupestris* [135, 136] are opposite and basally fused; internode length of the stems varies. Non-cremnophilous

forms (*C. rupestris*, *C. perforata*) have longer internodes. *Crassula rupestris* subsp. *marnierana* [135] and *C. perforata* subsp. *kougaensis* [131] have very short internodes (leaf pairs touching), forming a subcylindrical body.

4.6.1.3.1 Cylindrical leaves

The cylindrical shape is commonly associated with succulent plants growing on cliffs (Van Jaarsveld & Van Wyk 2003a). Cremonophytes with cylindrical assimilating branches have been dealt with above. Many succulent cremonophytes have cylindrical or subcylindrical leaves. Examples include *Bulbine ramosa* [36], *Drimia mzimvubuensis*, [72], *Tylecodon buchholzianus* [152] and *Senecio pondoensis* [92]. *Senecio talinoides* subsp. *talinoides* [94] has cylindrical grey-green leaves. *Gasteria rawlinsonii* [48] has long, leafy stems bearing long-lived, subterete leaves. *Gasteria batesiana* var. *dolomitica* [42] grows on south-facing dolomite cliffs. It has mottled subterete leaves. *Gasteria batesiana* var. *batesiana* [41] has dorsiventrally flattened, triangular, lanceolate leaves.

4.6.1.4 Bulbous cremonophytes; leaf and bulb scales

Cremonophilous bulbs are well adapted to life on a cliff and plants are characterised by their compact cluster-forming growth. All cliff bulbs have fleshy leaf scales (modified leaves) and are therefore treated here. Their leaves vary from distinctly succulent as in *Ornithogalum pendens* [79], to slightly fleshy or leathery. Some 30 such species have been identified, including members of the Amaryllidaceae (11 species), Hyacinthaceae (18 species) and Oxalidaceae (one species). Bulbs on cliffs mostly display epigeous growth, and the bulbous portion is photosynthetically active (Van Jaarsveld & Van Wyk 2003b). They vary in shape, size and growth form. Already mentioned above, the smallest is *Drimia uniflora* [73] with the bulbs only a few mm high. One of the largest is *Cyrtanthus falcatus* [2] of which the bulbs are longer than 300 mm. The bulbs are usually oval and tunicate, others with modified fleshy bulb scales (tunics), usually tightly packed in an imbricate body. The leaves are mostly spirally arranged (multifarious).

Cremonophilous bulbs are extremely drought tolerant. The functional leaves (upper portion of the bulb scale) vary considerably in shape, size and succulence. The leaves of these bulbs also vary in duration, some being annually replaced (deciduous) while others are evergreen. The leaves vary in shape from short, strap-shaped and ascending to elongated and

drooping. The texture also varies from densely hairy to glabrous. *Ornithogalum pendens* [79] has glaucous leaves (covered in a powdery bloom).

4.6.1.4.1 Bulb scales and their modification

Bulb scales are fleshy organs adapted for water storage. They vary from standard tunicate scales to modified loose scales. Although both states are also found in plants on non-cliff sites, there tends to be an increase in drought tolerance on the cliff.

4.6.1.4.1.1 Tunicate bulbs

Bulb scales are long-lived moisture-storage organs. The outer tunics often wither, forming a cover that protects the fleshy inner bulb scales against water loss. Such tunics are seen in bulbs of members of *Cyrtanthus*, *Ledebouria* and *Ornithogalum*. The tunics are sometimes shortened and truncate as in *Haemanthus*. Most tunicate bulbs grow in dense clusters and sometimes lose their leaves during times of drought or in the dormant season.

4.6.1.4.1.2 Bulb scales

Drimia cremnophila [69] and *D. mzimvubuensis* [72] have exposed photosynthetically active, fleshy, club-shaped bulb scales. When becoming detached the scales can function as vegetative propagules. Similar bulb scales are found in *D. haworthioides*, a non-cremnophilous species occurring among gravel, the bulb scales well camouflaged. The bulb scales in this species are not as succulent nor as pronounced as in the two cremnophytes. *Drimia mzimvubuensis* has firm, drooping, evergreen, semiterete leaves and similar club-shaped bulb scales (leaves of *D. cremnophila* are dorsiventrally flattened). Both have persistent assimilating (green) inflorescences (after the flowers have been shed).

4.6.1.4.2 Bulb leaves

Bulbs on cliffs vary considerably in the density, shape and size of the leaves. Most leaves are strap-shaped and linear. Leaves of most species are very adaptable, especially in size, and according to the situation. The direction of growth varies from ascending to pendent.

4.6.1.4.2.1 Leaves ascending

Most cremnophilous bulbs have ascending leaves. They can become drooping under shady conditions (*Ornithogalum longibracteatum* [78]).

4.6.1.4.2.1.1 Leaves few, narrow

Dwarf clustered bulbs often form dense, tight mats with a rosette of a few ascending linear leaves, the outer bulb scales sometimes becoming the main assimilating organ. The few ascending to spreading, linear leaves are often tightly packed into a narrow neck and play a minor role in photosynthesis but maximise penetration of light to the bulb. These photosynthetically active bulbs occur mostly on shady cliff faces (open shade). Examples are the dwarf *Drimia uniflora* [73] and *Ornithogalum juncifolium* var. *emsii* [77].

4.6.1.4.2.1.2 Leaves numerous

In members of *Ledebouria* the leaves are usually leathery, broad and produced in a conspicuous central rosette. They can be mottled (*L. cremnophila* [75]) or glaucous (*L. venterii* [76]) and the bulbs are the main assimilating organs. Species with larger bulbs (*Ornithogalum longibracteatum* [78] (both bulb and seed assimilating organs) and *Albuca batteniana* [63]) have elongated, ascending-spreading, strap-shaped, leathery, green leaves tapering at the tip. However, on shady cliffs the leaves of both species elongate and will become pendent. *Cyrtanthus herrei* [5] has erect, often spirally twisted, leathery leaves with an entire margin. The leaves are glaucous, evergreen and well adapted to dry conditions on the cliff face. Plants occur in large clusters on cliffs in northern Namaqualand and the Hunsberg of southern Namibia. *Cyrtanthus junodii* [7] (winter-deciduous), *C. flammosus* [3], *C. montanus* [9] and *C. labiatus* [8] all have leathery, glaucous, ascending leaves. *Cyrtanthus junodii* and *C. flanaganii* [4] occur on cliffs at higher altitudes and are winter-deciduous.

Although most bulbous cremnophytes have bulbs above ground, *Oxalis pocockiae* [219] (Western Cape) is the exception. It has a subterranean bulb well hidden in cliff crevices, with leaves ascending and typical of most members of *Oxalis*.

4.6.1.4.2.2 Bulbs with drooping leaves

Drooping leaves are displayed by some cremnophilous bulbous species such as *Albuca cremnophila* [64] and *A. thermarum* [68] and four species of *Drimia*. The shape of the lamina is usually linear and elongated, varying from dorsiventrally flattened to terete. There are two types of drooping leaves—those that become drooping owing to gravity and those with epinastic growth.

4.6.1.4.2.2.1 Leaves drooping due to epinastic growth

Albuca cremnophila [64] is evergreen and has firm, linear, deeply channelled leaves up to 1 m long (margin entire). These leaves have epinastic growth (also in cultivation) and are geotropically positive. The leaves of *A. cremnophila* are dark green, leathery and often with a centric translucent band (up to 5 mm in diameter) on the adaxial surface. Plants often occur on shady south-facing cliff faces, the translucent band allowing light to penetrate deep into the assimilating succulent tissue. Other bulbous species displaying epinastic leaf growth include *A. thermarum* [68] and *Cyrtanthus falcatus* [2]. The latter has strap-shaped, falcate, glaucous leaves that become deciduous in winter. It grows on inaccessible cliffs along the foothills of the Drakensberg.

4.6.1.4.2.2.2 Leaves drooping due to gravity

Drimia flagellaris [70] (southern KwaZulu-Natal and Eastern Cape) and *D. loedolffiae* [71] (Eastern Cape) have epigeous bulbs with linear, terete leaves that become drooping on the cliff. The cylindrical leaf shape is an effective moisture-storage solution in an arid climate (Van Jaarsveld & Van Wyk 2003a).

4.6.2 Leaf duration on the cliff

Leaves can be short-lived, remaining active during the rainy season or becoming deciduous with the onset of dry or cold conditions (e.g. *Cyrtanthus falcatus* [2]). *Albuca cremnophila* [64] has long-lived perennial leaves (rainfall spread throughout the year). *Ornithogalum pendens* [79] has pendent, distinctly succulent leaves.

4.6.3 Assimilating organs other than leaves

Schizobasis and *Bowiea* have annual assimilating inflorescences, pendent and softly succulent in *B. gariopensis* (cliffs and screes in the Northern Cape) and erect, stiff and less succulent in *Schizobasis* (mainly cliffs in the eastern parts of South Africa). Leaves in both groups are small and short-lived (rudimentary). The inflorescence of *Drimia flagellaris* [70] tends to be persistent after the seeds have been released, acting as an assimilating organ (Van Jaarsveld & Van Wyk 2006a). The same phenomenon occurs in *D. mzimvubuensis* [72].

4.6.4 Leaves of non-bulbous succulent geophytes

Non-bulbous succulent geophytes on cliffs appear to be confined to the winter-rainfall region and are winter-active. *Tylecodon singularis* [158] occurs on dolomite cliffs and steep southern

slopes of the Hunsberg, southern Namibia. It has a tuberous roots base, a solitary leaf, and becomes deciduous in spring. The solitary leaf is a paradox and unique among the cremnophytes. The blade is large (up to 100 mm) and concave, with a hairy epidermis. The petiole is channelled towards the base and moisture from fog is trapped by the blade and channelled via the petiole to the base of the plant near its roots.

Other non-bulbous geophytes include *Crassula nemorosa* [127] and *Bulbine pendens* [35]. These species occur on shady south-facing cliffs, reacting to winter moisture and aestivating during the long, dry summers. *Bulbine pendens* is a deciduous geophyte from the Rosyntjieberg (Richtersveld) and Skaaprivierspoort annually producing soft, linear, terete, drooping leaves from a succulent tuber (Williamson & Baijnath 1995). *Trachyandra tabularis* [62] from cliffs in the Western Cape also produces a rosette of subterete, succulent, pendent leaves up to 1 m long.

4.6.4.1 Succulent plants (non-bulbous) with leaves in acaulescent rosette

The leaves of many cremnophilous succulent plants are arranged in rosettes. They vary considerably in shape, size and function. The leaves are sometimes pendent as a result of gravity or epinastic growth.

4.6.4.1.1 Pendent leaves from acaulescent rosette due to epinastic growth

Leaves in these plants display epinastic growth and curve downwards even when cultivated. *Bulbine cremnophila* [31], *B. meiringii* [33], *B. latifolia* var. *curvata* [32] and *Gasteria croucheri* subsp. *pendulifolia* [43] have acaulescent rosettes of pendent, fleshy leaves. In the last-mentioned, leaves can become almost 1 m long.

4.6.4.1.2 Leaves becoming pendent due to gravity

Pyrrosia schimperiana [1] is a poikilohydric succulent-leaved fern from cliffs along the Blyderivierspoort (Mpumalanga). It grows in ample soil on south-facing ledges of quartzitic sandstone cliffs. It has a basal rosette of fleshy, drooping leaves (without epinastic growth) during the summer rainy season that become semidesiccated during the dry winter months or dry spells. The young leaves are densely hairy, a further protection against water loss, later becoming glabrous.

Streptocarpus kentaniensis [164] is an evergreen succulent from shady shale cliffs along tributaries of the lower Kei River in the Eastern Cape. It has linear, ascending to drooping leaves from a central rosette and deviates from all other members of *Streptocarpus* in the markedly fleshy midrib of the leaves as well as the decumbent fleshy petiole, this rendering it well adapted to the xeric cliff environment (Hilliard & Burt 1971). The prominent succulent midrib (prominent on lower leaf surface) is the main water-storage tissue of the leaf. Apart from succulence, the leaves are semi-poikilohydric. They often become pendent owing to gravity.

4.6.4.1.3 Leaves in a rosette (or rosette-like clusters), short, non-drooping

Most cliff-hugging cremnophytes have short, succulent leaves in a central rosette (compact phyllotaxy). This includes both monocotyledons and dicotyledons such as members of *Gasteria*, *Haworthia* and *Crassula*. Members of *Haworthia* have multiple rosettes (from division or basal stolons), often forming globose clusters. *Haworthia angustifolia* var. *baylissii* [50] occurs on shady cliffs of the Witterivier (Suurberg, Eastern Cape). It has recurved, triangular leaves exposing the inner rosette to as much sunlight as possible. Its non-cremnophilous relative (*H. angustifolia* var. *angustifolia*) has narrow, erect leaves and grows in exposed rock crevices in the Suurberg. *Haworthia gracilis* var. *picturata* [55] and *H. cymbiformis* var. *setulifera* [53] grow on shady cliffs. Their soft-textured, glabrous, cymbiform, fleshy, green leaves have distinct apical windows that allow light into the inner translucent leaf tissue (Schanderl 1935).

Most cliff-dwelling members of *Haworthia* grow in dense, rounded clusters or mats in rock crevices. *Haworthia glabrata* [54] (shale cliffs) and *H. attenuata* [51] (Enon Formation) grow on exposed north-facing cliffs. They differ by their firm leaves with a thick epidermis and the leaves are often reddish green (anthocyanin) or covered with white tubercles. *Gasteria glauca* [45] and *G. glomerata* [46] grow on sheer south- and east-facing cliffs along the Kouga River in the Eastern Cape, forming globose compact clusters. The leaf epidermis is glaucous and tuberculate. Both grow in mineral-poor, quartzitic sandstone rocks.

Species of *Crassula* confined to south-facing cliffs usually have broader leaves (compensating for the lower light intensity) while those on exposed sites have narrower leaves. In *C. cremnophila* [116] the leaves are dorsiventrally flattened and arranged in tight, imbricate, flattened to spherical rosettes. The three subspecies of *C. exilis* [118–120] all have dwarf rosettes, forming dense mats. *Adromischus* spp. growing on cliffs have elongated,

succulent leaves in basal rosette-like clusters. In *A. schuldianus* subsp. *brandbergensis* [103] the upper leaf surface is retuse, with an obscure window.

Kleinia galpinii [85] has glaucous, oblong, obovate, succulent leaves in a basal rosette. The margin is entire. *Aloe haemanthifolia* [19] is quite an exception with distichous leaves in dense clusters. These clusters, unlike in most other cliff huggers, are large. The green leaves are broad, strap-shaped, firm and erect, well adapted to shady and open-shade cliffs. The species also occurs on sunny cliffs.

Members of *Conophytum* (Mesembryanthemaceae) have opposite leaves, fused into an obconic body, in dense globose clusters. The leaves are annually replaced, the moisture recycled from the older to the younger leaf pair. During the dry summer season the plants aestivate and the younger, fleshy leaves remain tightly covered by the dry remains of the older ones.

Some leaves are flexible and adjust to the availability of moisture. The differences between the leaf shape of obligate cremnophilous members of *Conophytum* and related non-cremnophytes are often subtle, with some essentially similar whereas others differ markedly. However, there tends to be an increase in leaf shapes that maximise water-holding capacity—cylindrical or terete, biconvex, subcylindrical, club-shaped and triquetrous.

4.6.4.1.4 Leaves in pendent caulescent rosettes (pendent megachamaephytes) with non-assimilating stems

In most cremnophilous members of *Aloe*, *Bulbine* and *Gasteria* the leaves are in an apical rosette, some becoming cauline. *Aloe corallina* [16] and *A. dabenorisana* [17] have pendent rosettes; leaves of the former are pendent, those of the latter recurved. *Aloe corallina* has firm, greyish to whitish green, incurved leaves with a thick, firm epidermis. It occurs on dark-coloured dolomite cliffs in the very hot Kunene Valley (Namibia) in desert or arid savanna. The epidermis is light grey-green and reflects some of the sunlight, the outer leaves protecting younger leaves within. The leaves of *A. corallina* display epinastic growth. *Aloe dabenorisana* is a desert species from the dry lower Orange River Valley and grows on shady south-facing aspects. It has an open rosette and the older leaves re-curve, maximising radiation intake and compensating for its shady habitat (open shade).

Aloe meyeri [22] and *Gasteria rawlinsonii* [48] have long-lived leaves and consequently (apart of the apical rosette) also a leafy stem. Both are slow growers on mineral-poor quartzitic sandstone cliffs. In *A. hardyi* [20], *A. corallina* [16], *A. omavandae* [25] and *A. meyeri* the leaves display epinastic growth, curving down from the cliff faces (a feature retained in cultivation).

4.6.4.1.5 Succulent leaves on a leafy stem

Stems of a group of succulent cremnophytes are extended (short or longer), covered by perennial long-lived leaves. These leaves vary considerably in arrangement (phyllotaxy) and shape.

4.6.4.1.5.1 Leaves arranged in a subcylindrical body (internodes short)

Crassula rupestris subsp. *marnierana* [135], *C. perforata* subsp. *kougaensis* [131] and *Plectranthus purpuratus* [171] have very short internodes and consequently the leaves become tightly packed into a subcylindrical body. *Crassula rupestris* subsp. *marnierana* is an excellent example of this growth form, having leaves tightly packed into a cylindrical body (leaves decussate, each pair fused at the base). The stems are initially flaccid and succulent, often becoming woody with age. *Plectranthus purpuratus* from the KwaZulu-Natal Midlands is well adapted to life on cliffs. The leaves and stems are adjustable—under dry conditions the internodes become shortened and the leaves tightly packed into a subcylindrical body but in moist, shady environments the stems become elongated and the leaves much larger.

4.6.4.1.5.2 Leaves evenly spread (internodes extended)

Succulent leaves in most species of *Delosperma* are usually decussate, with longer internodes, thus more widely spaced. Leaves of *D. tradescantioides* [202] from shady cliffs are dorsiventrally flattened (oval). *Senecio muiirii* [91] has succulent stems and dorsiventrally flattened leaves. The leaves are ascending, obovate and glaucous, each bearing three conspicuous translucent veins on the abaxial surface. *Senecio talinoides* subsp. *talinoides* [94] and *S. pondoensis* [92] have terete, ascending leaves, those of the latter with a central elongated window.

Pelargonium mutans [162] (stem succulent) has leaves (non-succulent) on slender petioles that become deciduous in winter. Members of *Aeollanthus* and some cremnophilous species of *Plectranthus* have fleshy leaves that become deciduous in winter (*A. haumannii* [165] and *P. ernstii* [168]). *Cotyledon pendens* [108] has very succulent spindle-shaped leaves,

sometimes densely arranged (nodes becoming shortened when growing in full sun), and densely covered in a powdery bloom. The stems are epinastic, soon becoming pendent on cliffs.

4.6.4.1.6 Leaves in drooping clusters

Jensenobotrya lossowiana [211] and *Carruanthus peersii* [174] have club-shaped (sometimes almost rounded) leaves, maximising moisture intake. In both species the heavy, clustered, grape-like leaves become drooping on cliffs.

4.6.4.1.7 Leaves in ascending clusters

Cotyledon tomentosa subsp. *tomentosa* [109] is a dwarf cliff squatter (short, compact shrubs). The leaves are somewhat dorsiventrally compressed and densely hairy. They are large (compared to plant size), green and broad, adapted to shady cliff faces.

4.6.5 Leaf epidermis

The epidermis (with cuticle) of plants is important as the interface of the plant with its environment. Succulent plants often have modifications of the epidermis that help them to cope with drought stress. These waterproofing measures include features such as thickened outer periclinal epidermal cell walls, epidermal wax, a grey colour, epidermal hairs and a sunken position of the stomata.

4.6.5.1 Epicuticular waxes

The outer periclinal cell walls are mostly thickened in succulent plants, especially in cremnophytes. Leaves are often covered in insoluble epicuticular waxes, causing the characteristic ‘powdery bloom’. These are all adaptations that reduce water loss via transpiration and evaporation. Surface waxes are laid down on a continual basis.

Cremonophytes can also adjust their wax production according to their needs, especially during hot, dry spells (Lovegrove 1993).

4.6.5.2 Colour

The colour of the surface is sometimes greyish white, additionally reflecting the rays of the sun. The green colour is due to the radiation reflected from chloroplasts. Von Willert *et al.* (1992) have shown that colouring induced by light stress lowers the absorptivity in visible solar radiation. A whitish epidermal cover as found in some cremonophytes (*Adromischus leucophyllus* [101], *Cotyledon barbeyi* var. A [106], *C. pendens* [108]) increases reflectivity

(Eller & Willi 1977; Eller *et al.* 1983). A dense whitish indumentum as in *Senecio medley-woodii* [90] (from cliffs in KwaZulu-Natal) reduces penetration of light (Gates *et al.* 1965).

Cremnophytes growing on exposed north-facing aspects often have leaves with a very hard, firm, whitish to glaucous epidermis. Examples include *Aloe corallina* [16], *A. meyeri* [22] and *A. dewinteri* [18]. These taxa are usually associated with the very arid northern subtropical summer-rainfall regions. The epidermis is covered with a waxy or powdery bloom. This is also typical of cliff forms of the widespread *Cotyledon orbiculata* (leaves soft) and has been observed on cliffs on the southern slopes of the Aasvoëlberg (Willowmore), the Auas Mountains (Windhoek) and the upper cliffs faces of the Baynes Mountains (northern Namibia).

4.6.5.3 Papillae

In contrast to the cremnophilous Crassulaceae, leaves of many non-cremnophytes are distinctly papillate. *Crassula perfoliata*, which is also frequently encountered on cliffs, has dense, flask-like epidermal papillae with silicified walls (Rowley 2003). *Gasteria glomerata* [46], *G. glauca* [45] and *G. rawlinsonii* [48] grow on shady cliffs. Unlike most other members of *Gasteria*, their leaves are uniform in colour, not mottled. The epidermis is asperulous or tuberculate. The leaf surface consists of large numbers of raised silicified papillae, some of which are pointed. The function of these papillae is not clear, but they may act as windows (Haberlandt 1909) and could also serve to impede water loss by minimising the disruption of the boundary layer caused by wind (Lovegrove 1993).

4.6.5.4 Epidermal hairs

The function of epidermal hairs can be two-fold, namely to prevent moisture loss during hot, dry periods and to trap moisture, especially along the fog belt of the west coast of South Africa and Namibia.

4.6.5.4.1 Epidermal hairs reducing moisture loss

Plants benefit from a layer of epidermal hairs by maintaining a water pressure boundary layer. This impedes movement of moist air, thus reducing water loss (Lovegrove 1993). Most species of *Cotyledon* have smooth leaves. *Cotyledon tomentosa* subsp. *tomentosa* [109], an obligate cremnophyte of the semi-arid Baviaanskloof (Eastern Cape) and Gourits River (Western Cape), has a very hairy epidermis. *Senecio medley-woodii* [90] has a cover of dense,

white, felt-like hairs, all features that may help to reduce water loss through transpiration. Epidermal hairs also reflect some of the solar radiation, thus reducing heat levels of the plant.

4.6.5.4.2 Epidermal hairs and fog-trapping abilities

Epidermal hairs of succulent plants and fog-trapping abilities are associated with regions along the west coast that receive frequent fog. This relates to most of the succulent cremnophytes growing within the Namib coastal fog belt (Namaqualand and southern Namibia). *Tylecodon singularis* [158] grows on dolomite cliffs at Sonberg, Kuamsibberg and Konsertinaberg. It has large, heart-shaped leaves (solitary, rarely more than one) that are concave and densely hairy. The petiole is channelled and serves to guide moisture to the roots. *Tylecodon longipes* [156] and *T. ellaphieae* [155] also have large hairy leaves with fog-trapping abilities. *Conophytum stephanii* subsp. *stephanii* [190] and *C. ernstii* [179] have a hairy epidermis and the plants are dependent on regular fog from the Atlantic Ocean. *Conophytum stephanii* subsp. *stephanii* grows on south-facing cliffs of the Rosyntjieberg (receiving frequent fog) and has the longest trichomes in the genus (Opel 2002).

4.6.5.4.3 Epidermis glabrous

Conophytum ricardianum [189] is an obligate cremnophyte of which the range also falls in the fog zone, but it has a glabrous epidermis. The dense leafy clusters of *Jensenobotrya lossowiana* [211] (leaves club-shaped and glabrous) become moist during the regular foggy periods, dripping with moisture during dense fog at Dolphin Head along the coastal Namib (100 km north of Lüderitz).

4.6.5.5 Stomata

Stomata are important structures of the epidermis for allowing efficient gas exchange and transpiration. Stomata of succulent plants are often modified, ensuring conservation of water, and many open only at night when the vapour pressure of the air is higher. Deeply sunken stomata certainly reduce moisture loss by retaining moist air for longer periods. Members of *Aloe* and their close relatives (*Gasteria*, *Haworthia*) have deeply sunken stomata, often with cuticular rims (Von Willert *et al.* 1992).

The genus *Conophytum* is an exception and very few of its members have sunken stomata (Opel 2002). This could perhaps be attributed to their moist winter-growing period (also high dew incidence and high humidity during winter nights). The seven species of

Conophytum with sunken stomata according to Opel (2002) are confined to very dry habitats. The stomata of the leaf epidermis of *Jensenobotrya lossowiana* [211] are also not sunken. The species occurs in a region subject to regular fog and high air humidity, the leaves often covered in droplets of moisture during periods of fog. Although not proven yet, the possibility exists that moisture from fog is directly absorbed through the epidermis. Moisture collected from its smooth, club-shaped leaves drips onto the soil and is undoubtedly utilised by surface roots.

4.6.5.6 Changeable epidermis

Plants of *Delosperma* sp. A [194] from the cliffs in dry river valleys of southern KwaZulu-Natal can switch the texture of their leaf epidermis according to the availability of moisture. Under moist conditions the leaves are smooth. During dry periods the plants grow new leaves with a hairy epidermis. This has also been observed in cultivation. Leaf epidermal changes have also been noted in *Crassula*.

4.6.5.7 Windows

Windows are commonly associated with certain plant groups such as *Lithops* and *Bulbine* (Schanderl 1935; Von Willert *et al.* 1992; Hammer 1993, 2002; Rowley 1994). In cremnophytes, windows are often present in the leaves of plants that grow on shady south-facing cliffs. The windows are translucent, allowing for deep penetration of solar radiation. They vary from micro-windows to larger striations to distinct patterns, the last-mentioned present and especially prominent in cremnophilous species of *Haworthia* that grow in shady situations. Cremnophilous species of *Conophytum* all have micro-windows. These light wells lie just below the epidermis (Von Willert *et al.* 1992) and are often visible as dots on the leaf surface.

Windows are also present in the leaves of most bulbous cremnophytes with long, linear leaves. *Albuca cremnophila* [64] has a median window running along most of the adaxial leaf surface. Other cremnophytes with a similar centric window on the upper leaf surface include *Drimia mzimvubuensis* [72] and *Albuca shawii* [67]. *Aloe challisii* [15] and *A. soutpansbergensis* [29] are two grass aloes growing at high altitudes under cool, moist conditions, often in south-facing or shady places. Both species have narrow windows along the leaf margins.

4.6.6 Leaf margin

The leaf margin represents a direct interface with the environment and it is important that it is strong enough to withstand disturbances caused by the weather and predators, for example. Leaf margins of cremnophytes therefore vary considerably, from dentate, ciliate, tuberculate, entire, leathery and firm to soft. In *Gasteria* and *Haworthia*, leaf margins can be variously tuberculate or entire, firm and leathery. In *Aloe*, margins are often toothed, as in *Aloe hardyi* [20] and other cremnophilous members. It is almost entire in *A. corallina* [16] and entire in *A. nubigena* [24].

Compared to the situation in non-cremnophilous relatives, there is a reduction in armament, but this is dealt with in more detail under 4.8.1 below. Also see Table 11.11.

4.7 Succulent cremnophyte growth rate and life cycle

Succulent cremnophytes vary in their rate of growth. This was tested in cultivation at Kirstenbosch National Botanical Garden. Plants were grown from seed or vegetatively from cuttings. The growth rate of plants reveals their ecological status. Fast-growing taxa can be interpreted as pioneer plants. They have a rapid turnover (seed to seed), therefore a faster evolutionary rate of adaptation. Slow growth (low metabolism) in spite of favourable conditions often reveals adaptation to mineral-poor soils. Slow-growing plants furthermore have a much longer life span and tend to have a slower evolutionary rate of adaptability.

4.7.1 Monocotyledons

Within the Asphodelaceae, members of *Bulbine* are rapid growers and opportunistic pioneer cremnophytes. Sown from seed, some will flower within a year, thus displaying a potentially rapid evolutionary adaptability. Most aloes are also fairly fast-growing, *Aloe hardyi* [20] and *A. kouebokkeveldensis* [21] can flower 3–4 years after sowing, whereas *A. meyeri* [22] and *A. dabenorisana* [17] are much slower. The rapid-growing species furthermore tend to be of solitary growth, with large flowering panicles ensuring a large seed set. The rate of growth for *Haworthia* is medium, plants taking about two years to flower from seed. This mainly includes the soft-leaved species (e.g. *H. cymbiformis* var. *setulifera* [53]). *Haworthia* species with thick-textured leaves (e.g. *H. attenuata* [51]) usually grow more slowly.

The slowest growers in the group, however, are the gasterias. These plants take a long time to mature. *Gasteria rawlinsonii* [48] and most other cremnophilous gasterias have a slow

rate of growth and only flower about 4–5 years after sowing. They gradually increase by vegetative means, but with less investment in flowering (evolutionarily also the most basal species) (Zonneveld & Van Jaarsveld 2005). Many of the slower-growing species are also associated with mineral-poor quartzitic sandstone rocks (e.g. *Aloe meyeri* [22], *G. rawlinsonii*, and other *Gasteria* spp.). Most cremnophilous members of the Hyacinthaceae and Amaryllidaceae are of medium to slow growth. The Amaryllidaceae are the slowest, especially the genus *Haemanthus*.

4.7.2 Dicotyledons

The family Mesembryanthemaceae is known for rapid growth. Cremnophilous mesembs are also fairly rapid-growing, especially members of *Delosperma* and *Lampranthus*, which are fairly short-lived perennials. Members of *Conophytum* have a medium growth rate and will soon flower after sowing. There are, however, one exception—*Jensenobotrya lossowiana* [211] from the coastal Namib between Lüderitz and Walvis Bay. This cliff hanger is endemic to coastal cliffs at Dolphin Head. The plant grows isolated on low cliffs without any disturbances from predators. Around 1951, Hans Herre, Curator of the Stellenbosch University Botanical Garden, received a stem from E. Jensen, a succulent enthusiast of Lüderitz. It was 1.18 m long, with a thick woody portion, the main branch with a circumference of 230 mm (Schwantes 1957). Herre, author of this peculiar monotypic genus, estimated plants to be well over 200 years old. I can corroborate this as I was privileged to visit the habitat in December 2007—a plant photographed by Giess in 1974 and again by me in December 2007 did not appear much larger. Small portions of the stem had become leafless but the plant did not seem to have changed much over the 33 years (see Van Jaarsveld 2008).

Growth rate in the Crassulaceae varies, but most members are fairly fast-growing, the slowest being *Crassula rupestris* [135, 136] and *C. badspoortense* [113]. Cremnophytes in the Lamiaceae have a medium rate of growth, with *Plectranthus ernstii* [168] one of the slowest; it grows in pockets on mineral-poor, quartzitic sandstone rocks. *Dewinteria petrophila* [221] is semisucculent. It is a rapid-growing biennial, weak perennial or annual, flowering and completing its life cycle within the growing season. It compensates for its reproductive specialisation (see Chapter 5).

4.8 Cremnophyte defence

Sheer cliffs are inaccessible to most larger herbivores and other animals. Although some strict cremnophytes can show various degrees of defence, the general pattern is one of a decrease in defence adaptations against herbivores.

4.8.1 Armour

There is a clear reduction in armament in cremnophytes, not only a reduction in spines but also a reduction in firmness (see Table 11.11). *Aloe nubigena* [24] has soft, fragile leaves without any spines and in older specimens of *A. corallina* [16] the leaf margin is almost spineless or carries only small remnants of teeth. When this species is grown from seed, the leaf margin of the seedlings has more pronounced prickles, but the prickles decrease with maturity. This indicates a reduction and relaxation in armament. Relatives from conventional habitats, however, are usually armed with many well-developed teeth. Furthermore, many cremnophytes have very soft, fragile leaves and stems (see Table 11.14), for example species of *Haworthia* from south-facing cliffs, *Bulbine cremnophila* [31] and *B. pendens* [35].

Conophytum species [175–193] on cliffs also have a very fragile leaf epidermis that is easily damaged. *Conophytum ricardianum* [189] from Sonberg occurs on sheer south-facing cliffs. It has a soft, fragile epidermis that is easily damaged compared to the situation in *C. wettsteinii* (the same group), which has leaves with a firm texture and occurs in the same area, but as a chasmophyte in exposed terrain above the cliff face. *Senecio pondoensis* [92] has soft, pruinose leaves compared to the related *S. talinoides* subsp. *talinoides* [94] and *S. ficoides*. *Jensenobotrya lossowiana* [211] from Dolphin Head north of Lüderitz has very fragile leaves and stems. The plants grow on an isolated promontory without any herbivores or other disturbances.

4.8.2 Camouflage

Gasteria species usually have mottled green leaves or tubercles that make them difficult to spot in the thicket vegetation where many of them grow. In the cremnophilous *Gasteria glauca* [45], *G. glomerata* [46] and *G. rawlinsonii* [48], there is a reduction in leaf spots (Van Jaarsveld *et al.* 2003). In fact, some of the cremnophilous taxa are quite conspicuous as there is no need for camouflage because it is so difficult for herbivores to reach them (also see Table 11.13).

4.8.3 Chemical defence

Aloes are known for their bitter leaf sap. However, most cremnophilous aloes such as *Aloe challsii* [15], *A. haemanthifolia* [19], *A. kouebokkeveldensis* [21], *A. hardyi* [20], *A. nubigena* [24], *A. reynoldsii* [28], *A. soutpansbergensis* [29], *A. thompsoniae* [30] and *A. corallina* [16] are not as bitter-tasting as their relatives growing in more accessible places (Table 11.12). When the seeds of cremnophilous plants germinate in accessible terrain, the seedlings are rapidly grazed (see Figure 19d). The same is true of *A. arborescens*, a near-cremnophilous endemic (hence the Afrikaans name *kransaalwyn*).

CHAPTER 5

REPRODUCTION ON THE CLIFF

Obligate cremnophytes are exiled to life on a cliff and are effectively adapted to their vertical habitat where there is no (or limited) disturbance by larger mammals. Very few plants other than succulents can sustain life on a cliff, and the few non-succulent species that do survive, display a shift in reproductive strategy. Obligate cremnophytes cannot compete in conventional (non-cliff) accessible habitats and even if they do germinate in a non-cliff situation, the plants will soon be grazed. All plants are dependent on moisture, nutrients and sufficient solar radiation and cremnophytes have to cope with gravity in special ways. Furthermore, sustained life on a cliff demands an effective reproductive strategy. The overall reproductive behaviour of obligate cremnophytes deviates from that of their non-cremnophilous relatives in accessible habitats.

The emphasis in this chapter is on cliff-adapted reproductive strategies. Apart from their sexual reproduction, most (204 or 93% of the taxa studied) obligate succulent cremnophytes have an *in situ* vegetative propagation backup. There is therefore a clear shift to vegetative propagation on the cliff and many cremnophytes are dependent on this asexual mode of reproduction. Both sexual and asexual reproduction are discussed below.

Semisucculent plants such as *Dewinteria petrophila* [221], *Stemodiopsis rivae* [222] and *Colpias mollis* are less succulent but have additional strategies such as active cremnocarpy and cremno-amphicarpy. *Colpias mollis* and *D. petrophila* are almost ephemeral or weak perennials.

The vertical habitat and the constant presence of gravity demand an effective seed dispersal strategy. Cliffs are known for updrafts and birds of prey are often observed as they glide on thermals above cliff faces. Small wonder that 162 (73%) of cremnophytes have seeds that are dispersed by wind.

5.1 Sexual reproduction

5.1.1 Pollination

Gene exchange is vital for sexual reproduction and necessitates an effective pollination strategy. Most pollinators of cremnophytes are free flying, and consequently effective in

accomplishing pollination. However, the fact that cliffs are often large and very sparsely populated with plants demands an effective advertisement strategy. Attracting the right pollinator is accomplished by either sight or aroma (or both). These mechanisms include special adaptations for pollinator attraction, seed dispersal and vegetative reproduction.

5.1.1.1 Insect pollination

The flower architecture of most cliff plants (184, 83%) suggests insect pollination. Honeybees (*Apis mellifera*), which often have their nests on cliff faces, perhaps play the major role in insect pollination. Very little research, if any, has been done on the pollination of cremnophytes. *Drimia mzimvubuensis* [72] and *D. cremnophila* [69] (river valley cliffs, Eastern Cape) both have drooping white flowers (conspicuous against the dark Beaufort shales) and pollen is released only by the vibration of thoracic wing muscles of honeybees—vibratile or ‘buzz’ pollination. The other cremnophilous *Drimia* species have open protandrous flowers, pollinated by honeybees.

The cremnophilous *Haemanthus pauculifolius* [12] has condensed inflorescences pollinated by butterflies. Most cremnophilous *Crassula* species also have condensed inflorescences and are also pollinated by butterflies. *Bulbine* flowers are protandrous, with open flowers that are bee-pollinated (melittophilous flowers).

Bright single radiate Mesembryanthemaceae flowers are clearly insect-pollinated (Hartmann 1991). She recognises three subtypes among these melittophilous flowers (protandrous and producing copious amounts of pollen): (1) The *stamen carpet flower type* is found in all members of *Delosperma*, *Drosanthemum* and *Esterhuysenia* and in *Jensenobotrya lossowiana* [211]. In this open flower type, the centre of the flowers is densely covered in stamens during the male phase, followed by the female phase during which the stigmas become spreading. (2) The *central cone flower* is found in the cremnophyte *Ruschia promontorii* [216], with the stamens collected into a central cone in the flower, later to be overtopped by the stigmas. During the first phase, pollen is rubbed off onto the sternum of the insect and during the second phase, onto its head. (3) *Recess flowers* are modified flowers with a hidden cavity in the centre. The insect is forced to crawl into the cavity, where it comes into contact with the pollen. Cremnophilous examples include species of *Conophytum*. Of the 19 cremnophilous species of *Conophytum*, four have nocturnal flowers, which are also scented and thus attracting night-flying insects. Other generalists with open-flower pollination include members of *Ledebouria*, *Ornithogalum*, *Trachyandra*, *Othonna*, *Senecio* and *Kleinia*.

The tubular floral shape of the cremnophilous species of *Haworthia* and *Adromischnus* suggests long-tongue flies as possible pollinators. The flowers of *Plectranthus* and *Aeollanthus* also suggest long-tongue flies. In *Adromischnus*, the nectar droplets secreted on the outside of the floral tubes have an ant association, which is believed to protect the flowers (Nicolson 2007).

5.1.1.2 Bird pollination

The species (35, 16%) with large, tubular, usually reddish flowers (with copious amounts of nectar) are clearly bird-pollinated. The flowers are protandrous and this encourages cross-pollination. Flowers are produced on a sturdy peduncle that can support the weight of the bird. Sunbirds are commonly found throughout South Africa and Namibia and are the main pollinators of cremnophilous members of *Aloe*, *Gasteria* and *Cotyledon*. Sunbirds are also able to reach cremnophytes easily.

5.1.1.3 Rich flowering

Cremonophilous plants are compelled to make themselves visible during flowering so as to maximise their chances of attracting pollinators. Snogerup (1971) studied cremonophytes in the Mediterranean and found an increase in flower size compared to the level-ground relatives. He refers to the phenomenon as 'rich flowering'. In the present study, 28 (13%) of the plants examined have rich or near-rich flowering (see Tables 5.1 and 5.2).

Cyrtanthus flammosus [3] occurs on cliffs in the Kouga region and does not produce bulbils. The inflorescence is reduced to a large, conspicuous, solitary, bright red flower that opens in late summer and is thought to be pollinated by the butterfly *Meneris tulbaghia*. This butterfly is also responsible for pollinating many other red-flowered species such as *Crassula coccinea* and *Disa uniflora* on Table Mountain. *Cyrtanthus labiatus* [8] (sunbird-pollinated) and *C. montanus* [9] (butterfly-pollinated) occur sympatrically. Although both have conspicuous flowers, they, unlike *C. flammosus*, also produce vegetative bulbils from the base of the bulbs. The bulbils increase vegetatively, forming large groups that occupy entire crevices. The solitary *C. flammosus*, on the other hand, puts more energy into its 'advertisement campaign' than into vegetative output.

All *Gasteria* species are sunbird-pollinated. *Gasteria glomerata* [46], a dwarf cremnophilous endemic from Kouga Dam, also has conspicuous flowers. The gasteriform portion of its flowers is about 10 mm in diameter, thus markedly larger and more conspicuous than in its level-ground relatives (see Table 5.2). *Crassula perfoliata* var. *minor*, a near-cremnophilous endemic, has very large, conspicuous red flowers or inflorescences and is also thought to be pollinated by butterflies (butterflies visit these flowers regularly at Kirstenbosch National Botanical Garden).

Othonna armiana [86] (Asteraceae) is another dwarf cremnophyte from the Rooiberg cliffs near Eksteenfontein (Richtersveld, Northern Cape) with conspicuous flowers. Relative to the size of the plants, the flowers are large—a case of rich flowering. It is pollinated by insects. *Tylecodon ellaphieae* [155] on the Rosyntjieberg is another dwarf species with larger tubular flowers compared to those of its non-cremnophilous relatives. The Mesembryanthemaceae mostly have large, open, radiate flowers with multiple shiny petals and are typically insect-pollinated. Most have honeybee-pollinated (melittophilous) flowers (Vogel 1954).

Lampranthus affinis [212] has large pink flowers that open even on shady south-facing cliffs. By remaining open, they maximize on pollination. Most other members of *Lampranthus* are dependent on bright sunlight for the opening of their flowers. *Lampranthus affinis* and members of the genus have a relatively short but distinct floriferous flowering period and when in flower, the plants are very conspicuous. *Delosperma* species, on the other hand, flower more sparingly over a longer period and the plants are generally longer-lived. They also have melittophilous flowers, but of a type known as stamen carpet flowers (Vogel 1954; Hartmann 1991). The protandrous flowers are open and flat and covered by stamens during their male phase. This is followed by the lengthening and spreading of the stigmas, thus encouraging cross-pollination.

The genus *Conophytum* comprises dwarf succulent members of the Mesembryanthemaceae. Most dwarf mesembs occurring on gravel display rich flowering, compensating for their small size and semi-arid habitat. The *Conophytum* cremnophytes (18 taxa) all have large, showy flowers described as butterfly-pollinated (psychophilous). They do not differ from their non-cremnophilous counterparts and the flower consists of a long, narrow tube (connate stamens and staminodiums) and is dependent on insects such as butterflies (Hartmann 1991).

As shown in Table 5.3, most cremnophytes have conspicuous flowers that are generally larger than those of their non-cremnophilous relatives. *Conophytum quaesitum* subsp. *quaesitum* var. *rostratum* [188] differs in its smaller, nocturnal, scented, moth-pollinated (phalaenophilous) flowers. Flowers are pale-coloured, for example whitish (Hartmann 1991). The cremnophilous *Senecio medley-woodii* [90] has large yellow flower heads and cliff-face forms of *Haemanthus humilis* subsp. *humilis* [11] from near Graaff-Reinet have conspicuous bright pink flowers.

5.1.2 Dispersal

5.1.2.1 Seed

Seed is described by Kessler & Stuppy (2006) as ‘A major keystone in the evolution of land plants, the first seeds appeared some 360 million years ago. Since then they have developed into highly sophisticated propagules that enable seed plants to dominate the earth’s surface and conquer almost every possible habitat from the Antarctic to the hottest deserts.’ Seeds have a dual function, namely reproduction and dispersal, and in most cases seeds are the only mobile phase in the life of a plant. In this chapter the seed of cremnophytes and their dispersal mode (travelling adaptation) are investigated. Strategies of seed dispersal in deserts have been reviewed by Gutterman (1994). However, seed dispersal of succulent plants and bulbous succulent plants on cliffs has not been considered before. Dispersal of seed on cliffs can be divided into anemochory (dispersal by wind), hydrochory (dispersal by water), autochory (self-dispersal), zoochory (dispersal by animals) and amphicarpy (aerials and *in situ* deposit in crevices) (see Table 5.5). The cliff habitat is vertical and because of gravity most seed will become airborne, whether wind-adapted or not. However, ending up at the base of a shaded gorge is not ideal for a seed and the various strategies observed in the present study are discussed below.

5.1.2.1.1 Wind (anemochorous diaspores)

Owing to their vertical orientation, cliffs often experience turbulence and updrafts of rising warm air that help to carry light seeds upwards. This is a very effective way of dispersal and, depending on the wind or storm, seeds can be carried to adjacent cliff faces. The author has experienced strong winds on cliffs at various sites and intervals. However, various potential problems are involved in the dispersal of seed on the cliffs. The seeds have to be effectively

trapped and anchored in crevices—but they fall at random. Small wonder that most cremnophytes (in fact 162 or 74%) rely on the wind to disperse their diaspores, especially members of the Asphodelaceae, Crassulaceae, Asclepiadaceae, Hyacinthaceae and Asteraceae (Table 5.5). This is in agreement with the findings of Müller (1955) that the seeds of about 60% of alpine flora and 50% of the Mediterranean garigue are wind-dispersed. Flattish or winged seeds are more buoyant. Size is also important and owing to the haphazard nature of wind and the limited habitat, investment in numbers is crucial. Most of the disk-like airborne seeds of the Asphodelaceae are relatively small (2–3 mm in diameter) and, together with the dust diaspores, these tiny seeds are the prevailing state in most cremnophytes.

Although most members of the Mesembryanthemaceae make use of dispersal by water (44, 20% of all cremnophytes), there is a shift towards wind dispersal. Mesembs usually have capsules that close again after rain, but in the cremnophilous *Lampranthus affinis* [212], *Scopelogena verruculata* [218] and *Drosanthemum anemophilum* [206] the capsules remain open permanently and the light, flattened, disk-like seeds are adapted to dispersal by wind. Although the hygrochastic seed capsules of *Conophytum* mostly remain on the plant, strong winds can dislodge and blow them over considerable distances.

The shape of wind-dispersed seed (roughly four types representing 157 taxa, 74% of the 220 cremnophytes) is diverse, ranging from lateral-winged (7 taxa, 4%), flattish and disk-like with a marginal wing (70 taxa, 43%), dust diaspores (67 taxa, 41%, mainly Crassulaceae) to the silky parachutes of members of the Asclepiadaceae (plumed diaspores, 13 taxa, 8%).

5.1.2.1.1 Flattish or disk-like winged diaspores

Members of *Aloe*, *Gasteria* and *Haworthia* produce disk-like, angular, papery seeds that are obscurely winged along the margins. Seeds of monocotyledonous cremnophytes, as indicated below, are quite similar and do not differ markedly in size or in shape. Carried on extended inflorescences, the capsules become erect after fertilisation. The capsules dehisce loculicidally, usually with only the upper portion open. Under conditions of moderate or no wind, most of the seeds will be retained within the capsule. Strong winds are required to remove them from the capsules. Thus, the seeds are retained temporarily and would become airborne and be dispersed only when the wind is strong enough. Larger seeds in smaller numbers would mean a smaller chance of establishment.

Widespread *Aloe* species on the Karoo flats such as *A. variegata* and *A. claviflora* have distinctly winged seeds, much larger than those of cremnophytes. The open habitat is so much larger, with a much greater chance of establishment compared to conditions under which cremnophytes grow. *Gasteria acinacifolia* has large seeds and occurs widespread on beaches in the eastern coastal parts. Seeds of *Drimia flagellaris* [70] and *D. loedolffiae* [71] are small and markedly oblong. Those of *Tylecodon viridiflorus* [161] are unusual—flattened, winged seeds of $3 \times 0.5\text{--}1.0$ mm compared to the minute dust diaspores of other species of *Tylecodon*.

5.1.2.1.1.2 Diaspores with a single lateral wing

The capsules of *Cyrtanthus* and *Drimia* species dehisce spontaneously, followed by the release of the seed. *Cyrtanthus flammosus* [3] has flattened seed with a single lateral wing and ‘helicopter spiralling’, maximising buoyancy.

5.1.2.1.1.3 Seed with a parachute (plumed diaspores)

Plumed diaspores are associated with many families, especially the Asteraceae and Asclepiadaceae. According to Van der Pijl (1982), plumed diaspores are least common in forested habitats but mostly associated with open habitat such as savanna or grassland. Seeds of the Asclepiadaceae are known for their symmetrical comas of hair (so-called parachutes).

The cremnophilous stapeliads (*Tromotriche*, *Huernia* and *Lavrania*) all have paired follicles that typically release heavier seeds (spontaneous seed release, less dependent on wind turbulence for dispersal), attached to an aerodynamic parachute. There is no marked difference between the seeds of these cremnophytes and their counterparts in non-cliff habitats.

In *Othonna* and *Senecio*, both belonging to the Asteraceae, the seeds have a typical hairy pappus (modified calyx), not markedly different from those of non-cremnophilous relatives. In *Pelargonium* the seed has an extended spiralled hairy tail initially enabling it to become airborne.

5.1.2.1.1.4 Dust diaspores

Crassulaceae, with one or two exceptions, all have very fine seeds that easily become airborne with wind. These small seeds have less endosperm and therefore come at a cost but allow for larger numbers and thus a better chance of landing in a suitable habitat. The same applies to *Streptocarpus kentaniensis* [164], which has very fine seed. The possibility is great that germination of small seeds is associated with mycorrhizal activity.

5.1.2.1.1.5 Wind-ballists (anemoballists)

Drosanthemum anemophilum [206] is an exceptional mesemb. Clearly belonging to the genus *Drosanthemum*, it has long, slender, erect stems 1.5–2.0 m or taller. Unlike other species of *Drosanthemum*, the capsules remain open and the seeds are dispersed by jactitation caused by strong winds. It is a near-obligate cremnophyte endemic from Rooinek Pass near Laingsburg in the Western Cape.

5.1.2.1.2 Water dispersal (hydrochory)

Most Mesembryanthemaceae have hygrochastical fruit capsules, the cell lids forced open by their hygroscopically expanding keels (closing again when dry). The seeds are released by falling raindrops—Van der Pijl (1982) uses the term ombrohydrochory. In mesembs, this mechanism can be divided into four broad categories (Hartmann 1991).

5.1.2.1.2.1 Wash-out dispersal

The smaller species of *Conophytum* have capsules without covering membranes but with large valve wings that expand the saucer shape. The seeds are simply washed out and dispersed by water action (Table 5.5). These capsules close again upon drying out, thus retaining any remaining seed and releasing them only during the next rain event. *Delosperma* species and *Drosanthemum expersum* [207] have a similar mechanism.

Compared to non-cremnophilous species of *Conophytum* (see Tables 5.3 and 5.4), cremnophilous members of the genus all have relatively large seeds. These seeds are usually tuberculate to grossly tuberculate (Hammer 2002) and when dispersed by water runlets, they lodge in crevices where they germinate.

Lichens and mosses are groups frequently encountered on cliffs. They provide anchorage for cremnophytes such as species of *Conophytum* by enabling them to obtain a firm hold, especially dwarf succulents or lithophytic orchids. Seeds are deterred or held back by the often dense growth of these organisms. Lichens and mosses are important pioneers on some cliffs in that they prepare the habitat for the establishment of other cremnophytes at a later stage.

5.1.2.1.3 Bird-dispersed diaspores

Birds play a minor role in the dispersal of cremnophytes (Table 5.5). *Rhipsalis baccifera* [95], an obligate cremnophyte or epiphyte, has small, fleshy, many-seeded berries dispersed by birds. *Haemanthus albiflos* [10], *H. humilis* subsp. *humilis* [11] and *H. pauculifolius* [12] have conspicuous, fleshy, orange berries also dispersed by birds. According to bulb grower Mr Cameron McMaster (pers. comm.), *H. humilis* subsp. *humilis* has sticky seeds that would easily lodge in crevices on sheer cliffs.

5.1.2.1.4 Autochory (*in situ* dispersal)

This involves seed dispersed by the plant itself (*in situ* dispersal) (Table 5.5). Autochory is often associated with plants in specialist habitats, therefore with a local dispersal strategy. Members of *Ledebouria* have large seeds in fruits that become pendent. The seeds are dropped within the vicinity of the mother plant (*L. cremnophila* [75], *L. venterii* [76]).

Members of *Aeollanthus* have four rounded nutlets protected within a funnel-shaped 5-lobed (2-lipped) calyx with a protective indumentum at its throat. The nutlets are spontaneously released by a circumscissile cut (Ryding 1986) when the calyx matures. Some of the seeds, however, can be retained within the released calyx part and can act as a roller (Ryding 1986). The seeds become mucilaginous on becoming wet and are spontaneously released in the vicinity of the mother plant. The mucilaginous epidermis can adhere to crevices and act as anchorage. The pendent cremnophilous members of *Plectranthus* also have four rounded nutlets protected within the calyx and spontaneously released at maturity. The calyxes are usually persistent.

5.1.2.1.5 Dimorphic dispersal strategy (amphicarpy) of semisucculent cremnophytes

The terms amphicarpy and geocarpy are defined in Chapter 2.

There are two semisucculent obligate cremnophytes that display amphicarpy in the study area. *Dewinteria petrophila* [221] (Kaokoveld, Namib Desert, summer rainfall) and *Stemodiopsis rivae* [222] (Limpopo Province, summer rainfall) are clearly amphicarpic.

Dewinteria petrophila [221] is a remarkable chasmo-cremnophyte displaying a unique dimorphic facultative reproduction strategy (Van Jaarsveld & Van Wyk 2007a; Van Jaarsveld

et al. 2009). It is a semisucculent biennial (rarely annual) or weak perennial. It grows under desert and semidesert conditions on the Otjihipa Mountains in the northern Namibia. In addition to its conventional aerial branches with insect-pollinated flowers and wind-dispersed seed, it produces specialised shoots that are negatively phototropic and enter crevices. These shoots bear small cleistogamous flowers developing heart-shaped capsules with fewer but large, differently shaped seeds (*in situ* dispersal) (Van Jaarsveld *et al.* 2009).

Stemodiopsis rivae [222] (dry savanna, Limpopo Province) exhibits only a single type of dispersal, after the arboreal flowers have been fertilised. In this species, the fruits bend into a crevice, where the seeds are then dispersed. It is a form of geocarpy, here termed cremnocarpy. Cremnocarpous plants thus bury their fruit in crevices of cliff faces. *Cymbalaria muralis* (Scrophulariaceae) from the Mediterranean region of Europe is a classic example of a cremnocarpous plant. *Colpias molle* (Namaqualand, winter rainfall) is another non-succulent example displaying cremnocarpy.

The dispersal strategy of *Dewinteria petrophila* [221] (see below) could also be termed cremno-amphicarpy, and pertains to amphicarpy on cliffs. This species displays a unique amphicarpic state, with both atelechorous and anemochorous dispersal methods. This is an unusual adaptation and the first of its kind recorded for an obligate cremnophyte. The large seeds are a self-preservation strategy, ensuring long-term survival in its cliff-face habitat. This atelechorous form of seed dispersal ensures self-cloning, and the conventional small anemochorous seeds (from insect-pollinated flowers) ensure interbreeding and dispersal to new sites. The larger seeds carry more reserves than the seedling needs after germination. The thread-like branches in the crevices ensure an almost 100% survival rate if the mother plant should die as a result of drought or from natural causes. The smaller capsules produce five or fewer seeds per capsule, whereas the conventional and much larger aerial capsules produce more than 50 seeds per capsule.

Winds on cliffs are often strong and updrafts ensure that seeds are effectively dispersed to other crevices. *Dewinteria petrophila* [221] flowers in the rainy season and disperses its seed in autumn. The seeds are covered with mucilage, a state often associated with plants from desert or semidesert regions. The mucilage helps to anchor the seeds to the substrate (Van der Pijl 1982). In addition, *D. petrophila* possesses extrafloral nectaries, a clear association with ants which protect the plant against insect herbivores.

5.2 Vegetative (asexual) reproduction

Of the 220 identified cremnophilous succulent plant taxa, 204 species (93%) have a vegetative dispersal backup (Table 5.6). The margin between dividing or proliferating clusters and active growth and rooting is often not clear cut. Vegetative dispersal of propagules has many advantages and they can simply root when conditions are favourable. Many plants are mobile, and can root and establish by means of active growth, thus establishing new colonies other than from seed.

5.2.1 Bulbil propagules

Many bulbous plants are known for the production of bulbils, which play an important role in the dispersal of a few local succulent cremnophilous bulbs and other succulent plants.

Atelechorous bulbous propagules are found in bulbous plants such as *Ornithogalum longibracteatum* [78], *O. juncifolium* var. *emsii* [77], *Cyrtanthus montanus* [9] and *C. labiatus* [8] (Table 5.7). Bulbils are formed (from the fleshy scales) at the base of the parent bulb and in this way an entire crevice can become populated. Eventually these bulbils spill over the rock face and will grow if they land on a suitable ledge.

5.2.2 Winged bulbils

Oxalis pocockiae [219] regenerates from brittle 4-winged bulbils which are dispersed by wind, a unique feature among succulent cremnophytes in the study area. These winged bulbils are formed in the centre of the plant during the rainy season and detach in the dry season when they become airborne. When falling into adjacent crevices, they root and establish new plants (Table 5.7).

5.2.3 Inflorescence propagules

Crassula setulosa var. *jenkinsii* [139] and a form of *C. montana* [125] (Skaaprivierspoort, Namaqualand) have inflorescences that produce vegetative propagules consequently dispersed close to the mother plant. These propagules root when they fall into adjacent crevices.

5.2.4 Leaf propagules

These propagules include leaves as well as bulb scales (modified basal part of leaves). The Crassulaceae (except *Cotyledon*) is known for leaves that root and sprout quite readily when becoming detached from the mother plant. This is especially prominent in the genera

Adromischus and *Crassula*, but there is not much difference between cremnophytes and non-cremnophytes in this behaviour. *Cotyledon pendens* [108] from cliffs along the lower Bashee River in the Eastern Cape is an exception, being the only *Cotyledon* that will root from leaves. Leaves will root when they land in a crevice.

Members of the genus *Gasteria*, with the exception of *G. rawlinsonii* [48], all have brittle leaves that will root when becoming detached. *Gasteria batesiana* var. *dolomitica* [42] has long, subterete, succulent leaves that are often slightly re-curved. They will root (whether detached or not) where they touch a rock crevice, becoming established as new plants. It is the only *Gasteria* with this dispersal mode, in all probability an adaptation associated with its cliff habitat.

5.2.5 Bulb scale propagules

Drimia cremnophila [69] and *D. mzimvubuensis* [72] have succulent, club-shaped bulb scales and when they become detached, they will root to form new plants.

5.2.6 Dividing or proliferating clusters

The overwhelming majority of cremnophytes in the study area consist of vegetative clusters, a state especially common among monocotyledons. They have a cluster-forming nature—a self-preserving vegetative backup. The plants start from solitary growth but end up as extensive dense clusters (clones). Should parts break loose, or others succumb to fungal infection for example, loose clusters will form new groups. Cremnophilous examples include members of *Aloe*, *Cyrtanthus*, *Drimia*, *Bulbine*, *Haemanthus*, *Haworthia*, *Gasteria*, *Trachyandra*, *Ledebouria* and *Ornithogalum*. It is also found among dicotyledons such as *Crassula*, *Tylecodon* and *Conophytum*, which will root and form new plants even when they have become detached from their root system.

5.2.7 Active growth

Senecio muiirii [91] and members of *Delosperma* and *Plectranthus* have extended stems that sometimes become pendent on the rock face. These stems will root when new crevices are reached. The same happens in cremnophilous stapeliads (e.g. *Huernia* and *Tromotriche*), *Othonna capensis* [87] and many of the trailing *Crassula* species, forming new plants by active growth during the rainy season.

Tromotriche baylissii [83] and *T. choanantha* [84] have stems that display epinastic growth. The stems proliferate from the base and these side shoots can enter adjacent crevices by means of subterranean growth, not only anchoring the plant but also contributing to vegetative expansion. *Aloe meyeri* [22] and *Bulbine suurbergensis* [39] have long, pendent stems that root when they touch ledges or crevices.

5.3 Establishment

Successful germination of seed in obligate cremnophytes is dependent on the right crevice, aspect and moisture content as well as the right temperature.

5.3.1 Crevices

The seeds of most cremnophytes are dispersed by the wind. Monocotyledons usually have flattened to winged seeds. Updrafts on cliffs are well known and seeds landing in a crevice germinate when conditions are favourable. Seeds of mesembs are dispersed by water—the hydrochastical capsules open when it rains and seeds are then washed out. Most species of *Conophytum* have tuberculate seeds that are larger than those of their non-cremnophilous relatives (see Table 5.3). The larger seeds become stuck in crevices and germinate in autumn or winter. In *Othonna*, seeds germinate at the onset of cool conditions and shorter day lengths. Even when seeds are sown in summer, germination is delayed until autumn. Cremonophilous succulent Crassulaceae have small dust diaspores dispersed by wind. *Pelargonium mutans* [162] also has wind-dispersed seed; seedlings of plants grown at Kirstenbosch National Botanical Garden become established in many other containers of the greenhouse as a result of local wind action that disperses the seeds.

5.3.2 Cliff-face lichen fields

Lichen fields on cliff faces are an indication of moist air, making it possible for seeds to germinate and establish. *Parmelia* spp. are often found on cliffs. Their robust thalli allow deposit of debris and their poikilohydric nature acts as a moisture trap, ideal for establishment of seeds of obligate cremonophilous succulents. At Wolfberg (Cedarberg) in the Western Cape, adult plants and seedlings of *Crassula montana* subsp. *montana* [125] and *Crassula nudicaulis* were observed on a south-facing cliff among a *Parmelia* sp. This lichen is ideal for trapping small seeds such as those of *Crassula*, *Conophytum* and lithophytic orchids.

5.3.3 Germination

Seed of many cremnophytes in the study area have been sown under artificial nursery conditions at Kirstenbosch. Germination of plants is usually easily accomplished and within about three weeks (when sown in their natural rainy season). Seeds of especially the monocotyledons germinate easily. *Ledebouria*, however, has not been tested. The seed viability of monocotyledons usually deteriorates after a year, but their shelf life (variability period) has not been tested. Some species of *Aloe* from arid and semi-arid regions have seeds that remain viable for at least two years (e.g. *Aloe dichotoma*). Most dicotyledonous cremnophytes are also fairly easy to germinate, but not all taxa have been tested.

TABLE 5.1—Floral segment dimensions and pollinators of two cremnophilous and three closely related non-cremnophilous *Cyrtanthus* species

Taxon	Flower segments (mm)	Pollinator	Creemnophyte	Non-creemnophyte
<i>C. flammosus</i> [3]	40–50 × 30–35	<i>Meneris tulbaghia</i>	×	
<i>C. elatus</i>	35–45 × 20–30	<i>Meneris tulbaghia</i>		×
<i>C. sanguineus</i>	40 × 18	<i>Meneris tulbaghia</i>	×	
<i>C. guthrieae</i>	43 × 19	<i>Meneris tulbaghia</i>		×
<i>C. galpinii</i>	20 × 7–9	?		×

TABLE 5.2—Plant size and diameter of the basal portion of the perianth of the cremnophilous *Gasteria glomerata* (example of rich flowering) compared to that of other non-cremnophilous *Gasteria* species

Taxon	Plant size	Diameter of perianth base (mm)	Creemnophyte	Non-creemnophyte
<i>G. glomerata</i> [46]	dwarf	9.0–10.0	×	
<i>G. baylissiana</i>	dwarf	6.0–7.5		×
<i>G. bicolor</i>	large	6.0–9.0		×
<i>G. ellaphieae</i>	dwarf	7.5		×
<i>G. brachyphylla</i>	large	5.0–7.0		×
<i>G. pulcra</i>	large	6.0–7.0		×
<i>G. armstrongii</i>	dwarf	5.0–8.0		×

TABLE 5.3—Flower and seed dimensions and other characters in cremnophilous and related non-cremnophilous *Conophytum* species (data extracted from Hammer 1993, 2002)

Taxon	Petal dimensions (length × width) (mm)	Flower colour	Seed diameter (mm) and surface texture	Cremnophyte	Non-cremnophyte
<i>C. auriflorum</i> subsp. <i>turbiniforme</i> [175]	10 × 2	yellow	0.65, sparsely tuberculate	×	
<i>C. auriflorum</i> subsp. <i>auriflorum</i>	8 × 2	yellow	0.55, tuberculate		×
<i>C. bolusiae</i> subsp. <i>bolusiae</i> [176]	10 × 2	brilliant magenta	0.70, grossly tuberculate	×	
<i>C. fraternum</i>	12 × 2	pink	0.60, pustulate		×
<i>C. obscurum</i> subsp. <i>obscurum</i>	12 × 2	magenta	0.60, wrinkled		×
<i>C. ricardianum</i> subsp. <i>ricardianum</i> [189]	15 × 3	white or pink	0.80, pustulate	×	
<i>C. wettsteinii</i>	20 × 3	magenta	0.65, finely pustulate		×
<i>C. ernstii</i> subsp. <i>ernstii</i> [179]	15 × 3	pink	0.70, grossly tuberculate	×	
<i>C. tantillum</i> subsp. <i>amicorum</i> [191]	8	golden yellow	0.70, tuberculate	×	
<i>C. tantillum</i> subsp. <i>tantillum</i>	15 × 2	pink	0.60, pustulate		×
<i>C. taylorianum</i> subsp. <i>rosynense</i> [193]	12–22 × 1.8	magenta	0.85, tuberculate, with large papillae	×	
<i>C. taylorianum</i> subsp. <i>taylorianum</i>	8 × 2	pink-lilac	0.70, tuberculate		×
<i>C. obscurum</i> subsp. <i>sponsaliorum</i> [186]	8 × 1	rose-purple	0.65, densely pustulate	×	
<i>C. obscurum</i> subsp. <i>obscurum</i>	11 × 1	rose-purple	0.55, wrinkled		×

TABLE 5.4—Seed diameter of some cremnophilous and non-cremnophilous *Gasteria* species (data from Van Jaarsveld 1994b)

Species	Seed diameter (mm)	Cremnophyte	Non-cremnophyte
<i>G. batesiana</i> [41, 42]	4–6	×	
<i>G. glomerata</i> [46]	2–3	×	
<i>G. glauca</i> [45]	3–4	×	
<i>G. rawlinsonii</i> [48]	3–4	×	
<i>G. croucheri</i> subsp. <i>pendulifolia</i> [43]	3–4	×	
<i>G. nitida</i>	3–4		×
<i>G. acinacifolia</i>	6–8		×
<i>G. pulchra</i>	2–3		×
<i>G. pillansii</i> var. <i>pillansii</i>	4–5		×
<i>G. bicolor</i>	2–4		×

TABLE 5.5—Seed dispersal in obligate and near-obligate South African and Namibian cremnophytes

Mode of dispersal	Number of taxa			
	Monocotyledons	Dicotyledons	Other	Total
Wind	74	87	1	162 (73%)
Rain wash		42		43 (20%)
Birds	3	1		4 (2%)
Autochory	3	8		11 (5%)

TABLE 5.6—Vegetative dispersal in obligate and near-obligate South African and Namibian cremnophytes (204 taxa, 93% of total)

Mode of dispersal	Number of taxa			
	Mono-cotyledons	Di-cotyledons	Other group (fern)	Total (204)
Bulbils	5			5
Winged bulbils (anemochorous bulbils)		1		1
Proliferating clusters and inflorescence propagules		3		3
Proliferating clusters and leaf propagules	8	34		42
Proliferating clusters and bulb scale proliferation	3			3
Dividing or proliferating clusters	59	22	1	82
Active growth and rooting	1	67		68

TABLE 5.7—Terminology relating to vegetative dispersal of obligate succulent cremnophytes

Terminology	Type	Subtype	Taxa
Atelechorous bulbil propagules	arboreal bulbils from bulb scales	bulbils dispersed close to mother plant	<i>Cyrtanthus montanus</i> [9], <i>Ornithogalum longibracteatum</i> [78], <i>Drimia flagellaris</i> [70]
Anemochorous bulbil propagules	arboreal winged bulbils	wind-dispersed bulbils	<i>Oxalis pocockiae</i> [219]
Proliferating clusters and inflorescence propagules	arboreal propagules	propagules dispersed close to mother plant	<i>Crassula setulosa</i> var. <i>jenkinsii</i> [139], var. <i>setulosa</i> [141]
Leaf propagules	detached leaves rooting and proliferating	local dispersal, close to mother plant	<i>Gasteria</i> , <i>Adromischus</i> , <i>Crassula</i> spp.
Bulb scale proliferation	detached bulb scales rooting and proliferating	local dispersal, close to mother plant	<i>Drimia mzimvubuensis</i> [72], <i>D. cremnophila</i> [69]
Dividing or proliferating basal clusters and stolons	plants producing basal stolons	forming dense compact clusters	<i>Haworthia</i> , <i>Gasteria</i> , <i>Albuca</i> , <i>Lavrana haagnerae</i> [82]
Active growth and rooting	stems rooting from pendent elongated growth	stems rooting when touching crevices, forming new colonies	<i>Tromotriche</i> , <i>Huernia</i> , <i>Delosperma</i> , <i>Senecio</i>

CHAPTER 6

PHYTOGEOGRAPHY OF OBLIGATE SUCCULENT AND BULBOUS CREMNOPHYTES

6.1 Background

The habitat of obligate cremnophytes are cliffs. The phytogeography of cremnophytes therefore strictly follows the cliff-face habitat. Cliffs in the study area vary in size, geology, aspect and altitude. They are found all over southern Africa, associated with mountains and uneven terrain, from sea level to about 3 000 m along the Drakensberg Mountains in the eastern parts of South Africa (see Tables 6.1 and 6.2).

The study area (South Africa and Namibia) consists of at least 2 000 000 km² and is situated between 17° and 35° S, ranging from the tropics (north of the Tropic of Capricorn) to the warm-temperate Mediterranean-type climate in the south (2 120 × 1 600 km). The physiography and topography reflect the geological history, climate and subsequent weathering patterns. The region is characterised by two distinct topographic features: the interior plateau (bordered by a distinct escarpment), which is surrounded by the second feature, the marginal zone fringed by the Atlantic Ocean in the west and Indian Ocean in the south and east.

The subcontinent in the south is tectonically stable, without recent volcanic activity. The terminology regarding the geology of South Africa and Namibia follows Johnson *et al.* (2006) and Mendelsohn *et al.* (2009) respectively. Obligate succulent cremnophytes on cliffs in South Africa and Namibia are clearly dependent on factors such as cliff size, geology and location (latitude, altitude, aspect and rainfall) as well as plant size. The most important, however, is cliff size.

6.2 Size of the cliff face

Obligate succulent cremnophytes can be regarded as ‘plant exiles’ confined to a vertical habitat. It is the features of the cliff face and uneven, near vertical topography with crevices that allow for a foothold and sufficient nutrients. Therefore, without sufficient growing space (supporting a self-sustaining population), succulent plants will not be able to establish.

Apart from providing sufficient space for establishment and growth, a cliff has to be large enough to hold a self-sustaining population (a viable genetic pool). The various collections made on cliff faces throughout the study area support this statement—small isolated cliffs usually have no or very few endemic cremnophytes, whereas the chances of finding endemics are far greater on large cliffs. Cliff size is therefore important and an extended cliff or a series of cliff faces of similar geological strata are necessary to sustain a viable population of any obligate cremnophyte. A large series of cliff faces will usually support a number of obligate succulent cremnophytes (very often narrow endemics).

Skaaprivierspoort (northern Namaqualand, Northern Cape), for instance, has at least four endemic obligate cremnophytes that are confined to sheer cliffs on either side of the river. The occurrence of obligate cremnophytes on a single, isolated and relatively small cliff is therefore highly unlikely, but there are a few exceptions (dwarf succulents, see below) in the winter-rainfall region, especially in Namaqualand. Nevertheless, smaller cliffs provide a habitat for many facultative cremnophytes.

6.3 Plant size

Plant size in relation to cliff size is also important. Cremnophytes with a relatively smaller body size can thrive on smaller cliff faces (a viable population of many dwarf plants can be crammed in). This is especially true of smaller cluster-forming species so well represented in the winter-rainfall Succulent Karoo region and summer-rainfall alpine regions.

Smaller cliffs faces can therefore sustain a large enough population of dwarf succulent cremnophytes, for example species of *Conophytum*, *Crassula* and *Tylecodon*. A small isolated cliff could therefore support a self-sustaining, genetically diverse, viable population. This is particularly true of the Namaqualand region of the Western and Northern Cape.

On the other hand, a larger succulent body size can deal better with thermoregulatory properties and water loss (Nobel 1988). The small succulent body size of so many cremnophytes seems to be paradoxical. However, southern Africa is exceptionally rich in dwarf succulent plants (mainly associated with cool growing conditions, and in areas with either summer or winter rainfall).

Small size imposes considerable constraints on succulent plants, especially on level ground. However, regular moisture supply during the growing season and shallow soil with little competition from larger plants are the main reasons for their diversification (Ihlenfeldt 1994; Cohan 1998; Schmiedel & Jürgens 1999).

Below is an account on the distribution of obligate cremnophytes in South Africa and Namibia.

6.4 Endemism

Although cremnophytes were encountered throughout the study area, most were found on cliffs associated with a particular mountain range or river drainage system and especially with the same geological formation. Their distribution is therefore limited to specific habitats. The larger the river system, or mountain range, the better the chances of finding obligate cremnophilous endemics. Mountain ranges and river systems throughout the study area were investigated and cliff faces that support viable cremnophyte populations were identified. The main habitats identified include the escarpment, coastal and inland mountain ranges, inselbergs and riverine as well as coastal cliffs (see Table 6.2).

6.5 South African and Namibian cliff faces

Cliffs in South Africa and Namibia can roughly be divided into five cliff-face types, namely:

- i Great Escarpment.
- ii Inland mountains on the plateau.
- iii Marginal zone (between the Great Escarpment and the coast, such as the Cape Fold Belt mountains and other mountains).
- iv Riverine cliffs (along larger drainage lines; found essentially throughout the region, though more abundantly in the marginal zone).
- v Inselbergs (isolated mountains such as the Brandberg and Blouberg).
- vi Coastal cliffs (wave or river action).

The interior plateau is the southern extension of the Great African Plateau. The plateau is fringed by the Great Escarpment, which reaches its highest level in the east (Drakensberg) of the study area, with extensive well-developed cliff faces. It includes the KwaZulu-Natal Drakensberg (2000–3400 m) and mountains further south in the Eastern Cape (1500–2700 m).

The southern margin of the interior plateau includes the towns Graaff-Reinet and Beaufort West (1000–2000 m) and the western margin the Bokkeveld and Kamiesberg (1000–2000 m), and north of the Orange River it continues to the Kunene River (Baynes Mountains at 1000–2000 m).

The inland plateau tilts gradually towards the west, but the incline from the Drakensberg in the east to the coast is sharp, with many drainage patterns (rivers systems) and well-developed cliff faces providing habitat for many plant species. The exposed stratigraphy of the plateau reflects the geological layers (historical events) of the past. They firstly include the five distinct layers of the Karoo Supergroup which overlie the greater part of South Africa.

The higher land of the central Drakensberg and Maluti Mountains in Lesotho (Drakensberg and Lebombo Groups of the Karoo Supergroup) consists of igneous rocks (basalt), the result of volcanic action during the Jurassic. These rocks reach their highest level at Thabana Ntlenyana (3482 m). The underlying rocks (older sedimentary Carboniferous and Triassic rocks) are exposed as four distinct strata. The youngest include the sandstone, mudstone and shale of the Stormberg Group (Molteno, Elliot and Clarence Formations), becoming exposed and encircling the inner higher ground—often resulting in spectacular scenic landscapes (Golden Gate National Park) and spectacular cliff faces. The older three layers below include the Beaufort, Eccca and Dwyka Groups, covering the larger part of the subcontinent (mainly shale, mudstone and sandstone). In the southeast (marginal zone below) the Beaufort Group extends to the sea (East London), traversed by deeply dissected dry river valleys and cliff faces.

The interior plateau varies from flat terrain to some areas with many smaller outcrops (koppies, often flat-topped) and dolerite intrusions, providing smaller cliff faces. The geology is mainly shale and sandstones (Karoo Supergroup) as well as dolerite intrusions. Very few obligate cremnophytes are confined to mountains of the inner plateau.

6.5.1 The cliffs of the Great Escarpment and inland

This region can be divided into five parts: the northern Mpumalanga Drakensberg, the KwaZulu-Natal and Eastern Cape, the Nuweveld and Roggeveld Mountains in the south, the Kamiesberg (Namaqualand), and Namibian region in the west.

Although cliffs are best represented here, only 29 species of obligate cremnophytes (13%) have been recorded from this region. The main reason for this low number is the harsh climate at high altitude, with most succulent plants not well adapted to temperatures below freezing (Werger 1983; Von Willert *et al.* 1992). Towards the west of the study area, the margin of the escarpment (including Namibia) is much lower in altitude and the climate not as severe. The southern and southwestern margin receives rain in winter or in winter and summer.

6.5.1.1 Cliffs of Mpumalanga Drakensberg (northeastern Great Escarpment)

Located in the northeastern part of South Africa, with the average altitude about 2000 m a.s.l. The geology consists of Black Reef and Wolkberg Quartzite Formations, the cliffs rich in crevices and ledges and well vegetated with subtropical plant elements.

The escarpment cliffs are well developed, especially near Graskop and the Blyderivierspoort. Rainfall is high (1500–2000 mm or more per annum), occurring in summer and with frequent fog. The climate is mild but with cold, dry winters. Vegetation in the region consists mainly of grassland, Afromontane forest (higher ground) and savanna on the warmer lower slopes.

Obligate cremnophytes include the smaller grass aloes *Aloe nubigena* [24], *Aloe challsii* [15] and *A. thompsoniae* [30], and *Crassula setulosa* var. *longiciliata* [140], *Delosperma knox-daviesii* [197], *Cyrtanthus junodii* [7], *Haemanthus pauculifolius* [12], *Kleinia galpinii* [85] and *Albuca shawii* [67].

6.5.1.2 Cliffs of KwaZulu-Natal and Eastern Cape Drakensberg (eastern Great Escarpment)

Located along the eastern margin of Lesotho, the mountains reach their highest point here (about 3000 m). The climate is harsh, with annual snowfalls. Rainfall is high (1500–2000 mm or more per annum) and occurs in summer, with frequent fog. The geology of the higher parts consists mainly of basalt, with sandstone below. Cliff faces are prominent, with sufficient crevices and ledges, and the vegetation is mainly grassland and forest.

Obligate cremnophytes consist mainly of *Delosperma nubigenum* [199] (basalt cliffs), *Crassula setulosa* var. *setulosa* [141] and *C. setulosa* var. *longiciliata* [140] (basalt), *Cyrtanthus falcatus* [2] (sandstone, shale, lower parts) and *C. flanaganii* [4] (basalt, upper parts).

6.5.1.3 Nuweveld and Roggeveld Mountains (southern Great Escarpment)

The Nuweveld and Roggeveld Mountains are located in the south (southern border of the Great Karoo), and average between 1500 and 2000 m in altitude. The climate is semi-arid and although the region receives predominantly summer rain, the influence of winter rainfall is significantly greater. The rainfall is about 400–700 mm per annum, with frost and occasional snow in winter. The geology consists mainly of Beaufort Group shale (sedimentary) of the Karoo Supergroup, often capped by dolerite sills so typical at Graaff-Reinet. Cliffs on the escarpment are prominent, with fractures, crevices and ledges (shale or dolerite) allowing for establishment of plants.

Obligate cremnophytes include *Adromischus fallax* [100], *Crassula exilis* subsp. *cooperi* [118], *C. lanuginosa* var. *lanuginosa* [124], *C. pubescens* subsp. *rattrayi* [134], *C. nemorosa* [127], *Drimia uniflora* [73], *Haemanthus humilis* subsp. *humilis* [11] and *Haworthia marumiana* var. *batesiana* [56].

6.5.1.4 Kamiesberg

Located in the northwestern Cape and consisting of granite domes of the Namaqua-Natal Metamorphic Province (Cornell *et al.* 2006). The region is semi-arid with prolonged dry summers and short wet winters, the vegetation consisting mainly of Succulent Karoo and Fynbos. Cliffs are not as well developed, the solid granite domes offering little foothold for the few obligate cremnophytes, for example the dwarf *Conophytum danielii* [178] and *C. hanae* [182], both occupying small fissures and crevices.

6.5.1.5 Namibia

The geomorphology of Namibia is complex. The eastern part is covered with sand of the Kalahari Group (Mendelsohn *et al.* 2002). In the west, most rock formations are exposed and therefore more dramatic. The Great Escarpment is always clear-cut owing to the Kalahari basin (tectonic equalising). The cliffs of the Hunsberg and its lower southern slopes and outliers in the south consist mainly of sandstone of the Kuibis and Schwarzrand Subgroups, or to a lesser extent dolomite (1300–1500 m a.s.l.) (Mendelsohn *et al.* 2002).

Obligate succulent cremnophytes include *Aloe pavelkae* [26], *Conophytum ricardianum* [189], *C. taylorianum* subsp. *ernianum* [192], *Tylecodon bruynsii* [151], *T. singularis* [158]

and *Cyrтанthus herrei* [5]. No obligate cremnophytes have been identified from the central part of Namibia. To the north, the Baynes Mountains (sandstone) support populations of *Aloe omavandae* [25] and *Tetradenia kaokoensis* [173]. The status of *Haemanthus avasmontana*, a possible obligate cremnophyte from the central part of Namibia, is uncertain. In spite of three expeditions, this plant of the mountains just south of Windhoek could not be relocated and was therefore omitted from the study.

Only 30 obligate succulent cremnophytes have been identified for Namibia, 21 (70%) of which are endemic. Most of them are confined to the arid Orange River Valley in the south and the Kunene River Valley in the north.

6.5.2 Cliffs of the marginal zone

The more low-lying marginal zone (60–240 km wide) between the coast and escarpment can be divided into six broad zones: Cape zone (south); Greater Namaqua zone (western parts of the Northern Cape and Namibia); Kaoko zone (northwest, tropics); Limpopo zone (northeastern parts of South Africa); Mpumalanga to KwaZulu-Natal zone (northeast and east); Pondo and Eastern Cape zone (southeast).

The Cape zone is located in the southern and southwestern parts, the Palaeozoic sedimentary quartzitic sandstone mountainous region (Cape Supergroup). Various rivers have dissected deep river valleys in this zone, resulting in cliffs where most obligate cremnophytes have been identified. Although they belong to this zone, the river valley cliffs are dealt with separately.

There are 72 species (38%) of obligate cremnophytes that occur on cliffs within the marginal zone (excluding the river valleys). Together with the river valleys, the clear majority of succulent cremnophytes are found here. The main reason for this is probably the mild semi-arid climate of the region. Moreover, the zone also covers of the Fynbos, Albany Thicket and Succulent Karoo Biomes, all rich in succulent plant species. Rainfall occurs mainly in winter and summer, but in the west (Namaqualand) only in winter.

6.5.2.1 Cape zone (Cape Supergroup, Cedarberg–Suurberg).

The Cape Fold Belt mountains of the Cape Supergroup average about 1–2000 m in altitude, reaching their highest limit near Ladismith (Seweweekspoort peak, 2326 m). The Cape

Supergroup consists of quartzitic sandstone mountains running parallel to the coast (Cedarberg, Hottentots Holland, Langeberg, Riviersonderend, Swartberg, Outeniqua, Kouga, Baviaanskloof and Suurberg Mountains).

The zone is sharply dissected by four major river systems: the Gamtoos River and its tributaries (draining the southeastern Karoo), the Gourits River (draining the central Karoo), the Breede River (draining most of the Western Cape mountains and the Tanqua Karoo), and the Olifants River in the northern part of the Cape Fold Belt mountains (Cedarberg). Cliffs are common on the upper slopes of the mountains and in the river gorges, the latter where most succulent cremnophytes are found. Less common are outcrops of the Cape Granite Suite, with known landmarks such as Paarl Rock, Paardeberg and exposed sites on the Cape Peninsula, Saldanha and east of Mossel Bay.

Enon Conglomerate cliffs are found between the Swartberg in the north and the Langeberg in the south. This formation has only one cremnophilous endemic, namely *Machairophyllum brevifolium* [213]. The vegetation of this region consists mainly of Fynbos and Succulent Karoo. Rainfall occurs mainly in winter in the west, with dry summers, but also in summer in the eastern parts (Caledon and further east). The climate is cool and influenced by the coast.

The southern Cedarberg and Ceres region supports obligate succulent cremnophyte endemics such as *Aloe haemanthifolia* [19], *A. kouebokkeveldensis* [21] and *Drosanthemum expersum* [207]. Further south, along the Hottentots Holland Mountains, the mesembs *Esterhuysenia stokoei* [210] and *Erepsia heteropetala* [209] can be found.

6.5.2.2 Greater Namaqualand zone

Geologically, the western portion of the marginal zone (Namaqualand and Bushmanland) consists of the Mokolian Namaqua-Natal Metamorphic Provinces (granite, sandstone and shale). It is located south of the Orange River (mountains in Namaqualand, Bushmanland—Pellaberg, Dabenorisberg and other isolated peaks near the Orange River as well as the eastern half of the mountains of the Richtersveld). Cliff faces occur in most of the mountainous terrain, especially adjacent to the Orange River (Pellaberg and Rosyntjieberg) and are rich in succulent cremnophytes.

Pellaberg and Dabenorisberg, habitat of *Aloe dabenorisana* [17] and *Tylecodon sulphureus* var. *armianus* [159], consist of metamorphosed quartzitic rocks (Namaqua Metamorphic Complex) and rise to over 1000 m. The Damara-Gariep Supergroup is less prominent (near Vanrhynsdorp and the western part of the Richtersveld and adjacent territory).

The Oograbies Mountains (also known as Vyftienmyl se Berge) consist of layered quartzitic sandstone of the Gariep Group and are extremely rich in succulent plants and a few cremnophilous species. The many crevices on the cliff faces maximise establishment of succulent plants. Endemic cremnophytes encountered here include *Conophytum bolusiae* [176], *C. francoiseae* [180], *Tylecodon buchholzianus* var. *fasciculatus* [152] and *T. bodleyae* [150].

The Vanrhynsdorp and Nama Groups (mainly sandstone) are represented near Vanrhynsdorp, but more so just north of the Orange River along the Hunsberg plateau, with magnificent cliff faces. To the north, the slightly younger Namibian Damara Gariep Supergroup is found.

6.5.2.3 Kaoko marginal zone

The Kaoko marginal zone includes part of the Namib Desert marginal area, with mountains such as the Otjihipa. The latter range is mainly granite and reaches almost 2000 m in altitude, with some cliff faces along the upper peaks. This formation is fringed by dolomites of the Otavi Group. It is located within the tropics, with a hot, dry desert climate.

The upper reaches of the mountains are cooler and harbour cremnophytes such as *Pelargonium vanderwaltii* [163], *Aeollanthus haumannii* [165] and *Tetradenia kaokoensis* [173] can be found on the cliffs. The eastern parts of the Otjihipa Mountains consist of dolomite (Otavi Group), with *Aloe corallina* [16] the main cremnophyte on this substrate.

6.5.2.4 Limpopo zone

The main mountains in this region include the Soutpansberg and Blouberg, two sandstone massifs that also lie within the tropics, their peaks at about 2000 m. For practical reasons, the Waterberg (Kransberg) has also been included in this zone. The Soutpansberg, Blouberg and Waterberg consist mainly of sedimentary sandstone and conglomerate rock, reddish in colour (red bed succession due to iron oxide). The vegetation of the region is savanna and the cliffs carry a number of succulent endemics.

The upper margin of the Soutpansberg experiences high summer rainfall and Afromontane forest vegetation with at least two endemic cremnophilous species, namely *Aloe soutpansbergensis* [29] and *Delosperma zoutpansbergense* [205]. The lower cliffs (savanna) support *Cotyledon barbeyi* var. A [106] with grey-green leaves, *Adromischus umbraticola* subsp. *ramosus* [105] and *Orbea conjuncta* (the latter a cliff near-endemic).

The Blouberg has massive cliff faces, the upper north-facing ones the habitat of *Aloe mutabilis* [23] and *Adromischus umbraticola* subsp. *ramosus* [105].

Cliffs of the Waterberg are especially well developed at the Marakele National Park (Kransberg). *Crassula cymbiformis* [117] is endemic to the south-facing cliffs. The Strydpoortberg towards the eastern portion is the habitat of *Aloe mutabilis* [23] and *Adromischus umbraticola* subsp. *ramosus* [105].

6.5.2.5 Mpumalanga to KwaZulu-Natal zone (Mpumalanga–Thukela)

This zone is geologically complex, with basement granite and greenstone mountains and koppies (Kaapvaal Province), hills and mountains and the low-lying Lebombo Mountains (rhyolite) along the eastern border of South Africa.

The climate is subtropical and the vegetation is savanna. Most of the cremnophytes are confined to deeply dissected river valleys, as discussed below (6.5.2.6).

In the south, granites of the Natal Metamorphic Province have been exposed. Sandstone (Natal Group and Msikaba Formation of the Cape Supergroup) is prominent from Port St Johns in the south to just west of Richards Bay. Other formations include shale of the Dwyka, Ecca and Beaufort Groups (Karoo Supergroup) and sandstone and shale of the Mozaan Group in the vicinity of Pongola.

6.5.2.6 Pondoland and Eastern Cape zone (Durban–Great Fish River)

Sandstone outcrops of the Msikaba Formation and Natal Group are prominent at Port St Johns (Mount Thesiger) and further north. The various rivers draining the southern Drakensberg have dissected impressive gorges in the region and they are the habitat for a number of cliff-face endemics, all associated with river gorges and discussed below (6.5.2.7). The climate is

subtropical, with Indian Ocean Coastal Belt vegetation. Inland parts are mainly underlain by shale of the Ecca and Beaufort Groups (Karoo Supergroup). Cremonophilous species include *Drimia flagellaris* [70], *Gasteria croucheri* subsp. *pendulifolia* [43] and *Plectranthus purpuratus* [171].

6.5.2.7 Riverine cliffs of the marginal and other zones (between Great Escarpment and the sea)

The drainage lines (of the marginal zone) below the inland escarpment are rich in succulent plant species. In fact, 109 (50%) of all the obligate cremonophytes belong here. They are confined to cliffs associated with river valleys.

The greatest diversity of river valley cremonophytes occurs along the Gamtoos River and its tributaries where the prevailing vegetation consists mainly of Albany Thicket and Fynbos (upper higher-lying ground). The Orange River follows with 21 taxa (Desert and Succulent Karoo). Within the Albany Thicket vegetation, 47 species have been identified, followed by Savanna with 32 species, Succulent Karoo with 13 species and the Indian Ocean Coastal Belt with 10 species.

The cliffs of the rivers and gorges discussed below are particularly rich in obligate (or near-obligate) succulent cremonophytes. *Schizobasis intricata* [80] and *Drimia uniflora* [73] are widespread on cliffs throughout the river gorges and are the only species with a wide distribution. *Gasteria batesiana* var. *batesiana* [41] grows from the Buffalo River in northern KwaZulu-Natal to Barberton, with the disjunct outlier *G. batesiana* var. *dolomitica* [42] near Penge along the Olifants River in the north. Except for the impoverished (in terms of cremonophytes) Olifants River in the north, the diversity of obligate cremonophytes increases southwards.

6.5.2.7.1 Levuvu Gorge (Savanna)

The Levuvu River (north of the Tropic of Capricorn) runs through the northern Kruger National Park and has well-developed cliffs in the Levuvu Gorge. The geology consists mainly of the Bushveld Complex and is either rhyolite or sandstone. *Huernia procumbens* is a near-obligate cremonophyte with drooping stems. Many other facultative succulents are also found in the gorge.

6.5.2.7.2 Olifants River (Savanna)

Five obligate cremnophytes (of which four are dolomite endemics) are found in the Mpumalanga and Limpopo Provinces (just south of the Tropic of Capricorn). The Olifants River has cut a deep gorge through the northern Drakensberg Escarpment (Black Reef quartz) as well as through the Malmani dolomite sequence. The dolomite cliffs have four obligate succulent cremnophytes and two near-obligate cremnophytes, *Aloe monotropa* and *Orbea hardyi*. The vegetation here consists of savanna. The four dolomite endemics are *A. hardyi* [20], *Gasteria batesiana* var. *dolomitica* [42], *Plectranthus dolomiticus* [167] and a possibly unnamed species of *Albuca*.

6.5.2.7.3 The Kaap River (Savanna)

This river, a tributary of the Crocodile River, is located near Barberton in Mpumalanga. Three obligate cremnophytes are found here, one of which is endemic. The dark-leaved form of *Gasteria batesiana* var. *batesiana* [41], *Haemanthus pauculifolius* [12] and *Ledebouria cremnophila* [75] (endemic) grow on cliffs of the Fig Tree Group. The vegetation is savanna.

6.5.2.7.4 Umbeluzi (Swaziland), Phongolo, White Mfolozi and Mkhuze Rivers (all KwaZulu-Natal) (Savanna)

Obligate cremnophilous succulent plants identified here include *Gasteria batesiana* var. *batesiana* [41], *Pelargonium mutans* [162] and *Schizobasis intricata* [80].

6.5.2.7.5 Thukela River (Savanna)

The Thukela River is the largest river in KwaZulu-Natal and drains the northern Drakensberg. This river and its tributaries have several obligate cremnophytes. They include *Aloe arborescens* subsp. *mzimnyati* [13], *Gasteria batesiana* var. *batesiana* [41], *G. tukhelensis* [49], *Delosperma velutinum* [203], *Ornithogalum longibracteatum* [78], which is a widespread cliff endemic, and *Pelargonium mutans* [162]. A near-obligate cremnophyte is *Kalanchoe longiflora* (endemic).

6.5.2.7.6 Mngeni River and its tributaries (Indian Ocean Coastal Belt)

The deep sandstone gorges (Natal Group; Msikaba Formation of Cape Supergroup) house several obligate succulent cremnophytes. They include *Drimia flagellaris* [70], *Gasteria croucheri* subsp. *pendulifolia* [43], *Pelargonium mutans* [162] and *Plectranthus purpuratus* [171].

6.5.2.7.7 Mzimkhulu, Mthamvuna, Mzamba, Mtentu and Msikaba Rivers (KwaZulu-Natal and Eastern Cape) (Indian Ocean Coastal Belt)

These rivers drain part of the southern Drakensberg and all form deep gorges through the quartzitic sandstones of the Msikaba Formation (Cape Supergroup).

Obligate cremnophilous succulent plants endemic to the region include *Crassula orbicularis* [128], *C. perforata* subsp. *perforata* [132] (cliff form), *C. streyi* [145], *Delosperma* sp. A [194], *Delosperma* sp. B [195], *Gasteria croucheri* subsp. *croucheri* (widespread, near-obligate cremnophyte), *Drimia flagellaris* [70] (widespread), *Ornithogalum longibracteatum* [78], *Plectranthus ernstii* [168], *P. saccatus* subsp. *pondoensis* [172], *Adromischus cristatus* var. *zeyheri* [98], *Senecio medley-woodii* [90], *S. pondoensis* [92] and an unnamed species of *Senecio*.

6.5.2.7.8 Mzimvubu River (Eastern Cape) (Valley Bushveld)

The Mzimvubu River and its tributaries (Mzintlava, Thina and Tsitsa Rivers) drain large parts of the southern Drakensberg and the deep gorges consist mainly of Beaufort and Ecca shales (Karoo Supergroup). The climate is mild and dry, with mainly summer rainfall. Northern tropical tree species such as *Spirostachys africana* (tamboti) and *Catha edulis* reach their southern limit here.

Obligate cremnophilous succulents include: *Adromischus cristatus* var. *mzimvubuensis* [96], *Gasteria croucheri* subsp. *croucheri*, *Crassula intermedia* [123], *C. foveata* [122], *Bulbine natalensis* [34], *Ornithogalum longibracteatum* [78], *Plectranthus mzimvubuensis* [170], *Drimia cremnophila* [69], *D. mzimvubuensis* [72], *Senecio medley-woodii* [90] and *Senecio talinoides* subsp. *talinoides* [94]. Of these 11 species, two (*Drimia mzimvubuensis* and *Plectranthus mzimvubuensis*) are considered endemic to the river system.

6.5.2.7.9 Mbashe River (Eastern Cape) (Valley Bushveld)

The Bashee River is another river similar in geology and vegetation to the adjacent rivers to the north and south. It has a number of obligate cremnophytes of which some are endemic. This includes *Adromischus liebenbergii* subsp. *orientalis* [102], *Cotyledon pendens* [108], *Aloe reynoldsii* [28], *Bulbine thomasiae* [40] and *Haworthia glabrata* [54]. Non-endemic cremnophytes include *Crassula intermedia* [123], *Drimia loedolffiae* [71], *D. uniflora* [73], *H. cymbiformis* var. *setulifera* [53], *Haemanthus humilis* [11], *Ornithogalum longibracteatum* [78], *Othonna capensis* [87] and *Huernia pendula* [81].

6.5.2.7.10 Kei River and its tributaries (Eastern Cape) (Valley Bushveld)

The Kei River is a large river that marks the old border of the Transkei and Eastern Cape. The shale cliffs (Beaufort shale) have a number of obligate cremnophilous succulent endemics. This includes *Drimia cremnophila* [69], *D. loedolffiae* [71], *Streptocarpus kentaniensis* [164], *Huernia pendula* [81] (near-endemic), *Delosperma tradescantioides* [202], *Gasteria excelsa* (near-obligate cremnophyte), *Crassula intermedia* [123], *Haemanthus albiflos* [10], *Drimia uniflora* [73], *Haworthia cymbiformis* var. *setulifera* [53] and *Othonna capensis* [87]. Of these, *Drimia loedolffiae* and *Streptocarpus kentaniensis* are endemic.

6.5.2.7.11 Great Fish River, Keiskamma River (Eastern Cape) (Albany Thicket)

Further south, the cremnophilous vegetation and geology of the Great Fish and Keiskamma Rivers are similar to that of the Kei River and its tributaries. Cliffs along the river are usually relatively small. *Crassula socialis* [144] and *Ornithogalum juncifolium* var. *emsii* [77] are two of the local cremnophilous endemics of the Great Fish River. Other cremnophytes include *O. longibracteatum* [78], *Delosperma tradescantioides* [202] and *C. intermedia* [123]. The river valleys in the Eastern Cape are dry (rain shadow), with Albany Thicket vegetation.

6.5.2.7.12 Gamtoos River and its tributaries (Eastern Cape) (Albany Thicket)

The Gamtoos River and its tributaries (Kouga River, Baviaanskloof River and Grootrivier) drain large parts of the eastern Karoo and eastern quartzitic sandstone mountains of the Cape Supergroup. The climate is mild, with rain in summer and winter. The upper reaches of the Gamtoos River have cut deep gorges in the hard quartzitic formation of the Cape Supergroup (Kouga Mountains, Baviaanskloof Mountains, Groot Winterhoek Mountains) and have created various cliff-face habitats suitable for obligate cremnophytes.

Obligate cremnophytes (31 taxa) present along all the tributaries include *Adromischus cristatus* var. *zeyheri* [98], *A. cristatus* var. *schonlandii* [97], *Albuca cremnophila* [64], *Bulbine latifolia* var. *curvata* [32], *B. natalensis* [34], *Cotyledon tomentosa* subsp. *tomentosa* [109], *Crassula capitella* subsp. *thyrsiflora* [115] (cliff form), *Cyrtanthus labiatus* [8], *C. montanus* [9], *Delosperma esterhuyseniae* [196], *Drimia uniflora* [73], *Haemanthus albiflos* [10], *Haworthia gracilis* var. *picturata* [55], *Lampranthus affinis* [212], *Ornithogalum longibracteatum* [78], *Othonna capensis* [87], *O. triplinervia* [89] (cliff form), *Schizobasis intricata* [80] and *Tromotriche baylissii* [83]. The Kouga tributary (seven taxa) has *Crassula cremnophila* [116], *Cyrtanthus flammosus* [3], *Gasteria glomerata* [46], *G. glauca*, [45], *Aloe*

pictifolia [27], *Crassula perforata* subsp. *kougaensis* [131] and *Bulbine retinens* [37]. The Baviaanskloof tributary (four taxa) has *Adromischus subdistichus* [104], *Bulbine cremnophila* [31], *B. rupicola* [38] and *Gasteria rawlinsonii* [48].

6.5.2.7.13 Gourits River and its tributaries (Eastern Cape) (Albany Thicket)

The Gourits River and its tributaries (Grootrivier, Olifants River, Dwyka River, Huis River) form a large river system draining the Little and central Great Karoo. It has cut deep gorges through the Swartberg (Huis River), Rooiberg (Badspoort) and Langeberg mountain ranges (e.g. Gourits Poort).

Widespread species (six taxa) include *Cotyledon tomentosa* subsp. *tomentosa* [109], *Crassula capitella* subsp. *thyrsoflora* [115] (cliff form), *Senecio muirii* [91], *Drimia uniflora* [73], *Ornithogalum longibracteatum* [78] and *Schizobasis intricata* [80].

A solitary taxon, *Adromischus leucophyllus* [101], was documented along the Grootrivier. Cliffs along the Olifants River tributary revealed six taxa at Badspoort, near Calitzdorp. They are *Albuca thermarum* [68], *Crassula badspoortense* [113], *C. montana* subsp. *montana* [125], *Tromotriche choanantha* [84], *Bulbine meiringii* [33] and *B. ramosa* [36]. An unnamed species of *Bulbine* was found to be confined to the lower Gourits River Valley (Langeberg to the mouth). Three obligate cremnophytes were documented, namely *Ledebouria venterii* [76], *Cotyledon eliseae* [107] and *Albuca kirstenii* [66].

6.5.2.7.14 Berg, Breede and Olifants Rivers (Western Cape) (Fynbos)

These larger river systems in the Western Cape are without prominent deep gorges, except their tributaries and upper reaches, which drain the greater part of the western and northern parts of the Cape Fold Belt mountains.

6.5.2.7.15 Buffalo River and its Skaaprivier tributary (Namaqualand) (Succulent Karoo)

The Buffalo River drains the main Namaqualand and Kamiesberg region. The granite cliffs of the southern portion do not harbour any cremnophytes. The Skaaprivier, however, drains the northern escarpment region of Namaqualand between Okiep and Steinkopf. It has cut a dramatic gorge, capped with sandstone and with numerous cliffs. Four endemic cremnophytes have been identified, namely *Tylecodon petrophilus* [157], *Ornithogalum pendens* [79], *Ornithogalum* sp. nov. and *C. auriflorum* subsp. *turbiniforme* [175].

6.5.2.7.16 Orange (Gariep) River (Richtersveld) (Desert and Succulent Karoo)

The Orange River is South Africa's largest river system (also forming the northern border with Namibia) and its upper reaches drain Lesotho and parts of Gauteng. Most cliff endemics occur relatively close to the river but mainly from Pofadder to the coast, a region where 21 obligate cremnophytes have been recorded. After the Gamtoos River system, this is the largest number of obligate cremnophytes found along any river system in the study area. Although the vegetation of the area adjacent to the Orange River has been classified as Desert (Mucina *et al.* 2005), in reality it is more similar to Succulent Karoo.

Along the Orange River to the east of the Richtersveld (both Northern Cape and Namibia) we find a series of mountains that house endemic cremnophytes. The geology is complex and consists of magmatic, sedimentary and metamorphic types. Most of the magmatic rocks belong to the igneous Vioolsdrif and Richtersveld Suite. Pellaberg and Dabenorisberg are situated northwest of Pofadder and close to the Orange River. They are on average about 1000 m high and consist of metamorphosed sedimentary rocks (Hom Formation, Bushmanland Group) belonging to the Orange River and Vioolsdrif Suite of the Namaqualand Metamorphic Complex. These mountains have a distinct series of cliffs but, owing to their isolation, they can also be viewed as inselbergs. Obligate cremnophytes include five taxa, two of which are endemic. They are *Aloe dabenorisana* [17], *Tylecodon sulphureus* var. *armianus* [159], *Conophytum fulleri* [181], *Crassula exilis* subsp. *exilis* [119] and *Adromischus diabolicus* [99]. Rainfall occurs in summer and winter.

The geology of the Rosyntjieberg (Richtersveld) consists of quartz belonging to the Rosyntjieberg Formation (Richtersveld Suite). The Rosyntjieberg has ten obligate cremnophytes, five of which are endemic. The endemics are *Aloe meyeri* [22], *Bulbine pendens* [35], *Othonna cremnophila* [88], *Tylecodon ellaphieae* [155] and *Conophytum taylorianum* subsp. *rosynense* [193]. In spite of the arid winter-rainfall climate, the Rosyntjieberg is subject to fog from the Atlantic Ocean. Precipitation from fog occurs on sheltered south-facing cliffs. Other non-endemic cremnophytes here include *Cyrtanthus herrei* [5], *Crassula pseudohemisphaerica* [133] and *Conophytum stephanii* subsp. *stephanii* [190].

Conophytum ernstii [179] occurs on granite rocks of the Vioolsdrif Suite. *Aloe pavelkae* [26], *C. ricardianum* [189], *Gasteria pillansii* var. *ernesti-ruschii* [47] and *Tylecodon bruynsii*

[151] occur on the Kuamsib and Sonberg (on reddish sandstone). *Conophytum taylorianum* subsp. *ernianum* [192], *T. singularis* [158], *Crassula sladenii* [142] and *Drosanthemum inornatum* [208] are found on dolomite cliffs of the same region. *Tylecodon bleckiae* [149] grows mainly on quartzite.

6.5.2.7.17 Kunene River (Desert and Savanna)

The Kunene River is located on the Namibia–Angola border and is well within the tropics. It is larger than the Orange River and has cut a prominent gorge through granite (Damara Granites), dolomite (Otavi) and sandstone (Huab and Grootfontein Metamorphic Complex). The climate is dry and tropical and the vegetation consists of desert and arid savanna. Obligate cremnophytes occurring in the vicinity of the river include *Aloe corallina* [16] (dolomite), *A. omavandae* [25] (sandstone), *Aeollanthus haumannii* [165] (granite), *Pelargonium vanderwaltii* [163] (granite) and *Tetradenia kaokoensis* [173] (granite, sandstone and dolomite).

6.5.3 Inselberg cliffs

Inselbergs are isolated mountains usually associated with deserts. The Brandberg is perhaps the best example, an isolated granite mountain massif about 20 km in diameter and on average about 2000 m in altitude. It is located in the northern part of the Namib Desert. It has many plant endemics, but only one succulent cremnophyte, *Adromischus schuldianus* subsp. *brandbergensis* [103]. Owing to their isolation, the Dabenorisberg and Pellaberg along the Orange River could also be seen as inselbergs. See above (6.5.2.7.16).

6.5.4 Coastal cliffs

Coastal cliffs are often the result of wave action. Although coastal cliffs are found at several sites along the southern African coast, they are not very well developed in South Africa and Namibia. Investigation of this habitat revealed six obligate succulent cremnophytes. They are *Albuca batteniana* [63] on Beaufort shale coastal cliffs just west of the Kei River mouth, *Delosperma saxicola* [200] on quartzitic sandstone coastal cliffs at Tsitsikamma National Park, *Crassula orbicularis* [128] at Waterfall Bluff, and *Ruschia promontorii* [216], *Senecio serpens* [93] and the near-obligate cremnophyte *Othonna dentata* on coastal cliffs along the Cape Peninsula (quartzitic sandstone, Cape Supergroup).

Dolphin Head is a clear promontory or peninsula in the Namib Desert. *Jensenobotrya lossowiana* [211] is restricted to these south-facing cliffs and adjacent territory. Owing to its

isolation from herbivores, plants of this species could establish on non-cliff terrain in some parts of the peninsula. The fragile, pendent habit is typical of an obligate cremnophyte.

6.6 Representation of obligate succulent cremnophytes in biomes

Obligate cremnophytes form part of the prevailing vegetation type within the biomes recognised in the study area and it is therefore necessary to summarise the various biomes, their climate and the main environmental driving forces. Two floristic kingdoms occur within the study area—the smaller Cape Floristic Kingdom (mainly winter rainfall and warm temperate climate) in the south and the adjacent (north of this region) summer-rainfall Palaeotropical Kingdom, merely a southern outlier of the larger tropical African flora and further east (Takhtajan 1986). Several local centres of floristic endemism have been recognised (Van Wyk & Smith 2001). Most obligate succulent cremnophytes clearly belong to the Cape Floristic Kingdom, their diversity following the same pattern as that of the rest of the flora. Within the two floristic kingdoms, nine biomes have been recognised within the borders of South Africa and Namibia (Rutherford & Westfall 1994; Mucina *et al.* 2005; Mucina & Rutherford 2006). The descriptions of the various biomes follow Mucina & Rutherford (2006).

6.6.1 Winter rainfall

6.1.1.1 Fynbos Biome

(6.6% of land surface area of South Africa)

With more than 9 000 species, Fynbos is by far the most species-rich of all the biomes. It has also been the focus of much ecological research (Mucina & Rutherford 2006).

Derivation of name: ‘Fynbos’ is an Afrikaans word (*fyn* = fine, *bos* = bush) pertaining to the use of this vegetation as a fire starter.

Region: Centred mainly in the southwestern and southern region of South Africa (mainly the Western Cape and parts of the Eastern Cape).

Area cover: 71 339 km²

Climate: Warm temperate climate, cool moist winters, dry windy summers.

Main environmental driving forces: Summer aridity, nutrient-poor soil, fire (intervals of 10–30 years) and prevailing southeasterly winds.

Precipitation: 350 mm to more than 2 000 mm per annum (mainly in winter).

Temperature: Moderate, low-lying regions almost frost-free, mean annual temperature about 16°C at the coast.

Main bioregions: Fynbos Bioregion (acid, sandy soils), Western Strandveld Bioregion (alkaline soil), Renosterveld Bioregion (clay-rich soils).

Composition of vegetation: Ericoid shrublands rich in Asteraceae, Ericaceae, Fabaceae, Iridaceae, Proteaceae, Restionaceae, Rhamnaceae, Thymelaeaceae and Rutaceae.

Number of taxa: More than 9 000 taxa.

Characteristics: Evergreen shrublands (leaf spinescence), poor in tree and grass species, rich in geophytes, poor in nutritive value, absence of disturbances by mammals.

Main adaptations: In response to fire, re-sprouters and re-seeders; long-lived (evergreen leaves), pyrophytes (fire-response annuals). Reproductive specialisation, conspicuous flowers, serotiny, myrmecochory. In response to poor soil, cluster (proteoid) roots. *Aloe plicatilis*, *Maytenus oleoides* and *Protea nitida* with corky bark.

Main succulent plant families represented: Crassulaceae, Mesembryanthemaceae, Euphorbiaceae.

Geology: Mainly nutrient-poor, sandy soils derived from quartzitic sandstone rocks of the Cape Supergroup.

Geomorphology: Cape Fold Belt mountains.

Topography: 0–2400 m a.s.l.

Cliffs: Scattered along the Cape Fold Belt mountains and main river systems within the biome.

Obligate succulent and bulbous cremnophytes: 19 taxa (9%) of the 220 obligate elements in the study area are confined to the Fynbos Biome.

6.6.1.2 Succulent Karoo Biome

(6.5% of land surface area of South Africa)

As its name implies, the Succulent Karoo is rich in succulents. It has been the focus of much ecological and taxonomic research. It has an extremely rich diversity of succulents, the Richtersveld region declared a world heritage site (2007).

Derivation of name: The name ‘Succulent Karoo’ (derived from Khoekhoe, *karoo* = dry place) pertains to a dry place rich in succulent plant species.

Region: Mainly centred in the western part of the Northern Cape (mainly west of western escarpment), parts of the Western Cape and the southwestern portion of Namibia.

Area cover: 100 250 km² of the study area (83 075 km², Namibia; 17 175 km², South Africa).

Climate: Warm temperate climate, cool moist winters, long dry moderate to hot summers (ameliorated by the coast).

Main environmental driving forces: Summer aridity, low but predictable winter rainfall, disturbance by various larger and smaller mammals and other animal species.

Precipitation: (25–)100–250(–300) mm to more than 2 000 mm per annum (cyclonic, and mainly in winter, low intensity, hail absent). Fog along the coast and cool nights with heavy dew.

Temperature: Moderate, low-lying regions almost frost-free, mean annual temperature 16.8°C. Frost absent from the coast and light elsewhere.

Main bioregions: Richtersveld Bioregion, Namaqualand Hardeveld Bioregion, Namaqualand Sandveld Bioregion and Rainshadow Valley Karoo Bioregion.

Composition of vegetation: Dwarf succulent-leaved shrublands, dwarf cluster-forming succulents rich in Mesembryanthemaceae, Crassulaceae, Asclepiadaceae, Euphorbiaceae, Hyacinthaceae, Portulacaceae, Asphodelaceae, Iridaceae and shrubs and small trees (Gondwana elements). Rich diversity of annuals.

Number of taxa: 2 125 taxa, with high degree of endemism (1 630 taxa).

Characteristics: Low evergreen succulent-leaved shrublands, moderate spinescence, poor in tree and grass species, rich in quartz-gravel-adapted succulent plants and geophytes. Stem succulent plants in moderation.

Main adaptations: Mainly evergreen leaf succulent shrublets and dwarf cushion and cluster-forming succulent plants (high proportion with CAM photosynthesis) in response to predictable winter rainfall, moderate winter temperatures and long dry summers. Occurrence of annuals is mainly a response to arid conditions and predictable winter rainfall. Smaller numbers of summer-aestivating plants, *Tylecodon* (summer-deciduous), *Conophytum* and many mesembs summer-aestivating. Mass flowering. Seed dispersal by wind and rain (hygrochastical capsules in the mesembs). Defence characteristics: moderate chemical defence and spinescence, rich in camouflage in gravel environment (stone plants).

Main succulent plant families represented: Mesembryanthemaceae, Crassulaceae, Asclepiadaceae, Euphorbiaceae, Geraniaceae, Hyacinthaceae, Portulacaceae, Asphodelaceae.

Geology: Diverse, sedimentary (sandstone shale), volcanic (Cape Granite Suite, dolerite), quartzitic sandstone nutrient-poor (Cape Supergroup). Gariep belt.

Geomorphology: Coastal flats, intermountain valleys and hilly terrain, mountainous towards escarpment and Richtersveld.

Topography: 0–800 (1000) m a.s.l.

Cliffs: Scattered along the Cape Fold Belt mountains, Orange, Olifants, Gourits Rivers and tributaries. Richtersveld Mountains.

Obligate succulent and bulbous cremnophytes: 58 taxa (26%).

6.6.2 Rainfall in summer and winter

6.6.2.1 Desert Biome

(0.5% of land surface area of South Africa)

The Desert Biome has a limited representation in South Africa, but is well developed in Namibia. It has also been the focus of much ecological and taxonomic research. It is rich in xerophytic plant diversity. The borders between Desert, Succulent Karoo and Nama-Karoo Biomes are not clear cut. The southern and coastal parts experience winter rainfall and the biome is subject to heavy dew and frequent fog.

Derivation of name: The name 'Namib' is of San origin and pertains to a barren place.

Region: Centred mainly in the extreme northwestern part of the Northern Cape and the coastal part of Namibia (mainly west of western escarpment) and southern coastal part of Angola.

Area cover: 111 152 km² (110 598 km², Namibia; 554 km², South Africa).

Climate: Warm to warm-temperate, with a moderating influence from the coast. Rainfall has a high inter-annual variability (often unpredictable).

Main environmental driving forces: Extreme aridity, sun radiation and very sparse rainfall mainly in summer (north) or winter or any time of year (south). The vegetation is subject to disturbances by various larger and smaller mammals and other animal species.

Precipitation: 75 mm or less per annum (convection or cyclonic). Fog along the coast and cool nights with heavy dew. Coastal parts in the south receive mainly winter rain.

Temperature: Moderate, low-lying regions frost-free, mean annual temperature 17.2°C at the coast and 23.3°C inland at Goodhouse, much higher north of the Tropic of Capricorn. Frost absent from the coast and light elsewhere.

Main bioregions: Northern Namib Bioregion, Namib Desert Bioregion and Gariiep Desert Bioregion.

Composition of vegetation: Sparse open terrain, rich in lichen species (characteristic lichen fields), annual and stem succulents and xerophytic shrubs and trees (Burseraceae, Fabaceae, Capparaceae, Geraniaceae). In northern and central parts the presence of *Welwitschia mirabilis* is characteristic. The cooler coastal parts with dwarf succulent-leaved shrublands (Acanthaceae, Asteraceae, Aizoaceae, Crassulaceae, Asclepiadaceae, Euphorbiaceae, Hyacinthaceae, Portulacaceae, Asphodelaceae) with shrubs and small to larger trees along riverbeds. Stem succulent plants in moderation (*Adenia pechuellii*, *Sesamothamnus benguellensis*, *Moringa ovalifolia*, *Euphorbia gregaria*, *E. damarana*, *E. virosa* and *Sisymbrium sparteae*).

Number of taxa: 1 200 taxa.

Characteristics: Open, sparse, sandy to rocky deserts with sparse xerophytic shrubs, moderate grass cover after rain and rich in spinescence.

Main adaptations: Xeromorphism, with dwarf shrubs and leathery leaves, mainly stem succulents. Succulent CAM plants. The occurrence of annuals is a response to dry opportunistic conditions. Many plants remain deciduous while dry conditions prevail. Seed dispersal mainly by wind, hygroscopically, explosively and by animals. Defence characters consist of chemical defence and armour (spinescence) or camouflage (resembling stony background).

Main succulent plant families represented: Asclepiadaceae, Asphodelaceae, Burseraceae, Crassulaceae, Euphorbiaceae, Hyacinthaceae, Mesembryanthemaceae, Portulacaceae and Zygophyllaceae.

Geology: Diverse, sand, gravel, calcrete, sedimentary (sandstone shale), volcanic (Cape Granite Suite, dolerite), Gariiep belt, Nama sandstones.

Geomorphology: Coastal flats, hilly terrain, mountainous towards escarpment.

Topography: 0–800(–1500) m a.s.l.

Cliffs: Scattered along the Kunene River and Kaokoveld Mountains in the north and lower Hunsberg outliers in the south. Also escarpment mountains, inselbergs (Brandberg, Spitskoppe), along dry river valleys and coastal cliffs (Dolphin Head, north of Lüderitz).

Obligate succulent and bulbous cremnophytes: 10 taxa (5%).

6.6.2.2 Albany Thicket Biome

(2.2% of land surface area of South Africa)

Characterised by a dense impenetrable thicket of shrubs (spiny and non-spiny), rich in succulents (Low & Rebelo 1996). The Albany Thicket Biome is confined to the southeastern parts of South Africa and the biome is best represented around Port Elizabeth, Grahamstown and Graaff-Reinet. It consists of flat to hilly terrain, often mountainous and with wide river valleys. The greatest portion lies at lower altitudes (below 1000 m a.s.l.). Climate is warm to hot (rainfall at any time of the year), with mild warm winters (frost is absent or mild).

Derivation of name: The name ‘Albany Thicket’ pertains both to the place Albany in the centre of this biome and to its main characteristic, a dense impenetrable thicket. Parts of it are also known as Noorsveld (noors = *Euphorbia*), Spekboomveld (*Portulacaria afra*) and Valley Bushveld. The vegetation merges with savanna and the boundaries are not always clear.

Region: Semi-arid parts, mainly centred in the southeast (Eastern Cape and parts of the Western Cape), low-lying semicoastal regions.

Area cover: 26 000 km².

Climate: The Albany Thicket Biome is semi-arid, with a dry, mild climate and rainfall that can occur at any time of the year. Winters are mild and frost is absent or mild.

Main environmental driving forces: Semi-arid conditions and rainfall that is evenly spread throughout the year. A major driving force is disturbance by large and smaller mammals and other animals (herbivores) (vegetation is appropriately adapted). The passive resistance of *Portulacaria afra* to grazing is well known when grazed by elephants. Most of the succulent plant component regenerates vegetatively upon disturbance. *Crassula* (Crassulaceae) and *Gasteria* (Asphodelaceae) regenerate from leaves, *Sansevieria* regenerates from subterranean stolons. Species such as *Azima tetraacantha*, *Putterlickia pyracantha* and *Searsia longispina* are armoured with spines (active resistance) and members of *Euphorbia* are well known for mechanical (spines) as well as chemical (latex) resistance.

Precipitation: (200–)300–950(–1 000) mm per annum (cyclonic cool weather and convectional thundershowers from moisture-laden warm air).

Temperature: Average daily maximum 22–30°C (daily minimum 12–15°C). Frost absent or mild in winter, with warm pleasant days. Summer temperatures high, as much as 37–40°C during heat waves.

Main bioregions: Divided into 14 units: Southern Cape Valley Thicket, Gamka Thicket, Groot Thicket, Gamtoos Thicket, Sundays Noorsveld Thicket, Sundays Thicket, Koega Bontveld Thicket, Kowie Thicket, Albany Coastal Belt Thicket, Great Fish Noorsveld Thicket, Buffels Thicket, Eastern Cape Escarpment Thicket, Great Fish Thicket and the Camdebo Escarpment Thicket.

Composition of vegetation: Mainly dense shrubby thicket and scattered smaller trees and a distinct succulent component (shrubby and thicket floor). Rich in *Aloe*, some geophytes (*Ledebouria*) and other forbs (*Blepharis*, *Barleria*). Typical thicket shrubs and trees include *Pappea capensis*, *Euclea* spp., *Ptaeroxylon obliquum*, *Acacia karroo*, *Euphorbia* spp., *Ficus burtt-davyi*, *Azima tetraacantha*, *Senecio linifolius*, *Rhus longispina*, *Portulacaria afra*, *Crassula ovata*, *Othonna triplinervia* and *Cotyledon velutina*. Smaller succulent plants include *Delosperma* spp., *Gasteria* spp., *Haworthia* spp., *Senecio* spp. and *Ledebouria socialis*. Others include *Strelitzia juncea*, *S. reginae*, *Aloe pluridens*, *A. africana*, *A. speciosa* and *A. ferox*. The biome is also rich in herbaceous plants and chamaephytes (*Barleria*, *Petalidium*) and many lianas (*Asparagus*, *Ceropegia*).

Number of taxa: 3 500. It has high levels of endemism.

Characteristics: Dense, tangled thickets rich succulent vegetation, with a high percentage of regeneration of vegetation as backup.

Main succulent plant families represented: Asphodelaceae (*Aloe*), Asteraceae (*Senecio Othonna*, *Kleinia*), Crassulaceae (*Kalanchoe*, *Crassula*, *Cotyledon*), Euphorbiaceae (*Euphorbia*), Lamiaceae (*Plectranthus*, *Aeollanthus*).

Geology: Diverse, mainly Cape Supergroup and Enon Conglomerate. Soils include loam, sandy to clay soils (sedimentary and volcanic), sandstone, Shale Karoo or dolerite intrusions. Soils variable, derived from the Cape Supergroup and volcanic rock (varying from sandy, dystrophic to richer alluvium deposits).

Geomorphology: Diverse, flat to very mountainous or hilly.

Topography: 0–1000(–1500) m a.s.l.

Cliffs: Well represented along the dry eastern river valleys. Cliff outliers also on inland mountains.

Obligate succulent and bulbous cremnophytes: 58 taxa (26%). This biome and the Succulent Karoo have the highest representation of obligate cremnophytes confined to the biome (e.g. *Cyrtanthus flammosus* [3], *Aloe pictifolia* [27], *Bulbine cremnophila* [31], *Gasteria glauca* [45], *G. glomerata* [46], *G. rawlinsonii* [48], *Albuca cremnophila* [64] and *A. kirstenii* [66]).

6.6.3 Summer rainfall

6.6.3.1 Nama-Karoo Biome

(19.5% of land surface area of South Africa)

The Nama-Karoo Biome is a large, open region in the western part of South Africa and southeastern Namibia. The greatest portion lies above the Great Escarpment and includes the larger part of the Great Karoo. Characterised by temperature extremes of -5°C to 43°C.

Derivation of name: ‘Nama’ pertains to one of the Khoe tribes and ‘Karoo’ to a dry or remote place.

Region: Centred mainly in the western interior of South Africa and southeastern Namibia. It is situated from south of the Great Escarpment to almost Kimberley in the north.

Area cover: 575 437 km² (360 029 km², South Africa; 215 408 km², Namibia).

Climate: The Nama-Karoo is characterised by climatic extremes (far from the coast and at higher elevations). Rainfall occurs mainly in spring, summer and autumn.

Main environmental driving forces: Winter aridity, sparse summer rainfall and extreme sun radiation. Disturbances by various larger and smaller mammals and also by other animal species.

Precipitation: (75–)100–300(–500) mm per annum (mainly convectional, and less often cyclonic). Cool to cold nights with heavy dew and regular frost in winter.

Temperature: Average daily maximum 20–24°C. Frost severe in winter, days warm. Summer temperatures high (up to 40°C on hot days).

Main bioregions: Bushmanland Bioregion, Upper Karoo Bioregion and Lower Karoo Bioregion.

Composition of vegetation: Sparse open terrain, rich in dwarf shrublets with xeromorphic characteristics, few annual and stem succulents. Smaller trees and shrubs are sparse and confined to rock outcrops (Asteraceae, Meliaceae, Euphorbiaceae, Fabaceae, Capparaceae, Poaceae). Endemism low. Characteristic shrubs include *Searsia erosa*, *S. undulata* and *S. pyroides*.

Number of taxa: 2 147 taxa.

Characteristics: Open, sandy to hilly, rocky deserts sparsely vegetated. Moderate grass and dwarf shrubby cover (grass especially after rain), moderate in spinescence.

Main adaptations: Xeromorphism, with dwarf shrubs and leathery leaves, sparse occurrence of leaf and stem succulents. Geophytes fairly common. Annuals rare. Many plants deciduous under dry conditions. Seed dispersal mainly by wind. Defence characteristics consist of chemical defence (*Euphorbia*) and armour (spinescence) or camouflage (resembling stony background).

Main succulent plant families represented: Asteraceae, Asclepiadaceae, Asphodelaceae, Crassulaceae, Euphorbiaceae, Mesembryanthemaceae and Portulacaceae.

Geology: Diverse, sand, gravel, calcrete, sedimentary (sandstone, Shale Karoo and Cape Supergroup) or dolerite intrusions (volcanic). Soils consist of rich sedimentary deposits.

Geomorphology: Flat with hills, and mountainous towards the escarpment. Characteristic karoo koppies (dolerite).

Topography: 800–1500(–2500) m a.s.l.

Cliffs: Scattered mainly along the southern and western parts of the Great Escarpment. Cliff outliers sparsely scattered and associated with inland mountains.

Obligate succulent and bulbous cremnophytes: Only one obligate cremnophyte, *Crassula tabularis*.

6.6.3.2 Grassland Biome

(27.9% of land surface area of South Africa)

The Grassland Biome covers a large portion of South Africa and is a region extensively used for agriculture. It occupies the eastern interior of the inland plateau at higher altitude, with cold dry winters and warm summers. The greatest portion lies above the Great Escarpment. Temperature extremes are severe. Grassland can be divided into moist grassland (higher altitude, rainfall < 700 mm) and dry grassland (lower altitude, rainfall < 500 mm).

Derivation of name: Pertains to the main dominant grassland vegetation of the region (high diversity of Poaceae).

Region: Centred mainly in the eastern interior of South Africa.

Area cover: 349 180 km².

Climate: Characterised by moist summers and short, dry winters. Winters are cold, with regular frost and snow at higher altitudes. Rainfall occurs from spring to autumn.

Main environmental driving forces: Winter aridity, frost, regular fires (winter), summer moisture, sun radiation. Fog along the eastern escarpment (high incidence of lightning and hail). Disturbances by various larger and smaller mammals and other animal species.

Precipitation: (400–)500–1 000(–2 500) mm per annum (mainly convectional thundershowers). Cool to cold nights, with heavy dew and regular frost in winter.

Temperature: Mean annual daily temperature 20–25°C. Winters are cold, with severe frost (above 1500 m), days usually warm and sunny. Summer temperatures high (up to 35°C on hot days).

Main bioregions: Drakensberg Grassland Bioregion, Dry Highveld Grassland Bioregion, Mesic Highveld Grassland Bioregion and Sub-Escarpment Grassland Bioregion.

Composition of vegetation: Dense, species-rich grass vegetation (Panicoideae such as *Andropogon*, *Panicum*, *Trachypogon*, *Heteropogon*, *Cymbopogon* and *Diheteropogon*, *Themeda* and *Hyparrhenia*). The biome is also rich in herbaceous dwarf shrublets (*Helichrysum* spp., *Felicia* spp. and *Aloe* spp.), with scattered small trees (*Cussonia paniculata*, *Euclea crispa*, *Diospyros lycioides*).

Number of taxa: 3 788 taxa.

Characteristics: Dense vegetation dominated by grass species (Poaceae). Open, flat to hilly terrain. Tree and shrubby component mainly confined to rocky outcrops. Geophytes and with herbaceous component.

Main adaptations: Annual fires during the dry winter months. *Cussonia paniculata* has a corky bark. Grazing by various antelopes. Geophytes and succulent grassland species are

fairly common. Many plants are deciduous during the dry winter period. Seed mainly wind-dispersed. Many of the grasses palatable, offering good grazing, also some with defence characteristics such as tannins.

Main succulent plant families represented: Asteraceae, Asphodelaceae, Crassulaceae, Euphorbiaceae, Mesembryanthemaceae and Portulacaceae.

Geology: Diverse (Kaalvaal Craton), including loam, sandy to clayey soils (sedimentary and volcanic), sandstone, Shale Karoo or dolerite intrusions. Soils rich sedimentary deposits.

Geomorphology: Diverse, flat to very mountainous or hilly. Very mountainous along the Great Escarpment, the highest topography recorded of all the biomes.

Topography: 800–3000 m a.s.l.

Cliffs: Well represented along the Drakensberg and eastern Great Escarpment. Cliff outliers also on inland mountains.

Obligate succulent and bulbous cremnophytes: 25 taxa (11%). Examples are *Albuca shawii* [67], *Aloe nubigena* [24], *A. challisii* [15], *A. thompsoniae* [30] and *Delosperma nubigenum* [199].

6.3.3.3 Savanna Biome

(32.5% of land surface area of South Africa)

A combination of grassland and tree parkland defines Savanna. The Savanna Biome is confined to the northern part of South Africa (32%) and Namibia. In South Africa the biome best represented in the Northern Cape (Kalahari), Limpopo Province and KwaZulu-Natal (large parts of Zululand). In Namibia it is confined to most of the central and northern parts (excluding the Namib Desert). It consists of flat to hilly terrain, often very mountainous, and extends northwards to tropical Africa. The greatest portion lies below the Great Escarpment. Climate is warm to hot, with summer rainfall and mild, warm winters (frost is absent or mild).

Derivation of name: ‘Savanna’ refers to a subtropical or tropical parkland landscape (dominant vegetation grassland and trees). In the study area it is locally known as Bushveld.

Region: Centred mainly in the north, below the Great Escarpment (Kalahari, parts of North West, Limpopo Province, low-lying regions of Mpumalanga, Swaziland and KwaZulu-Natal).

Area cover: 888 208 km² (485 246 km², Namibia; 402 962 km², South Africa).

Climate: Characterised by hot, moist summers and short, dry winters. Winters are mild. Rainfall occurs from spring to autumn.

Main environmental driving forces: Winter aridity, regular fires (winter), summer moisture, sun radiation. Convectional storms with high incidence of lightning and hail. Disturbances by various larger and smaller mammals and also other animal species.

Precipitation: (200–)500–1 000(–1 200) mm per annum (mainly convectional thundershowers from moisture-laden, warm air).

Temperature: Average daily maximum 25–30°C (daily minimum 15–17°C). Frost is absent or mild in winter, with warm pleasant days. Summer temperatures are high (38–47°C on hot days).

Main bioregions: Central Bushveld Bioregion, Mopane Bioregion, Lowveld Bioregion, Sub-Escarpment Bioregion, Eastern Kalahari Bushveld Bioregion and the Kalahari Duneveld Bioregion.

Composition of vegetation: Mainly grassland with trees, shrubs and smaller succulent plants, geophytes and other herbs. Typical savanna trees include members of *Acacia*, *Combretum*, *Terminalia*, *Euphorbia*, *Colophospermum*, *Commiphora* and *Ficus*. Grasses include Panicoideae such as *Panicum*, *Andropogon*, *Trachypogon*, *Heteropogon*, *Cymbopogon*, *Themeda* and *Hyparrhenia*. The biome is also rich in herbaceous plants (*Barleria* and *Petalidium*) and succulent chamaephytes (*Aloe Cotyledon*, *Kalanchoe*, *Kleinia*, *Sansevieria* and *Eulophia*), with scattered small trees.

Number of taxa: 5 788 taxa.

Characteristics: Open to dense parkland vegetation dominated by a tree and shrub layer and grass species (Poaceae). Also with a fairly high percentage of succulent plants, often shrubby stem succulents (*Euphorbia*, *Monadenium*). Terrain diverse, from open flat to hilly terrain.

Main adaptations: Short dry winters (little frost), annual fires in the dry winter months. *Erythrina latissima* and *Cussonia natalensis* with corky bark serving as insulation against fire. Many re-sprouting species. Disturbances by big game a major driving force (elephant, buffalo, rhino). Stolons of *Sansevieria* remain behind after grazed by rhino. Grazing by various antelopes. Many plants deciduous under dry winter conditions. Seed mainly wind- and animal-dispersed. Many grasses palatable, offering good grazing, but with defence mechanisms such as tannins on dystrophic soils.

Main succulent plant families represented: Asphodelaceae (*Aloe*), Asteraceae (*Kleinia*), Crassulaceae (*Kalanchoe*, *Crassula*, *Cotyledon*), Euphorbiaceae (*Euphorbia*, *Monadenia*) and Lamiaceae (*Plectranthus*, *Aeollanthus*, *Tetradenia*).

Geology: Diverse, (Kaaopvaal Craton) including loam, sandy to clay soils (sedimentary and volcanic), sandstone, Shale Karoo or dolerite intrusions. Soils variable from sandy dystrophic to richer volcanic soils (rich sedimentary and volcanic deposits).

Geomorphology: Diverse, flat to very mountainous or hilly.

Topography: 0–1000(–1500) m a.s.l.

Cliffs: Well represented along the dry eastern river valleys. Cliff outliers also occur on inland mountains.

Obligate succulent and bulbous cremnophytes: 38 (17%). Examples include *Aeollanthus rydingianus* [166], *A. haumannii* [165], *Gasteria batesiana* var. *dolomitica* [42], *Aloe hardyi* [20], *A. corallina* [16], *A. omavandae* [25] and *Tetradenia kaokoensis* [173].

6.6.3.4 Indian Ocean Coastal Belt

(1.1% of land surface area of South Africa)

At once characterised by its mild subtropical climate, vegetation that varies from subtropical coastal grassland and savanna to dense evergreen subtropical forest. The coast is characteristically covered with *Strelitzia nicolai*, which is probably the most characteristic species. The greatest portion lies at lower altitudes (below 300 m a.s.l.). Climate is warm to hot (rainfall at any time of the year, but more in summer), winters mild, warm (frost absent).

Derivation of name: The name pertains to the Indian Ocean coastline with its characteristic warm, tropical, south-flowing sea currents.

Region: Kei River Mouth (Eastern Cape) and the KwaZulu-Natal coastal part of South Africa to the Mozambique border. The area consists of hilly terrain and wide river valleys, rocky in some parts, with sheer cliffs (Waterfall Bluff, Port St Johns).

Area cover: 12 000 km².

Climate: The most tropical part of South Africa characterised by a mild, subtropical, frost-free climate influenced directly by the Indian Ocean.

Main environmental driving forces: Warm, moist climate, with fire and herbivory the main disturbance regimes. Large and smaller mammals occur within this region. Most plants are rapid growers and of subtropical origin. The succulent plant component regenerates vegetatively upon disturbance. *Plectranthus* spp. are common in forests and on rocky outcrops and root where stems touch the ground.

Precipitation: 800–1 200 mm per annum (convictional thundershowers from moisture-laden warm air and cyclonic winter rainfall). Although rainfall occurs throughout the year in certain parts, the main precipitation is received in summer.

Temperature: Average daily maximum is 22–25°C (daily minimum 14–16°C). Frost absent or mild in winter, with warm pleasant days. Summer temperatures 35–40°C during heat waves.

Main bioregions: Divided into five units: Maputaland Coastal Belt, Maputaland Wooded Grassland, KwaZulu-Natal Coastal Belt, Pondoland-Ugu Sandstone Coastal Sourveld and the Transkei Coastal Belt.

Composition of vegetation: Mainly a mosaic of grassland, dense shrubby thicket, forest and savanna. The flora is rich in endemism, especially the sandstone of the Msikaba Formation (Cape Supergroup). Characteristic species include *Strelitzia nicolai*, *Allophylus natalensis*, *Mimusops obovata*, *M. caffra* and *Ficus burkei*. Some endemics include *Searsia acocksii*, *Leucadendron pondoensis*, *Leucospermum innovans* and *Raspalia trigyna*. Succulents and bulbous plants are also fairly well represented (*Aloe*, *Ledebouria*) and other herbs (*Blepharis*, *Barleria*).

Number of taxa: Fairly high levels of endemism, especially the sandstone parts and shale parts (Cape Supergroup, Karoo Supergroup and KwaZulu-Natal Supergroup).

Characteristics: Varied, ranging from open grassland to forest and elements of Cape fynbos vegetation on sheltered slopes and dunes.

Main adaptations: High and evenly spread rainfall, but more in summer. Winters are warm, short and mild, without frost. Many re-sprouting species in response to fire or herbivory. Fairly high representation of succulent plants and with vegetative regeneration backup. Seed dispersal mainly by wind and birds. Disturbances from big game a major driving force (elephant, buffalo, rhino). The vegetation palatable in parts, offering good grazing to game.

Main succulent plant families represented: Asphodelaceae (*Aloe*), Asteraceae (Senecio, *Kleinia*), Crassulaceae (*Kalanchoe*, *Crassula*, *Cotyledon*), Euphorbiaceae (*Euphorbia*) and Lamiaceae (*Plectranthus*, *Aeollanthus*).

Geology: Diverse, aeolian sand to Mokolian-age granites as well as sandstone of the Natal Group (Cape Supergroup, Msikaba Formation) and shale and mudstone (Karoo Supergroup). Soils include loam, sandy to clay soils (sedimentary and volcanic), sandstone, Shale Karoo or dolerite intrusions. Soils variable, from very sandy to loam, clay-loam to mineral-deprived (Msikaba Formation Cape Supergroup).

Geomorphology: Hilly terrain and wide river valleys. The vegetation consists of subtropical and Cape elements.

Topography: 0–450(–600) m a.s.l.

Cliffs: Well represented along the Transkei (Eastern Cape) coast, as well as by the coastal cliffs between the Mboyeti and Luputana Rivers. Also the quartzitic sandstone of the Msikaba Formation (Cape Supergroup) and sandstone of the Natal Group.

Obligate succulent and bulbous cremnophytes: Succulent cremnophytes are fairly well represented by 11 taxa (5%). They include *Gasteria croucheri* subsp. *pendulifolia* [43], *Plectranthus ernstii* [168], *P. saccatus* subsp. *pondoensis* [172], *Senecio medley-woodii* [90], *S. pondoensis* [92], *Drimia flagellaris* [70], *D. cremnophila* [69] and *D. mzimvubuensis* [72].

6.6.3.5 Forest Biome

(0.08% of land surface area of South Africa)

The smallest biome recognised in the study region. Immediately characterised by its dense, evergreen cover of trees, consisting of distinct multilayered units such as an understorey layer, shrubby layer, lianas and climax forest species. Mostly of a patchy nature and confined as relicts on south- and east-facing aspects of mountains (mainly Cape Fold Belt mountains and Drakensberg). Also along the east coast; especially well developed in the Tsitsikamma, where it is the best represented in South Africa. The greatest portion lies at lower altitudes (at 0–1000 m a.s.l.), but along the Drakensberg some kloofs are up to 2500 m a.s.l. Along the southern coast the climate is mild to warm to hot (rainfall at any time of the year), but elsewhere along the Drakensberg with much lower temperatures. Frost mostly absent from the Forest Biome.

Derivation of name: Refers to forest vegetation immediately recognised by dense tree growth.

Region: Knysna (Western Cape), Storms River (Eastern Cape), Drakensberg (Eastern Cape, KwaZulu-Natal and Mpumalanga). Other coastal parts: Alexandria Forest (Port Elizabeth), along Eastern Cape coast (Port St Johns region) and further north to Zululand (KwaZulu-Natal).

Area cover: 0.08% of South Africa's land surface area (568 km²).

Climate: Coastal part characterised by mild, subtropical, frost-free climate directly influenced by Indian Ocean. Afrotropical forests on mountains with a warm-temperate (cool) climate.

Main environmental driving forces: High rainfall, warm moist climate along the coast, warm temperate climate along mountain ranges. Fire (rare but has an influence), herbivory and tree falls are the main disturbance regimes. Large and smaller mammals occur in this region. Most plants are rapid growers and those along the coast of subtropical origin. Members of *Plectranthus* are common in forests and on rocky outcrops, rooting where stems touch the ground.

Precipitation: 700–2 500 mm per annum (convictional thundershowers from moisture-laden warm air and cyclonic winter rainfall). Although it rains throughout the year in certain parts, the main precipitation is received in summer (throughout the year in the Western Cape but dryer in summer). Fog plays an important role along the mistbelt forests.

Temperature: Average daily maximum is 20–25°C (daily minimum 10–16°C). Frost absent or mild in winter, with warm pleasant days at lower altitudes. Summer temperatures mild but as much as 33°C during heat waves.

Main vegetation units: Divided into nine Zonal and Intrazonal Forest units: Southern Afrotropical Forest, Northern Afrotropical Forest, Southern Mistbelt Forest, Northern Mistbelt Forest, Scarp Forest, Southern Coastal Forest, Northern Coastal Forest, Sand Forest, Ironwood Dry Forest and lastly three smaller azonal forest types.

Composition of vegetation: Mainly a mosaic of tall trees (*Podocarpus*, *Olinia*, *Olea*, *Ilex*, *Harpephyllum*, *Ekebergia*), a shrubby layer (*Curtisia*, *Halleria*, *Cunonia*) and a ground layer (*Plectranthus*, *Chlorophytum*, *Drimiopsis*, *Clivia*). Lianas and epiphytes are also common, especially in the north (*Senecio tamoides*, *Rhoicissus*, *Secamone*, *Jasminum*). Epiphytes include *Rhipsalis baccifera* and species of *Cyrtorchis*, *Mystacidium* and *Bulbophyllum*.

Number of taxa: Fairly high levels of endemism, especially in the quartzitic sandstone parts (Msikaba Formation in the Eastern Cape and southern KwaZulu-Natal). Geldenhuys (1992) lists 1 438 species in 155 plant families.

Characteristics: Dense, evergreen layered nature. Varying in forest size and tree size. Pioneers after tree falls, fire or animal disturbances.

Main adaptations: High, evenly spread rainfall, but more in summer. Winters cool to warm, short and mild without frost. Many re-sprouting species in response to fire or herbivory. Low representation of succulents (those present with vegetative regeneration backup). Seed dispersal mainly by birds and wind. Competition within, disturbances by tree falls, animals (elephant, buffalo, bushbuck) and fire the major driving forces. Vegetation palatable in parts, offering good grazing.

Main succulent plant families represented: Asphodelaceae (*Aloe*), Crassulaceae (*Crassula*, *Kalanchoe*) and Lamiaceae (*Plectranthus*, *Aeollanthus*).

Geology: Diverse, granites, sandstone, shale, mudstone (Cape Supergroup). Soils include loam, sandy to clay soils (sedimentary and volcanic). Soils variable, from loam, clay-loam to sandy, mineral-deprived (Cape Supergroup).

Geomorphology: Very mountainous terrain. Confined to shady south-facing slopes or deep protected river valleys.

Topography: 0–2800 m a.s.l.

Cliffs: Well represented in biome, along Drakensberg Escarpment, Transkei (Eastern Cape) coast.

Obligate succulent and bulbous cremnophytes: Succulent cremnophytes are not well represented. Only one species, *Rhipsalis baccifera* [95], but it is not confined to the Forest Biome.

TABLE 6.1—Representation of obligate cremophilous taxa in the biomes of South Africa and Namibia (220 taxa) (Fyn = Fynbos, SC = Succulent Karoo, NK = Nama-Karoo, AT = Albany Thicket. Sa = Savanna, Gr = Grassland, Fo = Afromontane Forest, IOCB = Indian Ocean Coastal Belt, D = Desert)

Location of cliffs	Total	Fyn	SC	NK	AT	Sa	Gr	Fo	IOCB	D
1. Escarpment	29 (13%)	–	2	–	5	5	16	–	–	1
2. Cape Fold Belt & other mountains	72 (33%)	15	39	1	5	2	8	–	1	1
3. River	109 (50%)	1	15	–	47	31	–	1	10	4
4. Inselbergs	5 (2%)	–	2	–	–	–	–	–	–	3
5. Coastal	5 (2%)	3	–	–	1	–	–	–	–	1
Total	220	19 (9%)	58 (26%)	1	58 (27%)	38 (18%)	24 (11%)	1	11 (5%)	10 (5%)

TABLE 6.2—Frequency of cremophilous taxa in the biomes of South Africa and Namibia (Fyn = Fynbos, SK = Succulent Karoo, NK = Nama-Karoo, AT = Albany Thicket. Sa = Savanna, Gr = Grassland, Fo = Afromontane Forest, IOCB = Indian Ocean Coastal Belt, D = Desert)

Frequency state	Total 220	Fyn	SK	NK	AT	Sa	Gr	Fo	IOCB	D
Widespread	21 (10%)	2	–	–	7	4	6	1	1	–
Widespread but restricted to vegetation region	116 (53%)	13	28	1	31	20	10	–	7	6
Restricted	83 (38%)	6	27	–	20	14	9	–	3	4

CHAPTER 7

EVOLUTION OF CREMNOPHYTES

7.1 Introduction

Adaptations of plant life forms on earth are diverse and most habitats have been exploited and are occupied today. The present flora is a product of evolution—adaptations to an ever-changing environment, both abiotic and biotic. The end product reflects a long history of moulding, resulting in the adaptation of organisms to existing conditions. The tropics receive high rainfall and have a dense vegetation cover and a great diversity of tropical species. In arid habitats there is a decrease in plant cover, but an increase in drought-adapted features. Pressure from constant animal predation ensures a distinct increase in plant defence strategies (mechanical, chemical and camouflage) (Van Jaarsveld 1988a).

According to Stebbins (1952) and Axelrod (1967), the rate of evolution in arid regions increases for three reasons. Firstly, diversity of terrain (topography and geology) has a greater effect on plants in arid or semi-arid regions. Secondly, the broken geology of a local dry site tends to break up populations into smaller units that can interbreed, and this consequently leading to population (genetic) diversification—a pattern well supported by the present study. Thirdly, plants evolve specialised xeromorphic structures and physiologies to cope with aridity. Aridity, in combination with diversity of the terrain, is therefore the main driving force accelerating the various xeromorphic adaptations. The end product includes succulence (leaf, stem, root, bulbous, etc.), ephemeral life forms, sclerophyly and poikilohydricity or additional less obvious xeromorphic adaptations.

Specialised adaptations are particularly pronounced in obligate succulent or semisucculent cremnophytes. *Dewinteria petrophila* [221], a semisucculent chasmo-cremnophyte from the northern Namib Desert, displays a unique amphicarpic state (atelechorous and anemochorous dispersal), together with ant-attracting extrafloral nectaries. This species is one of the most specialised of all southern African cremnophytes (Van Jaarsveld & Van Wyk 2007a). *Welwitschia mirabilis* is another unusual and well-adapted xerophyte reflecting a long history of aridity along the west coast of the subcontinent (Bornman 1978).

Southern Africa is exceptionally rich in succulents (Van Jaarsveld 1988a), many of which display intriguing structural and physiological adaptations to extreme habitats such as fog deserts or quartz pebble fields and to fire, grazing pressure and other animal disturbances. A high proportion of these specialised xerophytes are local endemics (Schmiedel & Jürgens 1999; Van Wyk & Smith 2001). The rich diversity of succulent and succulent bulbous xerophytes in southern Africa, especially of succulents, can be ascribed to a combination of factors such as diversity of the terrain and a long history of aridity in parts of the region, as well as to local habitat isolation and the evolutionary plasticity and adaptive propensity of some plant families, notably the Mesembryanthemaceae (Van Jaarsveld 2000a; Klak *et al.* 2004).

Moisture during the cool season (or cool growing conditions) seems to have been conducive to the evolution of succulent plant taxa, especially forms displaying dwarfism (or minutism) and the alpine growth form. A typical alpine growth form includes small herbs displaying a very small, densely branched, globose growth. This is commonly found in plants from high altitudes that have to cope with a cool, windy growing season. This growth form is not confined to plants at high altitudes but is also prevalent in the cool, short winter growing season in the arid and semi-arid parts of South Africa and Namibia. This lilliputian world of dwarf succulents (together with terrain diversity) allowed for an evolutionary ‘explosion’ of dwarf succulent and bulbous taxa in the Mesembryanthemaceae (e.g. many cremnophilous *Conophytum* spp.) (Cohan 1998; Van Jaarsveld 2000a).

The flora of the subcontinent is furthermore enriched by succulents from two very different floristic regions, namely the temperate Cape Floristic Kingdom in the south and the subtropical Palaeotropical Kingdom in the north. Examples from the Cape include many members of the Mesembryanthemaceae, Crassulaceae, Euphorbiaceae and Asclepiadaceae. Subtropical succulents include members of the Bombacaceae, Asphodelaceae, Asclepiadaceae, Vitaceae and Passifloraceae (Van Jaarsveld & Struck 1995).

7.2 Evolution of cremnophytes

From genetically diverse with initial adaptive vigour to cul-de-sac cliff exiles, plants of the vertical cliff face habitat are renowned for their many adaptations and a high degree of local endemism (Van Jaarsveld 2002). The 220 obligate cremnophilous succulent taxa identified in the present study represent 13 plant families (monocotyledons three and

dicotyledons ten) and about 6% of the succulent plant flora in South Africa and Namibia. Obligate cremnophilous succulents are part of the local flora of the region, but shaped by the cliff habitat, and are therefore products of that particular cliff environment.

There is understandably a high degree of local endemism. It represents both neo-endemics (*Haworthia turgida* [60], *Crassula perforata* [132], *C. rupestris* subsp. *rupestris* [136]) and palaeoendemics (highly specialised growth forms such as *Gasteria rawlinsonii* [48]). Neo-endemic succulents are widely distributed, displaying much local genetic variation, and there are therefore many genotypes at various stages of evolutionary change. Such examples throw light on present and past evolutionary trends. They include highly variable and widely distributed species such as *Cotyledon orbiculata*, *Crassula rupestris* subsp. *rupestris* [136], *C. capitella* subsp. *thyrsiflora* [115] and *C. perforata* [132], which all have cliff-adapted variants (ecotypes). *Crassula perforata* is an obligate cremnophyte in the dry valleys of KwaZulu-Natal and Transkei (Eastern Cape), but in the Karoo it occurs commonly on accessible sites where the plants are more woody and have rigid stems. The Transkei forms represent distinct obligate variants which in time could become distinct specialists. The same applies to *Crassula capitella* subsp. *thyrsiflora*, with dwarf cremnophilous forms (Gamtoos and Gourits systems) as well as the larger widespread non-cremnophilous ones.

The present distribution, fragmentation and speciation patterns of neo-endemic ecotypes/forms in taxa such as *Aloe arborescens*, *Crassula perforata*, *C. rupestris* and *Cotyledon orbiculata* can therefore provide valuable clues to the evolution of cremnophytes. *Aloe arborescens*, for example, is widespread in southern Africa, from Malawi in the north to the Western Cape in the south. Although commonly found on cliffs, screes and rocky sites in most biomes (hence the Afrikaans name *kransaalwyn*), this species is extremely variable, with many local forms. Its soft, fragile leaves (not heavily armed; less bitter to the taste than those of its relatives) show that it probably used to be a widespread cremnophyte but that it has now (owing to the disappearance of larger game through hunting) found a foothold on other rocky (non-cliff) terrain as well. *Aloe mutabilis* [23] and *A. hardyi* [20] are cremnophytes, both closely related to *Aloe arborescens*. *A. mutabilis* is endemic to a diversity of substrates and *A. hardyi* to dolomites (Mpumalanga). *Aloe arborescens* subsp. *mzimnyati* [13] from the Buffalo River is close to *A. arborescens* subsp. *arborescens* but represents a distinct cliff ecotype on the hard quartzite cliffs. If a broader concept of *Aloe arborescens* is maintained, all the

various ecotypes or species mentioned above would represent fragmented local ecotypes that will become even more distinct over time.

Cotyledon barbeyi and *C. orbiculata* also have segregated into distinct cliff ecotypes. *Cotyledon barbeyi* var. A [106] from Wyllies Poort is a small cremnophilous form of the widespread and highly variable *C. barbeyi*. This Wyllies Poort form also has rounded dorsiventrally flattened leaves (occasionally terete), but covered with a white powdery bloom—probably a local adaptation to its extreme cliff-face climate. Cremnophilous forms of *C. orbiculata* from Willowmore (warm temperate) and also at Omavanda (within the tropics, northern Kaokoveld) are morphologically remarkably similar (almost certainly as a result of convergence). Cremnophilous forms in both areas have dorsiventrally flattened leaves covered with a dense, white, powdery bloom. Non-cremnophilous forms are usually less waxy, with considerable variation in leaf colour and size. The specialist requirements for successful establishment of succulents in the cliff habitat are severe and the selection process is harsh, the main reason for the relatively low numbers of obligate cremnophytes.

One of the major challenges of cremnophytes is reproduction in the vertical environment. The cliff habitat differs from all other terrestrial (non-aquatic) habitats in its vertical orientation, extreme lack of moisture and the absence of disturbance by larger herbivores. The result is a long-term, fairly stable and safe (from larger herbivore disturbance) environment, enabling adapted plants to occupy the habitat and evolve with the minimum disturbance but the ever-present driving force of an extremely arid and vertical habitat with little soil. The main challenge, therefore, is establishment and local dispersal.

Plants in locally unique habitats such as quartz fields or forests patches require local dispersal to enable them to remain in their restricted habitat. Consequently species of genera such as *Argyroderma* and *Lithops* and many other mesembs have a small seed dispersal range of not more than 1 m, thus enabling plants to remain in their habitat. The same for *Crinum moorei*, a forest dweller with elongated inflorescences (up to 1.8 m tall) and heavy seeds that are locally dispersed. The main means of seed dispersal on the cliff face is wind (to a lesser extent water), and updrafts caused by moving warm air are a driving force in addition to the ever-present gravitation. Small wonder that in spite of the limited habitat, wind is the major factor in the dispersal of the seed of cremnophilous plants. This is a paradox, as non-

cremnophilous plants with wind-dispersed seed (such as *Aloe variegata* and *A. dichotoma*) are usually and understandably widespread!

Wind, however, demands light and copious amounts of seed to be effective, and consequently a very small percentage of seed land in a suitable crevice. To compensate, most cremnophytes have a vegetative dispersal backup (e.g. vegetative propagules, cluster forming, the pendent stems rooting where crevices are encountered). Thus, many cremnophytes spray the cliff face with wind-dispersed seed, at the same time maintaining a strong vegetative foothold. Succulence enables cremnophytes to carry on and endure prolonged dry conditions. Vegetative dispersal is therefore very important as a long-term evolutionary adaptation for survival of cremnophytes. There is a strong selection in cremnophytes towards efficient vegetative dispersal systems.

The main requirements for surviving on a vertical cliff face are therefore wind dispersal of seed, vegetative reproduction backup and succulence. Dispersal of seed is dependent on ample seed-set, and efficient pollination and good floral advertisement are therefore required. This requirement manifests as the rich flowering seen in many cremnophytes. Natural selection for an efficient pollination ‘advertisement’ is essential, whether for flower size or scent. Structural adaptation further requires adjustments such as compact growth (huggers and squatters) and intensification of drought-adapted features (e.g. reduction in size, increase in hairy features, powdery bloom, reflecting colours, and windows on shady southern faces) or epinastic growth and a pendent habit (hangers).

One of the most important requirements for the evolution of cremnophytes is genetic variability and propensity of taxa. Post-Gondwana neo-endemic taxa as found in Asphodelaceae (*Bulbine*, *Haworthia*, *Gasteria*) and Mesembryanthemaceae have a high degree of genetic variability. However, over-specialisation of features can lead to a genetic dead end or cul-de-sac, with the plant permanently ‘exiled’ to its cliff where it could eventually face extinction when the cliff becomes eroded (Snogerup 1971). Perhaps the evolutionarily most specialised cremnophyte in the study area is the biennial or weakly perennial semisucculent *Dewinteria petrophila* [221], a chasmo-cremnophyte from the northern Namib Desert. It displays a unique amphicarpic condition (with both atelechorous and anemochorous seed dispersal methods), together with ant-attracting extrafloral nectaries (Van Jaarsveld & Van Wyk 2007a).

7.3 Adaptive trends

There is a strong selection towards morphological and reproductive adaptation in cremnophytes. It includes both an increase in xeromorphism (as found in dry habitats with non-cremnophytes) and several cliff-adapted features (huggers or hangers; reduction in size). The cremnophilous flora represents a mixture of both basal representation ('primitive' or 'evolutionarily older' *Gasteria rawlinsonii* [48], *G. glomerata* [46]) as well as younger neo-endemic ecotypes still in the process of adaptation (e.g. *G. batesiana* var. *dolomitica* [42] (Zonneveld & Van Jaarsveld 2005), *Crassula perforata* [131], *C. rupestris* [135] ecotypes). There are furthermore few fixed rules and many exceptions in evolution. Nevertheless, there is a trend among cremnophytes towards cylindrical leaves or stems (or both, as in *Crassula rupestris* subsp. *marnieriana* [135], *Huernia pendula* [81], *Rhipsalis baccifera* subsp. *mauritanica* [95] and *Cotyledon barbeyi* var. A [106]). In *C. barbeyi* var. A at Wyllies Poort, the cremnophilous and non-cremnophilous ecotypes co-occur (sympatrically) in the same habitat, with intermediates, perhaps pointing to a shift in direction from the one to the other.

To summarise the recorded adaptive trends in cremnophytes:

Morphological adaptation

- Increase in xeromorphism (e.g. succulence, shorter internodes).
- Specialist structural adaptations such as:
 - Epinastic growth, resulting in pendent growth (cliff hangers, pendent stems or leaves).
 - Reduction in size, and either compact tufted growth (cliff huggers) or solitary squat shrublets (cliff squatters).
 - Open rosettes and windows on shady, south-facing cliffs or grey-green leaves in a closed rosette on exposed cliffs.

Reduction in defence mechanisms

- Leaf sap less bitter (in *Aloe*) than in close non-cremnophilous relatives.
- Reduction in armour (absence of teeth or smaller and fewer teeth).
- Reduction in camouflage.

Reproductive adaptation

- Sexual:
 - Rich flowering.
 - Increase in wind dispersal of seed.
- Asexual:
 - Increase in vegetative dispersal backup.

Growth vigour

From experience with cultivation of plants, especially on a performance scale (ease of growth in cultivation), we can also gain valuable information on the evolutionary adaptations of cremnophytes. Most succulent cremnophytes are usually easily cultivated (propagated and grown). If considered for normal home garden cultivation in South Africa, as on a stoep, balcony or rockery, on a scale of 1 to 4 (1 = very easy, difficult to kill; 2 = easy; 3 = can be cultivated but with some care; 4 = difficult), the easiest in cultivation are species from the Albany Thicket (most would score 1), followed by species from the Savanna Biome and Indian Ocean Coastal Belt (a score of 2), and then the Fynbos Biome and Grassland Biome (a score of 3), and lastly species from the Desert Biome and arid inselbergs (a score of 4). This is also generally true of non-cremnophytes, especially plants from the Albany Thicket (Van Jaarsveld 2000b). The most difficult to grow are those from the winter-rainfall region, desert and desert inselbergs.

Creemnophytes from Albany Thicket receive rainfall at any time of the year and the growing season of these plants is more evenly spread, not markedly restricted to winter or summer. This rainfall pattern (although semi-arid) favours selection for opportunistic growth, or when moisture is received (a strategy of ‘keeping the options open’). Flowering patterns in this case are not dependent on rainfall patterns and are genetically fixed, but within most groups in the thicket the odd plants do flower at a different time (‘keeping the options open’). *Aloe pictifolia* [27], *Gasteria glomerata* [46], *G. rawlinsonii* [48] are all creemnophyte examples. This is also found in non-cremnophilous plants in Albany Thicket, for example *Aloe ciliaris*. Ease of cultivation of Albany Thicket plants is enhanced by vegetative propagules so typical of the thicket vegetation. This is not surprising as the highly palatable vegetation (in recent historical times) is evolutionarily strongly driven by the impact of large herbivores (Skead 1989). The succulent creemnophytes from the Albany Thicket Biome, Indian Ocean Coastal Belt and Savanna Biome clearly show this historical ‘genetic memory’ and are generally very easily cultivated and propagated.

7.4 Convergence of cremnophytes

There are remarkable morphological and behavioural similarities among cremnophytes from phylogenetically different families throughout the world. The adaptive solution to colonising a vertical habitat is restricted to a few basic types (leafy pendent clusters, pendent rosettes, pendent leafless pencil-like stems or tightly clustered plants), and the various evolutionarily vegetative moulds are therefore similar globally. This convergence is pronounced among cremnophytes. Similar long-term environmental selection pressures have given rise to similar life forms in phylogenetically distant groups. Examples include the pendent stems of the Mexican *Sedum burrito* and *S. morganianum* versus the pendent *Cotyledon pendens* [108] and *C. rupestris* subsp. *marnieriana* [135]. *Adromischus fallax* [100] (South Africa) and *Cremonophila linguifolia* (Mexico) are similar, and *Kleinia galpinii* [85] (South Africa) resembles *Graptopetalum superbum* from Mexico. The latter two have basal rosettes of grey-white leaves. *Arrojadoa rhodantha* subsp. *reflexa* (Cactaceae) (Mexico) resembles South African cremnophilous *Tromotriche* species (Asclepiadaceae). Both have long, pendent, pencil-like, succulent stems.

7.5 Distribution patterns (historical and present)

Most southern African cremnophytes are found on cliff faces below the Great Escarpment, thus a peripheral (in terms of the subcontinent) distribution and associated with river valleys. Therefore, if we roughly know the main erosion patterns of the past that resulted in the formation of various present-day cliffs, then we have a kind of predictive time scale.

7.5.1 Distribution and representation

Although obligate cremnophytes have a wide peripheral distribution, the greatest diversity is associated with large river systems in the south and southeast. This includes 108 taxa (50%) associated with river systems, 72 (33%) with mountain ranges, 29 (13%) from the Great Escarpment, 4 (2%) from coastal cliffs and 5 (2%) from inselbergs. It is therefore clearly along the river systems where the greatest diversity lies. In fact, the Gamtoos River and its branches (Kouga River, Baviaanskloof River and Grootrivier) are also the main centre of endemism for cremnophytes in the study area. The associated vegetation here is the Albany Thicket Biome (Mucina *et al.* 2005; Mucina & Rutherford 2006). Associated obligate cremnophytes include 57 (26%) taxa. This figure will rise considerably if the eastern Valley Bushveld regions of the former Transkei (thicket formation prominent in these valleys currently in a matrix of savanna and grassland) were to be included.

The second highest representation of cremnophytes includes 54 taxa (25%), associated with the Succulent Karoo Biome. The Savanna Biome is also fairly rich in cremnophytes and includes 38 taxa (17%), followed by 24 (11%) in the Grassland Biome (mainly Great Escarpment cliffs) and 19 (9%) in the Fynbos Biome. The Indian Ocean Coastal Belt includes 11 taxa (5%) and lastly the Desert Biome with 9 taxa (4%). The lowest representation is in the Afromontane Forest (1) and Nama-Karoo Biome (1). It is clear that more than half of the cremnophytes (58%) are associated with the Succulent Karoo, Fynbos and Albany Thicket Biomes, centred in the southern parts of South Africa (126 taxa southeast and southwest), and the rest 94 (43%) from the northern parts (see Tables 6.1 & 6.2).

If we analyse these distribution patterns, it is clear that the greatest diversity of cremnophytes lies in the Albany Thicket and Succulent Karoo in the south. It is also more or less located within the Cape Floristic Region, in particular the dystrophic soils of the quartzitic mountains of the Cape Fold Belt (Cape Supergroup rocks). Rivers are fairly evenly distributed along the marginal zone of South Africa and Namibia, but more so in the east (higher rainfall). The difference between the Succulent Karoo and Albany Thicket Biomes lies in their growth season. Growth of the winter-rainfall species is strictly in winter. For example, *Conophytum* taxa shut down in summer, even when moisture is experimentally applied, the growth season clearly genetically fixed. The Albany Thicket experiences rain more or less at any time of the year and growth is not restricted to a particular season. On the other hand, the northern summer-rainfall cremnophytes have a distinct summer growing season and aestivate in winter (*Cyrtanthus*, *Delosperma*, grass aloes and other summer-rainfall taxa).

7.6 Evolutionary history and origin of southern African cremnophytes

Mountain-building and erosion is a continual process and our understanding of the evolution and occurrence of cremnophytes is dependent on past and present cliff formation. Nothing on earth is static and even the most stable land mass is driven by tectonics. Mountain-building is caused mainly by uplift of the earth's crust. The nature and stability of cliffs reflect past geological processes. It is the result of continual erosion of softer martial and the exposure of solid rock formations. Cliffs have always been present to a greater or lesser degree. They are formed mainly by water erosion and our understanding therefore lies in local geomorphology and time of the consequent cliff formation. Some species adapt to new habitats created whereas others reach the end of their journey.

Willis (1922), Weimark (1941) and Cain (1944) suggested that centres of species diversity are also the centres of origin and our answers lie with southern Africa and the evolution of arid-adapted taxa. Few Tertiary plant fossil records exist (Cowling *et al.* 2005) and the narrative supplied below is based mainly on biogeographical affinities. Aridity and diversity of terrain are stimuli for succulent evolution, although succulents do not lend themselves to fossilisation (Speirs 1980). Palaeobotany plays an important role in providing indicators or clues. Speirs (1980) points out that certain facts on succulent plant evolution can be established without having any fossilised succulent on record. Succulent plants (with few exceptions) are flowering plants (angiosperms) that started to diversify only during the Cretaceous (140–65 million years ago). We therefore know that most of them are relatively recent and have evolved locally and that only a few cremnophilous genera are shared with continents outside Africa and its islands.

Arid climates in southern Africa were apparently uncommon from the time when angiosperms evolved until the Palaeocene and Eocene (65–38 million years ago) with the onset of warm, dry conditions. Africa was also situated further south. The main families that represent cremnophytes include Crassulaceae, Asphodelaceae, Mesembryanthemaceae, Hyacinthaceae and to a lesser extent Asteraceae, Amaryllidaceae and Lamiaceae. Except for the Mesembryanthemaceae, most of these families are also represented in other regions of the world and most probably must have originated before the breakup of Gondwana. Holland (1978) suggested that *Aloe* originated in the highlands of southeastern Africa in the late Mesozoic–early Tertiary, to become widespread during the late Tertiary. *Aloe* is today widespread in Africa and on its islands and one can assume that the group originated after the breakup of Gondwana and after India separated from Africa. *Aloe* is well represented on Madagascar and Kamstra (1978) suggested that the genus must have originated shortly before the island broke away from Africa in the late Cretaceous. Treutlein *et al.* (2003) suggest that most of the Asphodelaceae (*Aloe*, *Gasteria*, *Haworthia*) and relicts are monophyletic and include at least 600 African taxa. Two early branches represent *A. barberae* and *A. ciliaris*, both southern endemics (Cowling *et al.* 2005). The mesembs are another (almost endemic to southern Africa) young local group (Klak *et al.* 2004), their vigour and genetic plasticity supporting this idea.

During the Cretaceous, Africa was situated 15° south of its current position, and present-day southern Africa lay at cooler latitudes (Goldblatt 1978). The continents were densely forested, with temperate *Podocarpus* forest (fossil record) in the south (Scott *et al.* 1997). Three early rivers dominated the southern African region, namely the Limpopo system, the Karoo river draining the eastern highlands and the Kalahari river the central part, removing (through erosion) most of the Karoo Supergroup (McCarthy & Rubidge 2005). Since the early Tertiary, about 65 million years ago, pockets of aridity probably existed along the fringe of the tropics (Palaeocene and Eocene), caused by the prevailing high pressure systems (Goldblatt 1978). It is hypothesised that ancestral succulent plants (represented by the families mentioned above) made their appearance at this time. Davies *et al.* (2004) corroborate this suggestion that families with succulent and geophytic affinities could have originated in the Eocene. From the mid-Miocene the general global climate became colder and drier, a change that might have coincided with the evolution of early grassland. Retallack (2001) believed grassland had a major effect, and browsers were to a great extent replaced by grazers, the grasslands thus opening new terrain especially for the diversification of ungulates. With a drier climate, grassland fires and diversity of terrain, there was a selection process that favoured succulent plants. Cowling *et al.* (2005) suggest that at mid-Oligocene the vegetation of southern Africa was most probably a mosaic of subtropical thicket and proto-Fynbos. The southwestern coast experienced an aridification as a result of the cold ocean and early Benguela Current. There was furthermore a decline in global temperatures during the Neogene, resulting in the increase of the Antarctic ice sheet (Scotese 2001), but it was not until the end of the Neogene when winter-rainfall conditions appeared (Deacon *et al.* 1992).

7.6.1 Uplift events and the creation of cliffs during the Neogene

Two major uplift events in southern Africa probably played the major part in the creation of cliff-face habitats and in enhancing the evolution of succulent plant taxa in our region. The first happened in the early Miocene some 20 million years ago and the second during the Pliocene about 3–5 million years ago (Partridge & Maud 1987, 2000). Cowling & Procheş (2005) suggest that prior to these uplifts, a major stimulus occurred for speciation in thicket, a vegetation type to which so many cremnophytes are floristically related. Before this, during the Palaeogene, southern African was tectonically stable (Partridge & Maud 1987) and topographically less diverse (Cowling & Procheş 2005). The highly diverse thicket vegetation to the south was therefore derived from fragmentation of this less diverse original flora after the uplift events.

The diversity of cremnophytes (and other succulents) associated with major river systems in the study area today (below the escarpment), rather than with the Great Escarpment cliffs, can be attributed to three reasons. Firstly, the creation of rain shadows (and consequent aridification), secondly the continual erosion and creation of additional habitats (and cliffs) and thirdly the fact that succulent plants do not cope well with subzero temperatures. Africa was located further south and was therefore cooler. We can therefore safely assume that most of the early ancestors of succulents diversified on diverse terrain created by the river systems. During the first uplift event (20 million years ago), the terrain in the east was raised about 250 m and in the west only 150 m, resulting in an east–west tilt (Partridge & Maud 1987). The high eastern barrier (Drakensberg) formed an effective cloud trap, consequently losing most of its moisture and also causing a rain shadow to the west. The first uplift wave probably ensured the establishment and foothold of many succulents. However, the second uplift was more dramatic and occurred about 3–5 million years ago, with a major raise of an additional 900 m in the east, but only 100 m in the west and 200 m in the south (McCarthy & Rubidge 2005). The latter authors suggest a rainfall of at least 1 000 mm per annum along the east coast, less than 100 mm per annum along the west coast and the enhancement of rain seasonality. The inner escarpment was covered with extensive grasslands, enhancing the diversification of grazers and their predators. The major river systems eroded the deep gorges in the coastal parts (marginal zone of South Africa) and created many additional cliff faces and diversification of terrain—a major stimulus for the evolution of succulent plant taxa.

According to McCarthy & Rubidge (2005), ‘The uplift events in southern Africa, which involved tilting of the continent to the west, increased the slope of the major rivers, increasing their energy and thereby creating two pulses of erosion in the interior, producing new land surfaces known as the Post-African I and II Surfaces.’ According to these authors, most of the present-day Karoo koppies are the result of erosion during the first uplift 20 million years ago, and the dramatic eastern parts (Valley of a Thousand Hills, Thukela Valley and deep gorges Pondoland, Mzimvubu, Kei) and the south (e.g. Kouga, Storms River) were created during the second uplift, an event that occurred 3–5 million years ago. We can therefore speculate that most of our present-day cremnophytes (marginal between the escarpment and sea) most probably evolved during in the Pliocene (3–5 million years ago).

7.6.2 Origin of Albany Thicket

Cowling *et al.* (2005) suggest that, based on fossil data and phylogenetic evidence, the origin of typical thicket taxa dates back to the Eocene. According to these authors, Albany Thicket vegetation also shares elements from other biomes in South Africa. The Cotyledonoideae (Crassulaceae) diversified during this period, but for many other succulent taxa and geophytes they predict a more recent origin (mid- to late Tertiary) (Klak *et al.* 2004; Procheş *et al.* 2006). Cowling *et al.* (2005) suggest that the Miocene uplift was an important stimulus for speciation of thicket plant taxa (*Aloe*, *Diospyros*, *Euclea*) and perhaps the same can be said for succulents from other biomes in the study area such as the Succulent Karoo and Nama-Karoo Biomes.

In searching for clues to the historical distributions and evolution of cremnophytes, it is best to look at their present distribution. Although cremnophytes have very restricted distributions, a situation that points to local adaptation and speciation, some indeed have a widespread distribution. The highest concentration is clearly on the hard, mineral-poor sandstone rocks of the Cape Supergroup in the southeastern Cape and the associated Albany Thicket vegetation. The genus *Gasteria* has a peripheral distribution and is endemic to southern Africa, with most members not confined only to Albany Thicket (Van Jaarsveld 1994b). We can safely assume that older widespread cremnophilous taxa, such as the most basal *Gasteria* (*G. glomerata* [46] and *G. rawlinsonii* [48]) (Treutlein *et al.* 2003), evolved locally in the Baviaanskloof Mountains.

CHAPTER 8

CONSERVATION OF CLIFFS AND SUCCULENT CREMNOPHYTES IN SOUTH AFRICA AND NAMIBIA

8.1 Introduction

Biodiversity loss in southern Africa has never been as critical as at present as a result of human population expansion over the last few decades (Golding 2002), but cremnophytes have been mostly unaffected—mainly because of their inaccessible and relatively stable vertical habitat where they are well protected from larger mammals and other herbivores. Obligate cremnophilous plants in the study area can mostly be classified as rare as they are confined to cliffs, a rather uncommon habitat. The main disturbances on cliffs, such as storm damage, fire (rarely) and rock falls, are natural and normal.

Historically, humans have been associated with cliffs. Even in the recent past they have often used overhangs and caves as shelters. This is especially true of southern Africa and most rock shelters and cliffs are associated with Stone Age artefacts and rock paintings. These shelters are important archaeological sites. Today cliffs still draw humans from all over the world who use them mainly for their recreation and scenic value. There are very few cliffs that cannot be reached by specialist climbers today. Rock-climbing is a natural and challenging outdoor sport, in the past often a survival skill. Nests of honeybees are often associated with cliffs and the San people were good natural rock climbers who regularly harvested honey, for example in the Baviaanskloof (Eastern Cape). Remnants of their climbing aids to construct simple ladders (sticks jammed into crevices) can still be seen on some cliffs today.

About 50 years ago, the IUCN produced its first Red Data Lists of threatened animal and plant species in a first attempt at conservation of species in need of protection (Simon & Melville 1962). This international effort grew rapidly and the first list for South Africa and Namibia, *Threatened plants of southern Africa*, was compiled by Hall *et al.* (1980), Hall & Veldhuis (1985), followed by *Southern African Plant Red Data Lists* (Golding 2002). The latest *Red List of South African plants* (Raimondo *et al.* 2009) and *Red Data Book of Namibian plants* (Loots 2005) are the most recent contributions in this regard. For the present study, IUCN (2001), Dlamini & Dlamini (2002), Talukdar (2002), Loots (2005) and

Raimondo *et al.* (2009) were followed in assessing obligate cremnophytes in the region (see Tables 8.1–8.4).

8.2 Why cliffs should be protected

Cliffs are one of the world's last remaining pristine habitats and all cliffs (rather than individual plant taxa) should be protected, not only by a few individual countries, but globally. The evolutionary significance of cliffs as refugia cannot be over-emphasised (Larson *et al.* 2000; Van Jaarsveld 2003). Such a conservation approach should not only protect obligate cremnophytes but also other species growing on cliffs. During the course of the present study fortunately only limited damage to obligate cremnophilous plants by rock climbers has been noticed. However, cliffs with a high diversity of obligate cremnophytes should be climbed with caution to ensure minimal damage to the plants. Climbers are usually particular to the cliff type they climb and in most cases keep to fixed routes. Damage, if any, is therefore very limited and confined to the immediate vicinity of a route.

This chapter uses the South African and Namibian Red List Categories of Raimondo *et al.* (2009), Loots (2005) and an amendment of the IUCN Red List Categories and Criteria Version 3.1 (IUCN 2001) (see Table 8.1). In the author's opinion, most of the 220 obligate cremnophytes in the study area can be placed in the Least Concern category. The only taxa that remain under threat are those obligate cremnophytes collected for medicinal use—populations of both *Gasteria croucheri* subsp. *pendulifolia* [43] and *G. batesiana* [41, 42] have been considerably reduced by humans. Fortunately both are still common in many inaccessible sites and are also well protected within reserves (Table 8.2).

8.3 Threats to obligate cremnophilous succulent plants in the study area

8.3.1 Habitat loss

8.3.1.1 Dam construction

River valleys are under constant threat as the prime target for water accumulation to meet demands either from agriculture or urbanisation. Examples in the study area include the Kouga Dam and its negative impact on cremnophytes in the Hankey District of the Eastern Cape. The dam was constructed in a region previously known as Kouga Poort. The Kouga River in this part is characterised by a narrow, winding gorge through the Kouga Mountains.

No studies on the vegetation or the plants were undertaken before the dam was filled in the 1960s. At least five species new to science have been named from the region since the filling of the dam—*Aloe pictifolia* [27], *Cyrtanthus flammosus* [3], *Gasteria ellaphieae*, *G. glomerata* [46] and *Albuca cremnophila* [64]. Although many of these plants were flooded, fortunately enough habitat was left where the species occur in great numbers today. There are many other river valleys that are continuously under investigation for new dam sites. The lower Cunene River in Namibia is a case in point and it will result in extensive habitat loss if a new dam is to be built. Species at risk include *Aloe corallina* [16] and several other non-cremnophilous species.

8.3.1.2 Mining

Although mining is not a serious threat to cliffs at present, it is a potential hazard. The habitat at Lekkersing (Richtersveld, Northern Cape, South Africa) is currently mined for its diamond quartz, a potential threat to both *Gasteria pillansii* var. *ernesti-ruschii* [47] and *Tylecodon bodleyae* [150], and to *T. torulosus* [160], which grows on cliffs of the same geological formation.

8.3.1.3 Recreation

8.3.1.3.1 Hikers and climbers

Hikers and rock climbers frequently use cliffs and this can have a negative impact on the cliff face (Larson *et al.* 2000). During the course of the present study, the author visited a cliff in northern KwaZulu-Natal where new climbing sites had been opened. All vegetation had simply been removed from some crevices and thrown at the base of the cliff. Fortunately it did not include any obligate cremnophytes, but species such as *Petopentia natalensis*, *Aloe arborescens*, *Crassula* spp., *Delosperma lebomboensis* and *Schizobasis* sp. were removed. These routes are also frequently maintained and vegetation is regularly removed or trimmed back. Rock climbers usually follow fixed, maintained routes. This has the same effect on the cliff as trampling on a footpath. The only difference is that the vertical path carries a limited amount of vegetation in a smaller habitat. This can have a negative impact on rare obligate cremnophytes and, although not a major threat, should be addressed in localities with high levels of local obligate cremnophytes. Other uses of cliffs are mainly for their scenic or historic value.

8.3.1.3.2 Plant collectors

Plant collectors include those who gather plants for medicinal or magical purposes and plant enthusiasts who are interested in growing plants in a collection. The first-mentioned is a more serious threat since it includes the removal of plants in bulk.

8.3.1.3.2.1 Gathering of medicinal plants

Plants are widely used for medicinal purposes in southern Africa and a visit to a traditional medicinal plant market such as those in Durban and other urban areas, rapidly reveals the extent of the trade. Of the more or less 23 000 plant species indigenous to the *Flora of southern Africa* region, Arnold *et al.* (2002) identified no less than 3 689 as being of ethno-medicinal importance. This comprises 15% of the flora, including 11 cremnophilous taxa (see further on). Of the ethno-medicinally important ones, 159 are Red Data Listed, with *Gasteria croucheri* subsp. *pendulifolia* [43] the only obligate cremnophyte. Local traditional healers consider some plants that grow on cliffs to be ‘empowered’ and these plants are therefore popular in magical preparations (Van Jaarsveld 1992a; Smith *et al.* 1999). They include *Crassula setulosa* [139, 140, 141], *G. batesiana* var. *batesiana* [41], *G. croucheri* subsp. *pendulifolia*, *Haemanthus albiflos* [10] and *Rhipsalis baccifera* subsp. *mauritiana* [95]. Other cremnophytes recorded by Arnold *et al.* (2002) as being locally used for medicinal purposes include *Aloe mutabilis* [23], *Bulbine natalensis* [34], *Huernia pendula* [81], *Cotyledon barbeyi*, *Schizobasis intricata* [80] and *Delosperma velutinum* [203]. Of these species, *G. batesiana* var. *batesiana* and *G. croucheri* subsp. *pendulifolia* have become rare because of over-exploitation in certain regions of KwaZulu-Natal and Mpumalanga.

8.3.1.3.2.2 Plant enthusiast collectors

Damage caused by plant enthusiasts is very limited at present, especially with so much publicity on the conservation of local plants. Collectors usually focus on specific species and remove small amounts of seed or vegetative material (cuttings) without major damage to the plants or to the population. The material is used for growing on and for sharing with other plant lovers. Plants are propagated (by seed or vegetatively) and sometimes sold through nurseries specialising in succulents or rare plants. This is especially true for most obligate cremnophytes. Some species are well established in horticulture and can serve as examples of *ex situ* preservation.

The obligate cremnophilous elements are, however, only a small proportion of the plants that grow on cliffs. Cliffs are valuable refugia (Larson *et al.* 2000; Van Jaarsveld 2003).

8.4 Natural disturbances on the cliff face

Cremonophilous plants are normally well protected by their stable habitat. However, damage by natural rock falls, storms and some mammals does occur from time to time, but such events usually have little effect on the overall populations of the plants. Populations recover gradually and life on the cliff continues.

8.4.1 Rock falls

This is a continuing natural process caused by weathering and erosion. The frequency of rock falls depends on the type of rock. Unstable softer strata such as shale have a faster rate of weathering. Most cremonophytes will rapidly occupy new terrain after a rock fall.

8.4.2 Fire

Fires are frequent in the Fynbos, Grassland and Savanna Biomes and broader ledges with sufficient organic material will certainly burn. However, most cliffs lack sufficient woody and other combustible plant material and are therefore protected against fire.

8.4.3 Storm damage

Storm damage on cliffs is an annual occurrence and many cliffs visited after storms during the present study displayed plant material broken loose by high winds. This is one convenient way in which vegetative material is gathered at the base of a cliff. Most cremonophytes, however, grow well wedged or anchored and will re-sprout after damage. Vegetative bulbils and leaves of species of *Crassula* and *Adromischus* are also capable of sprouting when fragments land on ledges.

8.4.4 Mammals

Chacma baboons (*Papio ursinus*) are natural rock climbers and occur throughout the study area. There are few sites where these acrobatic primates cannot reach but their damage is limited because of the vast terrain and most baboons use the safety of cliffs only for sleeping at night. The only cliffs where baboons were not observed during the study, was at Dolphin

Head in the Namib Desert. The prickles on the leaves of *Gasteria rawlinsonii* [48] in the Baviaanskloof should act as an efficient baboon deterrent.

Rock dassies (*Procavia capensis*) are also commonly associated with cliffs throughout the study area but, although agile, they are not rock climbers like baboons and are limited to the safer ledges. Cremnophytes in reach of these two animals will be eaten and plants damaged by grazing rock dassies have been recorded (*Conophytum taylorianum* subsp. *ernianum* [192]).

The Namaqua rock rat (*Aethomys namaquensis*) is another small mammal (rodent) that lives on rocky outcrops but as in the case of the dassie, it is also limited in its capacity to reach obligate cremnophytes.

8.5 *Ex situ* conservation

8.5.1 Propagation in botanical gardens and other institutions

Most of the 220 cremnophytes from the study area have been grown at Kirstenbosch National Botanical Garden, Cape Town. Many cremnophytes have horticultural potential (as collectors' items or appealing to the general horticultural industry) and are easily propagated. Material of several cremnophytes has been made available through the Kirstenbosch annual plant sale or via the distribution of seed to other botanical gardens and institutions. Examples of succulent cremnophytes readily encountered in cultivation throughout the world include many cremnophilous species of, for example, *Aloe*, *Gasteria*, *Conophytum* and *Crassula*. An entire issue of the *American Cactus and Succulent Journal* has been devoted to the growing of cremnophilous and other hanging succulent plants (Van Jaarsveld 2006b).

TABLE 8.1—South African Red List Categories: IUCN Categories and Criteria Version 3.1 (2001), with additional categories developed specifically for the South African context (verbatim from Raimondo *et al.* 2009)

Category		
EX	Extinct	A taxon is Extinct when there is no reasonable doubt that the last individual has died. Taxa should be listed as extinct only once exhaustive surveys throughout the historic range have failed to record an individual.
EW	Extinct in the wild	A taxon is Extinct in the Wild when it is known to survive only in cultivation or as a naturalised population (or populations) well outside the past range.
CR PE	Critically Endangered (Possibly Extinct)	Critically Endangered (Possibly Extinct) taxa are those that are, on the balance of evidence, likely to be extinct, but for which there is a small chance that they may be extant. Hence they should not be listed as Extinct until adequate surveys have failed to record the taxon.
CR	Critically Endangered	A taxon is Critically Endangered when the best available evidence indicates that it meets any of the five IUCN criteria for Critically Endangered, and is therefore facing an extremely high risk of extinction in the wild.
EN	Endangered	A taxon is Endangered when the best available evidence indicates that it meets any of the five IUCN criteria for Endangered, and is therefore facing a very high risk of extinction in the wild.
VU	Vulnerable	A taxon is Vulnerable when the best available evidence indicates that it meets any of the five IUCN criteria for Vulnerable, and is therefore facing a high risk of extinction in the wild.
NT	Near Threatened	A taxon is Near Threatened when available evidence indicates that it nearly meets any of the five IUCN criteria for Vulnerable, and is therefore likely to qualify for a threatened category in the near future.
Critically Rare		A taxon is Critically Rare when it is known to occur only at a single site, but is not exposed to any direct or plausible potential threat and does not qualify for a category of threat according to the five IUCN criteria.
Rare		A taxon is Rare when it meets any of the four South African criteria for rarity, but is not exposed to any direct or plausible potential threat and does not qualify for a category of threat according to the five IUCN criteria.
Declining		A taxon is Declining when it does not meet any of the five IUCN criteria and does not qualify for the categories Critically Endangered, Endangered, Vulnerable or Near Threatened, but there are threatening processes causing a continuing decline in the population.
DDD	Data Deficient—Insufficiently Known	A taxon is DDD when there is inadequate information to make an assessment of its risk of extinction, but the taxon is well defined. Data Deficient is not a category or threat. However, listing of taxa in this category indicates that more information is required and that future research could show that a threatened classification is appropriate.
DDT	Data Deficient—Taxonomically Problematic	A taxon is DDT when taxonomic problems hinder its distribution range and habitat from being well defined, so that an assessment of risk of extinction is not possible.
LC	Least Concern	A taxon is Least Concern when it has been evaluated against the five IUCN criteria and does not qualify for the categories Critically Endangered, Endangered, Vulnerable or Near Threatened.
Thr*		Taxa that are likely to be threatened, but have been brought to the attention of the Threatened Species Programme too late for full assessments to be included in this publication. Please see the SANBI website for the final status of these taxa.

TABLE 8.2—South African cremnophilous succulent plants, listed by Scott-Shaw (1999), Victor (2002) and Raimondo *et al.* (2009): conservation status and threats (all taxa endemic except *Aloe meyeri*, which also occurs in Namibia)

Taxon	Scott-Shaw (1999)	Victor (2002)	Raimondo <i>et al.</i> (2009)	Van Jaarsveld, this study (2011)	Threats
AMARYLLIDACEAE					
<i>Cyrtanthus falcatus</i> [2]	LR-nt		Rare	LC	collecting
<i>Cyrtanthus flamosus</i> [3]		VU D2	CR	LC	
<i>Cyrtanthus herrei</i> [5]		LR-nt	NT	LC	collecting
<i>Cyrtanthus junodii</i> [7]			VU D1	LC	
<i>Haemanthus pauculifolius</i> [12]	LR-lc		Rare	LC	
ASCLEPIADACEAE					
<i>Huernia pendula</i> [81]			Rare	LC	medicinal
<i>Tromotriche baylissii</i> [83]				LC	
<i>Tromotriche choanantha</i> [84]				LC	
ASPHODELACEAE					
<i>Aloe dabenorisana</i> [17]		VU D2	Rare	LC	collecting
<i>Aloe haemanthifolia</i> [19]		LR-Lc		LC	
<i>Aloe hardyi</i> [20]		VU D2	Rare	LC	
<i>Aloe kouebokkeveldensis</i> [21]			Rare		
<i>Aloe meyeri</i> [22]		VU D2	Rare	LC	
<i>Aloe nubigena</i> [24]		VU D2	NT	LC	
<i>Aloe pictifolia</i> [27]		VU D2	Rare	LC	
<i>Aloe reynoldsii</i> [28]		VU A1cD2	Rare	LC	habitat degradation
<i>Aloe soutpansbergensis</i> [29]		VU B1B2be	Rare	LC	collecting
<i>Aloe thompsoniae</i> [30]		EN B1B2e	Rare	LC	collecting
<i>Bulbine cremnophila</i> [31]			Rare	LC	
<i>Bulbine pendens</i> [35]			CR	LC	
<i>Gasteria batesiana</i> var. <i>batesiana</i> [41]	LR-nt		NT	LC	
<i>Gasteria batesiana</i> var. <i>dolomitica</i> [42]			CR	VU	
<i>Gasteria croucheri</i> subsp. <i>pendulifolia</i> [43]				VU	
<i>Gasteria doreeniae</i> [44]			CR	LC	
<i>Gasteria glauca</i> [45]			CR	LC	
<i>Gasteria glomerata</i> [46]			CR	LC	
<i>Gasteria rawlinsonii</i> [48]			Rare	LC	
<i>Gasteria tukhelensis</i> [49]			Rare	VU	
ASTERACEAE					
<i>Othonna armiana</i> [86]		LR-nt	CR	LC	collecting
<i>Senecio medley-woodii</i> [90]	LR-Lc	LR-nt		LC	
<i>Senecio muirii</i> [91]		LR-nt	Rare	LC	
CRASSULACEAE					
<i>Adromischus cristatus</i> var. <i>mzimvubuensis</i> [96]			Rare	LC	
<i>Adromischus cristatus</i> var. <i>zeyheri</i> [98]			DDD	LC	
<i>Adromischus diabolicus</i> [99]			Rare	LC	
<i>Adromischus fallax</i> [100]			Rare	LC	
<i>Adromischus liebenbergii</i> subsp. <i>orientalis</i> [102]			Rare	LC	
<i>Cotyledon eliseae</i> [107]			Rare		



Taxon	Scott-Shaw (1999)	Victor (2002)	Raimondo <i>et al.</i> (2009)	Van Jaarsveld, this study (2011)	Threats
<i>Cotyledon tomentosa</i> subsp. <i>tomentosa</i> [109]			VU D1+2	LC	
<i>Crassula badspoortense</i> [113]			Rare	LC	
<i>Crassula brachystachya</i> [114]			Rare	LC	
<i>Crassula cremnophila</i> [116]			Rare	LC	
<i>Crassula cymbiformis</i> [117]			CR	LC	
<i>Crassula foveata</i> [122]			Rare	LC	
<i>Crassula pellucida</i> subsp. <i>spongiosa</i> [130]			Rare	LC	
<i>Crassula rupestris</i> subsp. <i>marnieriana</i> [135]			Rare	LC	
<i>Crassula sladenii</i> [142]			NT B1ab(v)	LC	
<i>Crassula socialis</i> [144]			Rare	LC	
<i>Crassula streyi</i> [145]	LR-lc		Rare	LC	
<i>Tylecodon bodleyae</i> [150]			Rare	LC	
<i>Tylecodon buchholzianus</i> var. <i>fasciculatus</i> [152]			Rare	LC	
<i>Tylecodon cordiformis</i> [153]			CR	LC	
<i>Tylecodon decipiens</i> [154]			Rare	LC	
<i>Tylecodon ellaphieae</i> [155]			Rare	LC	
<i>Tylecodon longipes</i> [156]			CR	LC	
<i>Tylecodon sulphureus</i> var. <i>armianus</i> [159]			Rare	LC	
<i>Tylecodon torulosus</i> [160]			Rare	LC	
<i>Tylecodon viridiflorus</i> [161]			Rare	LC	
GERANIACEAE					
<i>Pelargonium mutans</i> [162]				LC	
GESNERIACEAE					
<i>Streptocarpus kentaniensis</i> [164]			VU D2	LC	
HYACINTHACEAE					
<i>Albuca kirstenii</i> [66]			Rare	LC	
<i>Albuca thermanum</i> [68]			CR	LC	
<i>Ledebouria cremnophila</i> [75]			Rare	LC	
LAMIACEAE					
<i>Plectranthus dolomiticus</i> [167]			CR	LC	
<i>Plectranthus ernstii</i> [168]	LR-lc		NT D2	LC	
<i>Plectranthus mzimvubuensis</i> [170]			Rare	DD	
<i>Plectranthus purpuratus</i> subsp. <i>purpuratus</i> [171]				LC	
MESEMBRYANTHEMACEAE					
<i>Conophytum auriflorum</i> subsp. <i>turbiniforme</i> [175]			Rare	LC	
<i>Conophytum bolusiaae</i> subsp. <i>bolusiaae</i> [176]			Rare	LC	
<i>Conophytum carpiantum</i> [177]			Rare	LC	
<i>Conophytum ernstii</i> subsp. <i>ernstii</i> [179]		LR-nt	Rare	LC	
<i>Conophytum luckhoffii</i> [183]			Rare	LC	
<i>Conophytum marginatum</i> subsp. <i>littlewoodii</i> [185]			Rare	LC	
<i>Delosperma saxicola</i> [200]			Rare	LC	
<i>Delosperma velutinum</i> [203]		I	Rare	LC	

TABLE 8.3—Namibian cremnophilous succulent plants (Craven & Loots 2002; Loots 2005): conservation status, endemism and threats

Taxon	Global Red List status category (Craven & Loots 2002)	Global Red List status category (Loots 2005)	Conservation – Protected (P), Cites App. 1 (C1), App. 2 (C2)	Van Jaarsveld, this study (2011)	Endemism	Threats
AMARYLLIDACEAE						
<i>Cyrtanthus herrei</i> [5]		R		LC	Namibia & RSA	
ASCLEPIADACEAE						
<i>Lavrania haagnerae</i> [82]	EN B1B2eC2a	R	P	LC	endemic	collecting
ASPHODELACEAE						
<i>Aloe corallina</i> [16]	R (E P C2)	R	P C2	LC	Namibia & Angola	collecting
<i>Aloe dewinteri</i> [18]	VU D1	R	P C2	LC	endemic	collecting
<i>Aloe meyeri</i> [22]	EN B1B2e	R	P C2	LC	Namibia & RSA	collecting
<i>Aloe omavandae</i> [25]				LC	endemic	
<i>Aloe pavelkae</i> [26]				LC	endemic	
CRASSULACEAE						
<i>Crassula aurusbergensis</i> [112]	EN B1B2e	R		LC	endemic	collecting, mining
<i>Crassula nemorosa</i> [127]	VU D2	R		LC	Namibia & RSA	collecting
<i>Crassula pseudohemisphaerica</i> [133]	VU D2	LC		LC	Namibia & RSA	mining, collecting
<i>Tylecodon aridimontanus</i>	EN B1B2cd	NT		LC	endemic	mining, collecting
<i>Tylecodon aurusbergensis</i> [148]	EN B1B2cd	NT		LC	endemic	mining, collecting
<i>Tylecodon singularis</i> [158]	EN B1B2cd	R		LC	endemic	mining, urban expansion
MESEMBRYANTHEMACEAE						
<i>Conophytum quaesitum</i> subsp. <i>densipunctum</i> [187]	EN B1B2e	LC	P	LC	endemic	collecting
<i>Conophytum quaesitum</i> subsp. <i>quaesitum</i> var. <i>rostratum</i> [188]	EN B1B2ceC2a			LC	Namibia & RSA	collecting
<i>Conophytum ricardianum</i> subsp. <i>ricardianum</i> [189]	EN B1B2ceC2a	LC	P	LC	endemic	habitat degradation, mining, collecting
<i>Conophytum taylorianum</i> subsp. <i>ernianum</i> [192]	EN B1B2ceC2a	LC	P	LC	endemic	collecting
<i>Jensenobotrya lossowiana</i> [211]	EN B1B2ce	NT	P	LC	endemic	collecting
PEDALIACEAE						
<i>Dewinteria petrophila</i> [221]				LC		

TABLE 8.4—Cremnophilous succulent plants of Lesotho (Talukdar 2002) and Swaziland (Dlamini & Dlamini 2002): conservation status, endemism and threats

Taxon	Global Red List category	Endemism	Threats
<i>Delosperma nubigenum</i> [199]	DD	RSA & Lesotho	
<i>Haemanthus paucifolius</i> [12]	VU C2bD2	RSA & Swaziland	damming, grazing
<i>Senecio medley-woodii</i> [90]	DD	RSA & Swaziland	

CHAPTER 9

COMPENDIUM OF SUCCULENT CREMNOPHYTES AND THEIR FEATURES

9.1 Diagram (dendrogram) of obligate succulent cremnophyte growth forms

During the course of the study, 220 succulent plants have been identified as obligate or near-obligate cremnophytes. These 220 species were grown on in containers at Kirstenbosch National Botanical Garden and their behaviour was studied. This also made it possible to discern between genotypic and phenotypic behaviour.

Many cremnophytes show convergent trends. Although they were shaped by the one constant (cliff-face driving force in absence of larger herbivores), other environmental factors differ, depending on the particular cliff situation (e.g. geology, altitude, latitude, aspect). This uniform driving force resulted in similar adaptive trends, which led to a similarity in growth forms and adaptive features. These similarities have enabled the construction of a diagram or dendrogram depicting the various cremnophyte growth forms and adaptive pathways. It includes features such as the three main cremnophyte growth forms (based on stem length), the cliff hangers, the squat shrublets (cliff squatters) and the compact dwarf growth forms hugging the cliffs (cliff huggers).

Below follows a description of the diagram and the symbols used to depict the cremnophyte growth forms and other adaptive traits.

9.1.1 Cliff growth form formula

This section gives a description of the schematic diagram (**Diagram 9.1**), simply describing the various cremnophytes and their structural characteristics. The various traits and characteristics are represented as symbols. Each of the 220 study plants has been assigned a **growth form formula**. The formula is based on shared growth form and behavioural traits. Growth form formula pathways assigned to the individual taxa are given in Table 10.1 (Chapter 10) and in the species treatment (Chapter 12).

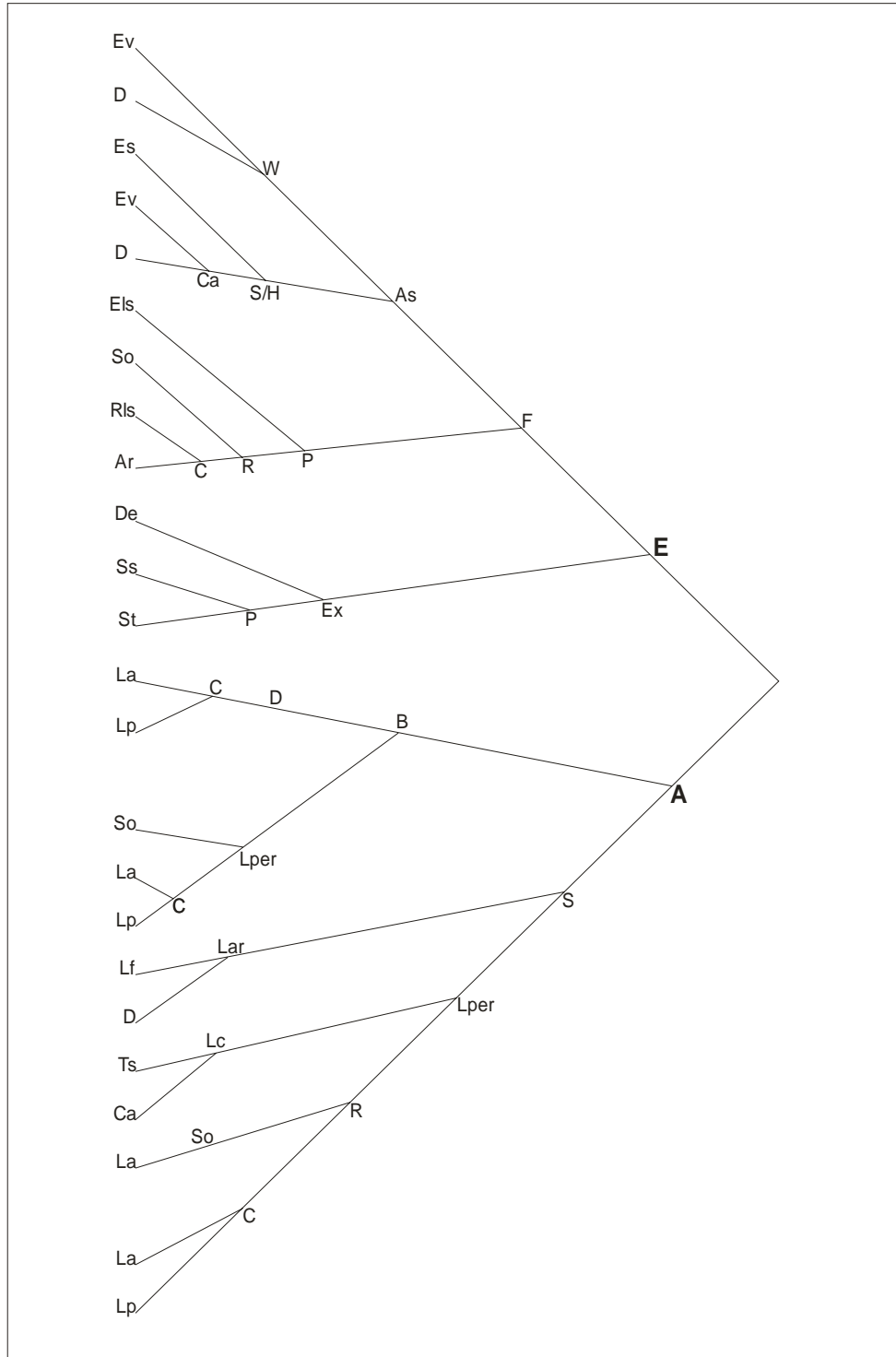


DIAGRAM 9.1. Schematic representation of the obligate or near-obligate growth forms (symbols explained in 9.1.2). The two main subdivisions are **A**: abbreviated stems, and **E**: extended stems. The diagram depicts the adaptive pathways of the 220 cremnophytes identified in this study.

The two main growth forms identified on cliffs (shown in Diagram 9.1) are based on stem length and are represented by the symbol **E** (extended stems, 94 taxa) and the symbol **A** (abbreviated stems, 126 taxa). The basal branches in Diagram 9.1 depict the main convergent plant adaptive traits. Each end of a branch represents from a single taxon to as many as 50 taxa.

Most cremnophytes identified in this study share the formula **A:S:Lper:R:C:La**. Abbreviated stems are represented by the symbol **A**, non-bulbous succulents by the symbol **S**, perennial leaves by **Lper**, rosette by **R**, cluster-forming by **C**, and ascending leaves by **La**. Most obligate cremnophytes identified are dwarf cluster-forming succulent plants with rosettes. They mainly include the cremnophilous members of *Haworthia*, *Gasteria* and *Crassula*, most of them associated with cliffs in the Eastern Cape.

Another example is the growth form formula of *Aloe hardyi* [20], which is **E:F:P:R:C:Ar(vb)(eg)**. The symbol **E** stands for extended stems, **F** for foliated stems, **P** for pendent growth, **R** for leaves in a rosette, **C** for clustered growth, **Ar** for apical rosette, **(vb)** for vegetative backup, and **(eg)** for epinastic growth. There are 11 cremnophilous aloes with the formula **E:F:P:R:C**.

9.1.2 Explanation of symbols

The following symbols are used in Table 10.1 (the check list in Chapter 10) and in the species treatment (Chapter 12).

A = Abbreviated growth, plants with shortened internodes, resulting in compact clusters.

Ar = Apical rosette, as in *Aloe dabenorisana* [17].

As = Ascending growth.

B = Bulbous or geophytic.

C = Clustered growth.

Ca = Caudiciform or swollen stem base.

D = Deciduous.

De = Decumbent.

E = Extended branch growth, including plants with extended internodes, thus lengthening.

(e) = Bulb epigeous.

(eg) = Epinastic growth.

Els = Evergreen leafy stem (not in a rosette).

Es = Evergreen succulent stems.

Ev = Evergreen.

Ex = Rudimentary foliage, as in *Lavrania haagnerae* [82], *Tromotriche* [83, 84].

F = Foliated stems, as in *Conophytum* [175–193], *Delosperma* [194–205], *Aloe* [13–30].

(fn) = Inflorescence negatively phototropic.

(ft) = Fog-trapping.

H = Herbaceous growth.

La = Leaves ascending.

Lar = Leaves annually replaced.

Lc = Leaves crowded.

Lf = Leaves fused, annually replaced, as in *Conophytum* [175–193].

Lp = Leaves pendent.

Lper = Leaves perennial.

P = Pendent growth.

(p) = Semi-poikilohydric.

R = Rosette, as in *Aloe pavelkae* [26], *Haworthia* [50–61].

(r) = Rich flowering.

(rd) = Reduction in camouflage.

Rls = Rosette extended into leafy stem, as in *Gasteria rawlinsonii* [48], *Aloe meyeri* [22].

S = Non-bulbous succulents.

So = Solitary growth.

Ss = Stems square, as in *Tromotriche* [83, 84].

St = Stems terete, as in *Rhipsalis baccifera* subsp. *mauritiana* [95], *Huernia pendula* [81].

Ts = Thin stems.

(vb) = Vegetative backup.

W = Woody growth.

9.1.3 Descriptive dichotomous key to the schematic Diagram 9.1

The key represents the various growth forms and general morphology. Numbers in brackets refer to the number of taxa represented within each pathway.

1a Extended growth	E	(94)
2a Stems with rudimentary foliage, succulent	Ex	(5)
3a Stems pendent	P	(51)
4a Stems square	Ss	(2)
4a Stems terete	St	(2)
3b Stem ascending (decumbent)	As	(36)
2b Stems foliated	F	(88)
5a Stems pendent	P	(51)
6a Rosulate	R	(14)
7a Solitary growth	So	(1)
7b Clustered growth	C	(14)
8a Rosette apical	Ar	(10)
8b Rosette extended into leafy stem	Rls	(3)
6b Extended leafy stems (not rosulate)	Els	(37)
9a Deciduous	De	(1)
9b Evergreen	Ev	(36)
5b Stems ascending or decumbent	As	(36)
10a Stems succulent/herbaceous	S	(29)
11a Stems caudiciform	Ca	(12)
12a Evergreen	Ev	(2)
12b Deciduous	De	(10)
11b Stems succulent, foliate	Es	(17)
10b Stems woody	W	(7)
13a Deciduous	De	(1)
13b Evergreen	Ev	(6)
1b Abbreviated (truncated) growth	A	(126)
14a Succulent (not bulbous)	S	(96)
15a Leaves annually replaced	Lar	(27)
16a Leaves fused, persistent (thin stem)	Lf	(19)
16b Leaves deciduous (thick stem)	D	(8)
15b Leaves perennial	Lper	(96)
17a Leaves rosulate	R	(59)
18a Solitary growth	So	(3)
19a Leaves pendent	Lp	(6)
19b Leaves ascending	La	(50)
18b Clustered growth	C	(56)
17b Leaves crowded	Lc	(10)
20a Stem base caudiciform	Ca	(2)
20b Branches thin	Ts	(8)
14b Bulbous	B	(30)
21a Leaves perennial	Lper	(21)
22a Solitary growth	So	(1)
22b Clustered growth	C	(20)
23a Leaves pendent	Lp	(7)
23b Leaves ascending	La	(13)
21b Leaves deciduous	D	(9)
24a Clustered growth	C	(9)
25a Leaves pendent	Lp	(4)
25b Leaves ascending	La	(5)
24b Solitary growth	So	(1)

9.2 Descriptions of growth forms according to Diagram 9.1

Below follows an account of the main structural adaptations as reflected in Diagram 9.1 and used in Table 10.1 (Chapter 10) and in the descriptions of the taxa (Chapter 12). Other facultative cremnophytes such as the cliff-dwelling *Ficus* species and lithophytic (epiphytic) orchids commonly encountered on cliff faces are also mentioned, but have not been included in the main text.

Most South African and Namibian succulent and bulbous cremnophytes can be grouped according to Raunkiaer's (1934) life forms, a classification based on the position of the renewal buds. Cremnophilous life forms include: phanerophytes, chamaephytes, hemicryptophytes, geophytes and therophytes. These include trees and shrubs as well as smaller perennial succulent and bulbous plants. There is also a solitary therophyte as well as a number of epiphytes and lithophytes. However, the latter two life forms have no obligate cremnophytes.

Warming (1909) classified the growth forms in a schematic tree diagram based on the length of their internodes. Two groups are clearly distinguishable, those with **abbreviated growth (A, 126 taxa)** and those with **extended growth (E, 94 taxa)**. These two groups depict the various growth forms according to their stem habit.

The largest group (abbreviated stems) of 126 taxa (57%) is the compact cluster group or cliff huggers, consisting of plants with very short internodes (abbreviated growth, symbol **A** on the schematic diagram) and consequently with compact growth. Included among the 126 taxa are most of the bulbous (**A:B**) and rosulate and other succulents (**A:S**). Their leaves are variable, from short to drooping. The group also includes clustered or tufted perennial growth types that form rounded to truncated mats and cushions, as in the genus *Conophytum*. Most of these plants are evergreen, but with a distinct resting phase (few exceptions). They tend to be concentrated more to the west and south and in regions with scanty rainfall.

The second group (longer well developed stems, three groups) of 94 taxa (43%) are the cliff hangers and cliff squatters—plants with extended internodes and their growth orthotropous (erect trees or woody or herbaceous, erect to decumbent, squat shrublets), plagiotropous (procumbent) or becoming pendent. The group includes mostly dicotyledonous plants but also some monocotyledons such as the long-stemmed pendent members of *Aloe* and *Bulbine*. Most taxa (55) in this group have pendent stems and come from the southern and

eastern parts of South Africa where summer rainfall has some influence and the rainfall is much higher. The pendent growth is due to gravity (plant growing on a vertical plane) or epinastic growth (genetic); 29 taxa with epinastic stem growth have been identified. Plants in this group are, with a few exceptions, evergreen.

I shall first deal with the growth forms (of cremnophytes) with extended stem growth; first the trees (*Ficus*) that are facultative cremnophytes and the arborescent obligate cremnophilous shrublets (squatters) and cliff hangers. This is the smallest group.

The various symbols assigned pertain to their discerning features. Pendent features are not confined to the extended growth category but are also found in the group with abbreviated growth (**A**) (cliff huggers with pendent leaves). This includes plants (17 taxa) with pendent leaves from a compact basal cluster or growth.

9.2.1 Extended stem growth (E, 94 taxa)

At present this includes 94 (43%) obligate cremnophilous taxa, most (55 taxa, 59%) with stems that become pendent. The others (37, 39%) have either decumbent or ascending growth, some also showing a degree of abbreviation to cope with gravity. This category includes both foliated species (evergreen or deciduous) (**F**) and those with rudimentary foliage (members of *Lavrania*, *Huernia*, *Rhipsalis* and *Tromotriche*). I will first discuss stem growth with rudimentary foliage of which there are two groups. Most taxa occur in the summer-rainfall region and are confined to the southeastern, eastern and northern parts of the study area.

9.2.1.1 Cremnophytes with rudimentary foliage (E:Ex, 5 taxa)

Mainly belonging to the Asclepiadaceae and Cactaceae, these cremnophytes have foliage that is highly reduced, modified and soon deciduous. There are two distinct growth forms, decumbent (**De**) and pendent (**P**).

9.2.1.1.1 Decumbent growth (E:Ex:De, 1 taxon)

Lavrania haagnerae [82] has leafless, green, assimilating stems typical of the stapeliads (Asclepiadaceae, **E:Ex:De:St**), with fleshy, cylindrical (terete), decumbent to erect stems. They grow in dense clusters on dolomite cliffs near Sesfontein in the Kaokoveld, with distinct decumbent stems.

9.2.1.1.2 Pendent growth (E:Ex:P, 4 taxa)

The obligate cremnophyte component here belongs to the Asclepiadaceae, with one member of the Cactaceae. The stems (square, terete or pencil thickness) are usually rope-like and flaccid, often branched from near the base. Plants vary from form sparsely branched to dense clusters. Stems of *Tromotriche baylissii* [83] and *T. choanantha* [84] can become 1 m or longer, the basal stolons often with epinastic growth, and stems will grow into crevices, thus extending their clusters by vegetative means. *Rhipsalis baccifera* subsp. *mauritiana* [95] can also occur as an epiphyte. Four taxa belong to this category, *Huernia pendula* [81], *Tromotriche baylissii*, *T. choanantha* and *Rhipsalis baccifera* subsp. *mauritiana*. *Huernia procumbens* from Levuvu Gorge and *Tromotriche longii* occur on cliffs as well as level ground.

9.2.1.2 Foliated cremnophytes (F, 88 taxa)

This group includes plants with distinct foliage (evergreen or deciduous). Two groups have been identified—plants with ascending growth (**As**) and the pendent group (**P**). For the sake of completeness, members of *Ficus* commonly encountered on cliffs are also mentioned, but they are not obligate cremnophytes in the study area. *Ficus muelleriana* (Mozambique) appears to be an obligate cremnophyte (Burrows & Burrows 2005), but it grows just outside the study area.

9.2.1.2.1 Trees and shrubs (facultative cremnophytes, 8 species)

Ascending trees and shrubs are commonly encountered on cliffs when a foothold is available. Chasmophytic members of the genus *Ficus* are known as rock-splitting figs. Although not obligate cremnophytes, they are frequently encountered on cliffs in the study area (Burrows & Burrows 2005). This includes eight species of the genus *Ficus* (Moraceae), namely *F. abutilifolia*, *F. burtt-davyi*, *F. cordata*, *F. glumosa*, *F. ilicina*, *F. ingens*, *F. salicifolia* and *F. tetensis*. They are typical large, ascending shrubs or trees. Frugatory birds, fruit-eating bats and other mammals spread their seed, which is adapted to germinating in crevices. They have wandering aerial roots seeking better ground. These aerial roots can grow in all directions, but are mostly geotropically positive. The seedling stage holds the key to their initial survival. The young seedling develops a temporary caudex in the form of a thick, succulent, water-storing basal part of the stem (Van Jaarsveld 1983; Van Jaarsveld & Van Wyk 2003a), the plant thus starting life as a succulent (temporary phase). However, the amazing aerial roots wander and seek out crevices. The plants gradually extend their growth until the roots reach the base, side or top of the cliff face, the other adventitious roots firmly anchoring the plants.

9.2.1.2.2 Ascending herbaceous and succulent-stemmed foliated shrubs or shrublets

(E:F:As:S/H, 29 taxa)

This group includes 29 mainly herbaceous- and succulent-stemmed chamaephytes. Two groups are involved—those with thick stem bases (12 taxa, caudiciform) and a second group with succulent stems, but lacking in markedly swollen stems (17 taxa). They vary from smaller dwarf shrublets to larger shrubs (evergreen or deciduous). Growth is erect or decumbent and some have shortened growth, where the distinction between the extended or abbreviated growth is blurred. Most are evergreen, including *Aeollanthus haumannii* [165] with large succulent phyllopodia, and *A. rydingianus* [166]. Both occur in savanna regions in northern Namibia. *Plectranthus mzimvubuensis* [170] is a tall, leaning, evergreen shrub 2–3 m high and known only from cliffs along the Mzimvubu River in the Eastern Cape. Some *Tylecodon* taxa belong to this group; all have succulent stems and are summer-deciduous (Succulent Karoo, Western and Northern Cape). Members of *Adromischus*, *Cotyledon*, *Crassula* and *Senecio* have decumbent stems (evergreen). *Delosperma laxipetalum* [198] is an ascending shrublet with succulent herbaceous stems bearing linear succulent leaves, and *Senecio medley-woodii* [90] has herbaceous stems and fleshy leaves. The leaves of *S. medley-woodii* are partially covered with dense, felt-like hairs. The same group also includes *Senecio pondoensis* [92] (Eastern Cape), *S. talinoides* subsp. *talinoides* [94] (Eastern Cape) and *S. serpens* [93] (Western Cape). *Othonna triplinervia* [89] (obligate cremnophilous form) is evergreen (rainfall at any time of year), with swollen succulent stems and stem base (Van Jaarsveld 2006c). *Plectranthus ernstii* [168] (sandstone cliffs, KwaZulu-Natal and Eastern Cape) is an evergreen decumbent shrublet with articulated, tapering, succulent stems and aromatic leaves. These plants also root where the stems touch the ground. Some individuals can also become pendent at times.

9.2.1.2.3 Ascending woody stemmed shrublets (E:F:As:W, 7 taxa)

The following species have woody stems and succulent leaves. Most members of this group have an erect to decumbent habit. *Lampranthus affinis* [212], an obligate cremnophyte, is a much-branched evergreen shrublet from cliffs along river valleys in the Eastern Cape. It has woody stems and linear, succulent leaves. The other four species are *Drosanthemum anemophilum* [206], *Ruschia knysnana* [215], *Scopelogenia bruynsii* [217] and *S. verruculata* [218]. *Tetradenia kaokoensis* [173] is an erect woody or herbaceous shrub with ascending, sparsely branched stems with large leaves and distinct woody phyllopodia (Van Jaarsveld & Van Wyk 2003c). There are many other near-obligate taxa fitting this category. These cremnophytes do not differ markedly

from level-ground mesemb associates, all having the same lignified stems. The young growth is soft and in some species can become pendent (phenotypic).

9.2.1.2.4 Pendent stems (51 taxa, E:F:P)

This category includes foliated plants that become pendent, some of which display epinastic growth. These 51 cliff-hanger taxa can be divided into two groups. Those with rosettes (first group) (**E:F:P:R**) include 14 taxa such as *Aloe*. The second group of 37 taxa have extended foliated stems lacking a rosette (**E:F:P:ElS**) and include plants such as *Delosperma* spp. and *Jensenobotrya lossowiana* [211].

9.2.1.2.4.1 Pendent rosettes (E:F:P:R, 14 taxa)

Included here are mainly monocotyledons, especially Asphodelaceae with representatives such as *Aloe* (11 species), *Bulbine suurbergensis* [39] and *Gasteria rawlinsonii* [48]. Plants are either solitary with long stems (bare or covered in dry leaves) and apical rosettes (*A. hardyi* [20], **E:F:R:Ar**), or drooping clusters (11 taxa) or shrubs with rosettes but extending into foliated stems as in *A. catengiana* [14], *A. meyeri* [22] and *Gasteria rawlinsonii*, **E:F:P:R:C:Rls**.

9.2.1.2.4.2 Pendent leafy stems (E:F:P:ElS, 39 taxa)

This is a large group (39 dicotyledonous taxa) consisting of plants with leafy plagiotropous stems becoming drooping on a vertical plane. Many are actively (vegetatively) increasing their growth size, forming dense to loose mats. Plants are often rooting at the nodes, thus forming extensive clones. This group is not always clear cut, some leaning towards plants with abbreviated growth, depending on the crevice and availability of solar radiation. Compared to counterparts growing in non-cliff habitats, there is an increase in succulence and reduction in size, thus a combination of drought- and cliff-adapted features. Forms of *Crassula perforata* [131, 132] usually have shorter internodes, together with its leaves resulting in almost cylindrical bodies. The largest plant in this group is *Jensenobotrya lossowiana* [211]. This amazing species has dense clusters of club-shaped leaves on stems up to 1 m long. The main branch can be as thick as a man's arm.

9.2.2 Abbreviated or truncated stem growth (A, 126 taxa)

The cliff huggers are clearly the largest group, with two clear-cut subgroups—the bulbous succulent plants of 30 taxa (**A:B**), and the 96 (44% of total) non-bulbous succulent cliff

huggers (A:S). Although they display a compact growth, some bulbous species bear long, pendent leaves. The plants have shortened stems with a compact growth hugging the cliff.

9.2.2.1 Bulbous cremnophilous succulent plants (A:B, 30 taxa)

The bulbous component (30, 14%) consists mostly of plants with epigeous bulb growth, with one or two exceptions from the Drakensberg and adjacent regions. In size they range from the miniature *Drimia uniflora* [73], probably the world's smallest bulbous species occurring from almost sea level to 3000 m, to the large robust *Cyrtanthus herrei* [5] of the Richtersveld and southern Namibia. Most bulbous species on terrestrial habitats have bulbs that are located below ground. Cremnophilous bulbous taxa usually grow in dense rounded clusters, with the exception of one that is solitary. Their bulbs (storage, fleshy scales) vary from loose bulb scales (*D. cremnophila* [69]) to well tunicated (*Haemanthus albiflos* [10]), sometimes covered with dried bulb scales (*C. flammosus* [3], *C. montanus* [9] and *C. labiatus* [8]). There are two groups, evergreen and deciduous plants.

9.2.2.1.1 Bulbs with perennial leaves (A:B:Lper, 21 taxa)

There are 21 bulbous taxa with evergreen leaves. Most of them form dense clusters (*Cyrtanthus herrei* [5], *C. montanus* [9], *C. labiatus* [8], *Haemanthus albiflos* [10] and *H. pauculifolius* [12]). They can be further divided into two groups—those with pendent and those with ascending leaves. Most of them are from the southeastern regions of the study area where rainfall is experienced at any time of the year and with mild winters. However, *C. herrei* from the winter-rainfall zone is an exception in that the leaves remain evergreen. *Cyrtanthus flammosus* [3] (Eastern Cape) is the only solitary bulbous species (So = solitary) growing with its bulb half exposed (semi-epigeous). To compensate for a lack of vegetative output, *C. flammosus* has very large, solitary flowers (rich flowering). The species mentioned above have mainly ascending leaves. Some of them have flaccid, drooping, perennial leaves, for example *Albuca cremnophila* [64] and *A. thermanum* [68]. Both are cluster-forming. *Albuca cremnophila* is a robust evergreen species confined to the Gamtoos River and its tributaries and grows horizontally to pendent along ledges. Its leaves are leathery, long-lived and also display epinastic growth. Plants do not proliferate from the base but divide to form small, dense clusters. *Albuca thermanum* from Calitzdorp Spa is the only evergreen species with drooping leaves occurring so far west (also subject to winter rainfall).

9.2.2.1.2 Bulbs with leaves that are deciduous or replaced annually (A:B:D, 9 taxa)

There are a number of cremnophilous bulbs with deciduous leaves. Those from the Drakensberg become dormant during cold winters. *Cyrtanthus falcatus* [2] is well adapted to cliffs and apart from the epinastic growth of its leaves, the bulb presentation is also often horizontal to pendent. *Albuca crudenii* [65] from the Grahamstown region is a winter-growing taxon (summer-deciduous) and in spite of summer rain, it remains deciduous during this period. *Albuca kirstenii* [66] (Gourits River and further west) is also summer-deciduous. *Albuca shawii* [67] forms dense clusters. It is widespread in the northeastern parts of South Africa and becomes deciduous where frost or snow is experienced. In warmer subtropical regions where frost is rare, it remains evergreen.

9.2.2.2 Non-bulbous succulents (A:S, 96 taxa)

This includes clearly the largest group of the obligate cremnophytes (96 taxa, 44%). It comprises both dicotyledons (e.g. Mesembryanthemaceae, Crassulaceae, Asteraceae) and monocotyledons (Asphodelaceae) that grow in dense clusters (rarely solitary) hugging the cliffs. There are two groups—plants in which the leaves are annually replaced or renewed (27 taxa; **Lar** = leaves annually replaced) and plants with long-term perennial leaves (69 taxa; **Lper** = leaves perennial).

9.2.2.2.1 Compact succulent plants, leaves annually replaced (deciduous or aestivating leaves) (A:S:Lar, 27 taxa)

Plants with leaves that are annually replaced fall in two distinct groups—those with leaves that are deciduous during the dry resting season (8 taxa) and those with leaves that are summer-aestivating (19 taxa). The latter group is represented by members of the genus *Conophytum* and, although the leaves are evergreen, moisture is annually translocated or recycled to a young new pair, the old leaves remaining intact as a dry skin enveloping the young pair.

9.2.2.2.1.1 Compact growth with fused leaves, the genus *Conophytum* (A:S:Lar:Lf, 19 taxa)

These 19 taxa all belong to the genus *Conophytum*. Plants are usually short-stemmed and grow in tight mats or clusters (shady south-facing cliffs) and the leaves are fused (**Lf** = leaves fused) into a characteristic club-shaped body, flat or lobed at the top. In the centre is a small orifice or opening from where the flower appears. During the dry summer season, plants aestivate and the body is gradually replaced by a new young pair of leaves. Although the cluster type can also be found on quartz flats and in other habitats in the Succulent Karoo, the

cliff huggers tend to be more fragile (sometimes bearing fog-trapping hairs or papillae) than the non-cremnohytes. Some non-cremnophilous species of *Conophytum* have a solitary growth form or are deeply sunken in the ground (only apical windows visible).

9.2.2.2.1.2 Compact cluster, succulent-stemmed, leaves deciduous during the long dry summer season, the genera *Tylecodon* and *Othonna* (A:S:Lper:D, 8 taxa)

This group represents plants like compact clusters in the genus *Tylecodon* of which the leaves become deciduous towards the summer months (A:S:Lar:D). The stems of these plants are succulent and compact. This includes species such as *T. longipes* [156], *T. ellaphieae* [155], *T. decipiens* [154], *T. singularis* [158] and *Othonna armiana* [86]. These taxa are mostly confined to crevices and ledges on shady south-facing aspects.

9.2.2.2.1.3 Compact succulent plants with perennial leaves (clustered, crowded leaves, or in dense rosettes) (A:S:Lper, 69 taxa)

This includes two groups, both evergreen—those with the leaves in clusters (*Adromischus* spp.) and those with distinct tight rosettes (*Haworthia* spp. and many *Crassula* spp.). They are mostly from an all-year- or summer-rainfall region, usually confined to south-facing cliffs.

9.2.2.2.2 Compact succulent plants with leaves crowded, the genera *Adromischus*, *Pyrrosia* and *Streptocarpus* (A:S:Lper:Lc, 10 taxa)

This group includes ten taxa, some members of the genus *Adromischus*, *Streptocarpus* and *Pyrrosia*. It comprises two groups—one with a caudex (Ca) and the other with thin succulent stems (Ts). *Streptocarpus kentaniensis* [164] has ascending leaves that become pendent on the cliffs (summer rainfall, Eastern Cape). *Pyrrosia schimperiana* [1] has short procumbent stems and ascending leaves that can become pendent. Members of *Adromischus* have crowded leaves. The caudiciform group (Lc:Ca) includes the dwarf *Anacampseros scopata* [220] and *Adromischus schuldianus* subsp. *brandbergensis* [103]. Both have a swollen caudiciform base. The stems of *Anacampseros scopata* are densely covered with long hairs with fog-trapping abilities—the species occurs within the fog range (Vyftienmyl se Berge, Port Nolloth).

9.2.2.3 Plants with leaves in tight (rarely loose) rosettes (A:S:Lper:R, 59 taxa)

There are 59 taxa, and two groups have been identified—those usually with a solitary or sparsely branched rosette (three taxa) and the other (56 taxa) with rosettes in tight to loose clusters.

9.2.2.3.1 Plants with solitary rosettes (A:S:Lper:R:So, 3 taxa)

It includes three species, *Aloe dewinteri* [18] (summer rainfall), *A. kouebokkeveldensis* [21] (winter rainfall) and *Bulbine natalensis* [34] (summer rainfall) (A:S:Lper:R:So). The aloes are quite large, rosulate plants and the *Bulbine* is smaller.

9.2.2.3.2 Plants with leaves in a tight rosette in dense to loose clusters (A:S:Lper:R:C, 56 taxa)

These plants (56 taxa) can also be divided into two groups—those (50 taxa) with ascending and those (six taxa) with pendent leaves. The first group consists of the compact cluster-forming members of *Haworthia*, *Gasteria* and *Crassula*, all with short ascending to spreading leaves. The second group is the smallest and often displays epinastic growth, as in *G. croucheri* subsp. *pendulifolia* [43]. Other examples include *Aloe soutpansbergensis* [29], *Bulbine cremnophila* [31], *B. meiringii* [33], *B. thomasii* [40] and *Trachyandra tabularis* [62]. Most of them (except *Trachyandra*) originate from summer-rainfall regions.

CHAPTER 10

CHECK LIST OF OBLIGATE AND NEAR-OBLIGATE CREMNOPHILOUS TAXA (220 TAXA, 203 SPECIES)

10.1 Introduction

Table 10.1 lists the 220 obligate or near-obligate succulent and bulbous succulent cremnophytes gathered in the study area. The two semisucculent taxa *Dewinteria* and *Stemodiopsis* were added as an outgroup. The total of 222 taxa belong to 16 plant families (ferns 1 family, 1 taxon; monocotyledons 3 families, 79 taxa; dicotyledons 10 families, 140 taxa; outgroup 2 families, 2 taxa). The families with the largest representation are the Crassulaceae (66 taxa, *Crassula* 38), followed by the Asphodelaceae (44 taxa, *Aloe* 18) and the Mesembryanthemaceae (44 taxa, *Conophytum* 19). These three are also the largest succulent plant families found in South Africa (Van Jaarsveld 1988a). Another family well represented by succulent plants in South Africa is the Asclepiadaceae. However, only four taxa that are obligate cremnophytes have been found in this family.

The check list has been compiled during the botanical survey of the succulent and bulbous succulent plants on cliff faces in South Africa and Namibia over more or less the past ten years. Propagation material (seed, cuttings or plants) was gathered from the native habitat and grown in a greenhouse at Kirstenbosch National Botanical Garden. The behaviour (morphological and reproductive) of the various plants was observed and the information extracted and documented.

10.2 Explanation of the check list

The fern is listed first, followed by the monocotyledons, dicotyledons and lastly the outgroup. Within a family, the genera and species follow an alphabetical arrangement. Each taxon was designated a number, which is used throughout the study. This was done to avoid repetition of author citations, which are given only in the check list and in Chapter 12 (Species treatment), thus saving space.

Each taxon has also been designated a growth formula, shown in the third column of Table 10.1. The symbols used in these growth formulae are explained in 9.1.2. A growth formula is merely a summary of the main characteristics (morphological and reproductive) of

the taxon in question. It classifies the taxon in one of the three main cremnophyte groups: cliff squatters, cliff hangers and cliff huggers. Other information such as occurrence, distribution, vegetation type, conservation status and environmental data (geology, aspect, altitude, rainfall) is also reflected in Table 10.1.

Plants were also grouped into three classes according to their weight: light = < 50 g; medium = 51–500 g; heavy = > 500 g. Within the various taxa, the weight of individuals varies according to size and the time of year. During sufficient rain, succulents become turgid, with a dramatic increase in weight; the opposite happens during periods of drought. Because of this variation in weight, it was decided to weigh the plants when fully turgid, during their rainy season. Average-sized mature plants were weighed. The weight of most taxa falls within the light- or medium-weight classes. Those below 50 g include mostly *Conophytum* and the smaller *Crassula* taxa. Only a few plants (five aloes) fall within the heavy-weight class.

10.3 The list is still growing

The check list in Table 10.1 represents plants found by the author as well as plants previously documented from cliffs in the study area. It is by no means a final list as many more species are continuously found on cliffs in southern Africa. The numbers are being updated as more information is gathered.

10.4 Layout of Table 10.1

Table 10.1 consists of 24 columns per taxon, each column summarising the particular attribute mentioned in the heading. Fitting all of this into A4 format has necessitated seven consecutively numbered pages for each set of species/infraspecific taxa, covering all 24 columns. For convenience and ease of reference, a guide to the seven-page clusters is supplied on the next page, i.e. the page preceding Table 10.1.

GUIDE TO THE LAYOUT OF TABLE 10.1

To fit in all the required columns, entries for each taxon are spread over seven consecutively numbered pages. Hence, to view all the information on a particular taxon (24 columns), consult all seven pages. The pages on which the various seven-page clusters can be found, each cluster covering the same set of taxa, are indicated below (for detailed treatment of each taxon, see Chapter 12).

Set of taxa	Page range
FERNS to taxon 30	167–173
<i>Bulbine</i> (Asphodelaceae) to taxon 62	174–180
HYACINTHACEAE to taxon 89	181–187
<i>Senecio</i> (Asteraceae) to taxon 116	188–194
117 <i>Crassula cymbiformis</i> (Crassulaceae) to taxon 147	195–201
<i>Tylecodon</i> (Crassulaceae) to taxon 173	202–208
MESEMBRYANTHEMACEAE to taxon 205	209–215
<i>Drosanthemum</i> (Mesembryanthemaceae) to taxon 222	216–222



TABLE 10.1—Check list of obligate and near-obligate cremnophilous taxa (220 taxa, 203 species)

No.	Taxon	Cremonophilous growth form	Degree of cliff occupation	Weight class
		See 9.1.2 for explanation of the symbols below	*** = strictly obligate cremnophyte, displaying cliff-adapted features ** = obligate cremnophyte * = predominantly on cliffs (80%)	light = < 50 g medium = 51–500 g heavy = >500 g
	FERNS			
	POLYPODIACEAE (1 species)			
	<i>Pyrosia</i> Mirb. (1 species)			
1	<i>P. schimperiana</i> (Mett. ex Kuhn) Alston	A:S:Lper:Lc:Ts (p)	**	medium
	MONOCOTYLEDONS (3 families, 79 taxa, 76 species)			
	AMARYLLIDACEAE (2 genera, 11 species)			
	<i>Cyrtanthus</i> Aiton (8 species)			
2	<i>C. falcatus</i> R.A.Dyer	A:B:D:C:Lp (e) (vb) (eg)	***	medium-heavy
3	<i>C. flammosus</i> Snijman & Van Jaarsv.	A:B:Lper:So:La (r)	***	medium
4	<i>C. flanaganii</i> Baker	A:B:D:C:La (vb)	**	medium
5	<i>C. herrei</i> (F.M.Leight.) R.A.Dyer	A:B:Lper:C:La (e) (vb)	**	medium
6	<i>C. inaequalis</i> O'Brien	A:B:Lper:C:La (e) (vb)	*	medium
7	<i>C. junodii</i> P.Beauv.	A:B:D:C:La (e) (vb)	**	medium
8	<i>C. labiatus</i> R.A.Dyer	A:B:Lper:C:La (e) (vb)	***	medium
9	<i>C. montanus</i> R.A.Dyer	A:B:Lper:C:La (e) (vb)	***	medium
	<i>Haemanthus</i> L. (3 species)			
10	<i>H. albiflos</i> Jacq.	A:B:Lper:C:La (e) (vb)	**	medium
11	<i>H. humilis</i> Jacq. subsp. <i>humilis</i>	A:B:D:C:La (e) (vb)	**	medium
12	<i>H. pauculifolius</i> Snijman & A.E.van Wyk	A:B:Lper:C:La (e) (vb)	**	medium
	ASPHODELACEAE (5 genera, 50 taxa, 47 species)			
	<i>Aloe</i> L. (18 species)			
13	<i>A. arborescens</i> Mill. subsp. <i>mzimyati</i> Van Jaarsv. & A.E.van Wyk	E:F:P:R:C:Ar (vb)	*	medium-heavy
14	<i>A. catengiana</i> Reynolds	E:F:P:R:C:Rls (vb)	**	medium-heavy
15	<i>A. challisii</i> Van Jaarsv. & A.E.van Wyk	E:F:P:R:C:Ar (vb) (eg)	***	light-medium
16	<i>A. corallina</i> I.Verd.	E:F:P:R:C:Ar (vb) (eg)	***	medium-heavy
17	<i>A. dabenorisana</i> Van Jaarsv.	E:F:P:R:C:Ar (vb) (eg)	***	medium-heavy
18	<i>A. dewinteri</i> Giess	A:S:Lper:R:So:La	***	heavy
19	<i>A. haemanthifolia</i> A.Berger & Marloth	A:S:Lper:R:C:La (vb)	***	heavy
20	<i>A. hardyi</i> Glen	E:F:P:R:C:Ar (vb) (eg)	***	heavy
21	<i>A. kouebokkeveldensis</i> Van Jaarsv. & A.B.Low	A:S:Lper:R:So:La	*	heavy
22	<i>A. meyeri</i> Van Jaarsv.	E:F:P:R:C:Rls: (vb) (eg)	***	medium-heavy
23	<i>A. mutabilis</i> Pillans	E:F:P:R:C:Ar (vb)	**	heavy
24	<i>A. nubigena</i> Groenew.	E:F:P:R:C:Ar (vb) (eg)	***	light-medium
25	<i>A. omavandae</i> Van Jaarsv.	E:F:P:R:C:Ar (vb) (eg)	***	medium-heavy
26	<i>A. pavelkae</i> Van Jaarsv., Swanepoel, A.E.van Wyk & Lavranos	E:F:P:R:C:Ar:(vb) (eg)	***	medium-heavy
27	<i>A. pictifolia</i> D.S.Hardy	A:S:Lper:R:C:La (vb)	**	medium
28	<i>A. reynoldsii</i> Letty	A:S:Lper:R:C:La (vb)	***	medium-heavy
29	<i>A. soutpansbergensis</i> I.Verd.	A:S:Lper:R:C:Lp (vb) (eg)	***	light-medium
30	<i>A. thompsoniae</i> Groenew.	A:S:Lper:R:C:La (vb)	*	light-medium



TABLE 10.1 (continued)—Check list of obligate and near-obligate cremnophilous taxa (220 taxa, 203 species)

No.	Taxon	Vegetative dispersal backup	Geology	Aspect
	FERNS			
	POLYPODIACEAE (1 species)			
	<i>Pyrosia</i> Mirb. (1 species)			
1	<i>P. schimperiana</i> (Mett. ex Kuhn) Alston	dividing or proliferating clusters	sandstone	S
	MONOCOTYLEDONS (3 families, 79 taxa, 76 species)			
	AMARYLLIDACEAE (2 genera, 11 species)			
	<i>Cyrtanthus</i> Aiton (8 species)			
2	<i>C. falcatus</i> R.A.Dyer	dividing or proliferating clusters	mudstone	S
3	<i>C. flammosus</i> Snijman & Van Jaarsv.	solitary	sandstone	S
4	<i>C. flanagani</i> Baker	dividing or proliferating clusters	basalt	N
5	<i>C. herrei</i> (F.M.Leight.) R.A.Dyer	dividing or proliferating clusters	sandstone, granite	E, S
6	<i>C. inaequalis</i> O'Brien	bulbils	sandstone	E, S
7	<i>C. junodii</i> P.Beauv.	dividing or proliferating clusters	sandstone	N
8	<i>C. labiatus</i> R.A.Dyer	bulbils	sandstone	N, E, S
9	<i>C. montanus</i> R.A.Dyer	bulbils	sandstone	N, E, S
	Haemanthus L. (3 species)			
10	<i>H. albiflos</i> Jacq.	dividing or proliferating clusters	sandstone, shale, mudstone	S, E, N
11	<i>H. humilis</i> Jacq. subsp. <i>humilis</i>	dividing or proliferating clusters	sandstone, shale	S
12	<i>H. pauculifolius</i> Snijman & A.E.van Wyk	dividing or proliferating clusters	quartz, mudstone	S
	ASPHODELACEAE (5 genera, 50 taxa, 47 species)			
	<i>Aloe</i> L. (18 species)			
13	<i>A. arborescens</i> Mill. subsp. <i>mzimnyi</i> Van Jaarsv. & A.E.van Wyk	dividing or proliferating clusters	sandstone	S, E, N
14	<i>A. catengiana</i> Reynolds	dividing or proliferating clusters	sandstone	E
15	<i>A. challisii</i> Van Jaarsv. & A.E.van Wyk	dividing or proliferating clusters	sandstone	W
16	<i>A. corallina</i> I.Verd.	dividing or proliferating clusters	dolomite	S, E
17	<i>A. dabenorisana</i> Van Jaarsv.	dividing or proliferating clusters	quartz	S
18	<i>A. dewinteri</i> Giess	solitary	dolomite	S,W
19	<i>A. haemanthifolia</i> A.Berger & Marloth	dividing or proliferating clusters	sandstone	W, N
20	<i>A. hardyi</i> Glen	active growth and rooting	dolomite	W, N
21	<i>A. kouebokkeveldensis</i> Van Jaarsv. & A.B.Low	solitary	sandstone	N, W
22	<i>A. meyeri</i> Van Jaarsv.	dividing or proliferating clusters	sandstone	S, E
23	<i>A. mutabilis</i> Pillans	dividing or proliferating clusters	sandstone	E, S, N
24	<i>A. nubigena</i> Groenew.	dividing or proliferating clusters	sandstone	E, S
25	<i>A. omavandae</i> Van Jaarsv.	dividing or proliferating clusters	sandstone	S, E
26	<i>A. pavelkae</i> Van Jaarsv., Swanepoel, A.E.van Wyk & Lavranos	dividing or proliferating clusters	sandstone	E, S
27	<i>A. pictifolia</i> D.S.Hardy	dividing or proliferating clusters	sandstone	E, W, N
28	<i>A. reynoldsii</i> Letty	dividing or proliferating clusters	mudstone	S, E, W
29	<i>A. soutpansbergensis</i> I.Verd.	dividing or proliferating clusters	sandstone	S
30	<i>A. thompsoniae</i> Groenew.	dividing or proliferating clusters	sandstone	W, E



TABLE 10.1 (continued)—Check list of obligate and near-obligate cremnophilous taxa (220 taxa, 203 species)

No.	Taxon	Altitude (m)	Rainfall (mm per annum)	Rainfall seasonality	Deciduousness
				S = summer W = winter W/S = any time of year	E = evergreen SA = summer-aestivating SD = summer-deciduous WD = winter-deciduous
	FERNS				
	POLYPODIACEAE (1 species)				
	<i>Pyrosia</i> Mirb. (1 species)				
1	<i>P. schimperiana</i> (Mett. ex Kuhn) Alston	1400–1600	100–1250	S	E
	MONOCOTYLEDONS (3 families, 79 taxa, 76 species)				
	AMARYLLIDACEAE (2 genera, 11 species)				
	<i>Cyrtanthus</i> Aiton (8 species)				
2	<i>C. falcatus</i> R.A.Dyer	1100–1800	1000–1500	S	WD
3	<i>C. flammosus</i> Snijman & Van Jaarsv.	250–500	400–500	W/S	E
4	<i>C. flanagani</i> Baker	2750–3000	1000–1500	S	WD
5	<i>C. herrei</i> (F.M.Leight.) R.A.Dyer	400–1500	150–250	W	E
6	<i>C. inaequalis</i> O'Brien	800–1200	200–300	W/S	E
7	<i>C. junodii</i> P.Beauv.	1500–2000	1500–1750	S	WD
8	<i>C. labiatus</i> R.A.Dyer	300–900	400–500	W/S	E
9	<i>C. montanus</i> R.A.Dyer	250–500	400–500	W/S	E
	Haemanthus L. (3 species)				
10	<i>H. albiflos</i> Jacq.	15–1500	300–1000	W/S	E
11	<i>H. humilis</i> Jacq. subsp. <i>humilis</i>	460–1400	400–1000	S	WD
12	<i>H. pauculifolius</i> Snijman & A.E.van Wyk	600–900	600–800	S	E
	ASPHODELACEAE (5 genera, 50 taxa, 47 species)				
	Aloe L. (18 species)				
13	<i>A. arborescens</i> Mill. subsp. <i>mzimyati</i> Van Jaarsv. & A.E.van Wyk	700–1000	800–1000	S	E
14	<i>A. catengiana</i> Reynolds	1800–2000	300–500	S	E
15	<i>A. challsii</i> Van Jaarsv. & A.E.van Wyk	1800–2000	1500–1750	S	E
16	<i>A. corallina</i> I.Verd.	400–1200	75–150	S	E
17	<i>A. dabenorisana</i> Van Jaarsv.	700–1000	75–150	W/S	E
18	<i>A. dewinteri</i> Giess	600–1200	75–150	S	E
19	<i>A. haemanthifolia</i> A.Berger & Marloth	500–1675	800–1000	W	E
20	<i>A. hardyi</i> Glen	850–1350	300–400	S	E
21	<i>A. kouebokkeveldensis</i> Van Jaarsv. & A.B.Low	400–600	700–800	W	E
22	<i>A. meyeri</i> Van Jaarsv.	300–1200	75–150	W	E
23	<i>A. mutabilis</i> Pillans	800–1800	700–800	S	E
24	<i>A. nubigena</i> Groenew.	1450–2100	1500–2000	S	E
25	<i>A. omavandae</i> Van Jaarsv.	1600–1900	300–500	S	E
26	<i>A. pavelkae</i> Van Jaarsv., Swanepoel, A.E.van Wyk & Lavranos	700–800	50–125	W	E
27	<i>A. pictifolia</i> D.S.Hardy	250–500	400–500	W/S	E
28	<i>A. reynoldsii</i> Letty	150–1000	800–1250	S	E
29	<i>A. soutpansbergensis</i> I.Verd.	1525–1750	1500–2000	S	E
30	<i>A. thompsoniae</i> Groenew.	1650–2100	1500–2000	S	E



TABLE 10.1 (continued)—Check list of obligate and near-obligate cremnophilous taxa (220 taxa, 203 species)

No.	Taxon	Fog	Biomes	Pollination
		*** = regular fog ** = occasional fog * = little fog – = no fog	IOCB = Indian Ocean Coastal Belt	
	FERNS			
	POLYPODIACEAE (1 species)			
	<i>Pyrrhosia</i> Mirb. (1 species)			
1	<i>P. schimperiana</i> (Mett. ex Kuhn) Alston	*	Forest	wind
	MONOCOTYLEDONS (3 families, 79 taxa, 76 species)			
	AMARYLLIDACEAE (2 genera, 11 species)			
	<i>Cyrtanthus</i> Aiton (8 species)			
2	<i>C. falcatus</i> R.A.Dyer	*	Grassland	bird
3	<i>C. flammosus</i> Snijman & Van Jaarsv.	**	Albany Thicket	insect
4	<i>C. flanagani</i> Baker	**	Grassland	bird
5	<i>C. herrei</i> (F.M.Leight.) R.A.Dyer	**	Succulent Karoo	bird
6	<i>C. inaequalis</i> O'Brien	*	Succulent Karoo	bird
7	<i>C. junodii</i> P.Beauv.	**	Grassland	insect
8	<i>C. labiatus</i> R.A.Dyer	–	Albany Thicket	bird
9	<i>C. montanus</i> R.A.Dyer	–	Albany Thicket	insect
	Haemanthus L. (3 species)			
10	<i>H. albiflos</i> Jacq.	–	Albany Thicket	insect
11	<i>H. humilis</i> Jacq. subsp. <i>humilis</i>	*	Grassland	insect
12	<i>H. paucifolius</i> Snijman & A.E.van Wyk	–	Savanna	insect
	ASPHODELACEAE (5 genera, 50 taxa, 47 species)			
	Aloe L. (18 species)			
13	<i>A. arborescens</i> Mill. subsp. <i>mzimnyi</i> Van Jaarsv. & A.E.van Wyk	–	Savanna	bird
14	<i>A. catengiana</i> Reynolds	–	Savanna	bird
15	<i>A. challisii</i> Van Jaarsv. & A.E.van Wyk	**	Grassland	bird
16	<i>A. corallina</i> I.Verd.	–	Savanna	bird
17	<i>A. dabenorisana</i> Van Jaarsv.	–	Desert	bird
18	<i>A. dewinteri</i> Giess	–	Savanna	bird
19	<i>A. haemanthifolia</i> A.Berger & Marloth	*	Fynbos	bird
20	<i>A. hardyi</i> Glen	–	Savanna	bird
21	<i>A. kouebokkeveldensis</i> Van Jaarsv. & A.B.Low	–	Fynbos	bird
22	<i>A. meyeri</i> Van Jaarsv.	**	Succulent Karoo	bird
23	<i>A. mutabilis</i> Pillans	–	Savanna	bird
24	<i>A. nubigena</i> Groenew.	**	Grassland	bird
25	<i>A. omavandae</i> Van Jaarsv.	–	Savanna	bird
26	<i>A. pavelkae</i> Van Jaarsv., Swanepoel, A.E.van Wyk & Lavranos	***	Succulent Karoo	bird
27	<i>A. pictifolia</i> D.S.Hardy	–	Albany Thicket	bird
28	<i>A. reynoldsii</i> Letty	–	Savanna	bird
29	<i>A. soutpansbergensis</i> I.Verd.	**	Grassland	bird
30	<i>A. thompsoniae</i> Groenew.	**	Grassland	bird



TABLE 10.1 (continued)—Check list of obligate and near-obligate cremnophilous taxa (220 taxa, 203 species)

No.	Taxon	Seed dispersal	Conservation status	Light requirements
			LC = Least Concern NT = Not Threatened VU = Vulnerable	BL = bright light DS = dappled shade FS = full sun
	FERNS			
	POLYPODIACEAE (1 species)			
	<i>Pyrosia</i> Mirb. (1 species)			
1	<i>P. schimperiana</i> (Mett. ex Kuhn) Alston	wind	LC	DS, BL
	MONOCOTYLEDONS (3 families, 79 taxa, 76 species)			
	AMARYLLIDACEAE (2 genera, 11 species)			
	<i>Cyrtanthus</i> Aiton (8 species)			
2	<i>C. falcatus</i> R.A.Dyer	wind	LC	FS, DS, BL
3	<i>C. flammosus</i> Snijman & Van Jaarsv.	wind	LC	FS, BL
4	<i>C. flanagani</i> Baker	wind	LC	FS
5	<i>C. herrei</i> (F.M.Leight.) R.A.Dyer	wind	LC	FS, BL
6	<i>C. inaequalis</i> O'Brien	wind	LC	BL, FS
7	<i>C. junodii</i> P.Beauv.	wind	LC	FS, DS
8	<i>C. labiatus</i> R.A.Dyer	wind	LC	FS, BL
9	<i>C. montanus</i> R.A.Dyer	wind	LC	FS, BL
	Haemanthus L. (3 species)			
10	<i>H. albiflos</i> Jacq.	bird	LC	FS, DS
11	<i>H. humilis</i> Jacq. subsp. <i>humilis</i>	bird	LC	FS, DS
12	<i>H. pauculifolius</i> Snijman & A.E.van Wyk	bird	LC	FS, DS
	ASPHODELACEAE (5 genera, 50 taxa, 47 species)			
	Aloe L. (18 species)			
13	<i>A. arborescens</i> Mill. subsp. <i>mzimnyi</i> Van Jaarsv. & A.E.van Wyk	wind	LC	FS, BL
14	<i>A. catengiana</i> Reynolds	wind	LC	FS, BL
15	<i>A. challsii</i> Van Jaarsv. & A.E.van Wyk	wind	LC	FS, BL
16	<i>A. corallina</i> I.Verd.	wind	LC	FS
17	<i>A. dabenorisana</i> Van Jaarsv.	wind	LC	BL
18	<i>A. dewinteri</i> Giess	wind	LC	FS
19	<i>A. haemanthifolia</i> A.Berger & Marloth	wind	LC	FS
20	<i>A. hardyi</i> Glen	wind	LC	FS
21	<i>A. kouebokkeveldensis</i> Van Jaarsv. & A.B.Low	wind	LC	FS
22	<i>A. meyeri</i> Van Jaarsv.	wind	LC	FS, BL
23	<i>A. mutabilis</i> Pillans	wind	LC	FS
24	<i>A. nubigena</i> Groenew.	wind	LC	FS, BL
25	<i>A. omavandae</i> Van Jaarsv.	wind	LC	FS, BL
26	<i>A. pavelkae</i> Van Jaarsv., Swanepoel, A.E.van Wyk & Lavranos	wind	LC	BL
27	<i>A. pictifolia</i> D.S.Hardy	wind	LC	FS, BL, DS
28	<i>A. reynoldsii</i> Letty	wind	LC	FS, BL
29	<i>A. soutpansbergensis</i> I.Verd.	wind	LC	FS, BL
30	<i>A. thompsoniae</i> Groenew.	wind	LC	FS, BL, DS



TABLE 10.1 (continued)—Check list of obligate and near-obligate cremnophilous taxa (220 taxa, 203 species)

No.	Taxon	Rich flowering	Reduction in armament	Cliff habitat
		*** = rich ** = exposed * = insignificant	*** = margin without teeth ** = margin with smaller teeth * = no significant change, same as other non-cremnophytes	C = coastal R = river E = escarpment M = mountain I = inselberg
	FERNS			
	POLYPODIACEAE (1 species)			
	<i>Pyrosia</i> Mirb. (1 species)			
1	<i>P. schimperiana</i> (Mett. ex Kuhn) Alston	*	*	R
	MONOCOTYLEDONS (3 families, 79 taxa, 76 species)			
	AMARYLLIDACEAE (2 genera, 11 species)			
	<i>Cyrtanthus</i> Aiton (8 species)			
2	<i>C. falcatus</i> R.A.Dyer	**	*	E
3	<i>C. flammosus</i> Snijman & Van Jaarsv.	***	*	R, M
4	<i>C. flanaganii</i> Baker	**	*	E
5	<i>C. herrei</i> (F.M.Leight.) R.A.Dyer	**	*	E, M
6	<i>C. inaequalis</i> O'Brien	**	*	R
7	<i>C. junodii</i> P.Beauv.	**	*	E
8	<i>C. labiatus</i> R.A.Dyer	**	*	R, M
9	<i>C. montanus</i> R.A.Dyer	**	*	R, M
	<i>Haemanthus</i> L. (3 species)			
10	<i>H. albiflos</i> Jacq.	**	*	R, C
11	<i>H. humilis</i> Jacq. subsp. <i>humilis</i>	**	*	E, M
12	<i>H. paucifolius</i> Snijman & A.E.van Wyk	**	*	E
	ASPHODELACEAE (5 genera, 50 taxa, 47 species)			
	<i>Aloe</i> L. (18 species)			
13	<i>A. arborescens</i> Mill. subsp. <i>mzimyati</i> Van Jaarsv. & A.E.van Wyk	**	*	E, R, M
14	<i>A. catengiana</i> Reynolds	**	*	E
15	<i>A. challisii</i> Van Jaarsv. & A.E.van Wyk	**	*	E
16	<i>A. corallina</i> I.Verd.	**	***	R
17	<i>A. dabenorisana</i> Van Jaarsv.	**	**	R, I
18	<i>A. dewinteri</i> Giess	**	**	R, E
19	<i>A. haemanthifolia</i> A.Berger & Marloth	**	***	M
20	<i>A. hardyi</i> Glen	**	*	R
21	<i>A. kouebokkeveldensis</i> Van Jaarsv. & A.B.Low	**	*	M
22	<i>A. meyeri</i> Van Jaarsv.	**	**	M, R
23	<i>A. mutabilis</i> Pillans	**	*	M, R
24	<i>A. nubigena</i> Groenew.	**	***	E
25	<i>A. omavandae</i> Van Jaarsv.	**	**	E
26	<i>A. pavelkae</i> Van Jaarsv., Swanepoel, A.E.van Wyk & Lavranos	**	**	R, M
27	<i>A. pictifolia</i> D.S.Hardy	**	**	R, M
28	<i>A. reynoldsii</i> Letty	**	*	R
29	<i>A. soutpansbergensis</i> I.Verd.	**	*	M, I
30	<i>A. thompsoniae</i> Groenew.	**	*	E, M



TABLE 10.1 (continued)—Check list of obligate and near-obligate cremnophilous taxa (220 taxa, 203 species)

No.	Taxon	Occurrence	Endemism	Windows
		W = widespread We = widespread but endemic to its vegetation region R = restricted	* = endemic Bots = Botswana Les = Lesotho Moz = Mozambique Nam = Namibia RSA = South Africa Swaz = Swaziland	Lm = on leaf margin Mw = micro-windows O = other
	FERNS			
	POLYPODIACEAE (1 species)			
	<i>Pyrrhosia</i> Mirb. (1 species)			
1	<i>P. schimperiana</i> (Mett. ex Kuhn) Alston	W	RSA	
	MONOCOTYLEDONS (3 families, 79 taxa, 76 species)			
	AMARYLLIDACEAE (2 genera, 11 species)			
	<i>Cyrtanthus</i> Aiton (8 species)			
2	<i>C. falcatus</i> R.A.Dyer	W	RSA*	
3	<i>C. flammosus</i> Snijman & Van Jaarsv.	R	RSA*	
4	<i>C. flanagani</i> Baker	We	RSA*	
5	<i>C. herrei</i> (F.M.Leight.) R.A.Dyer	We	RSA, Nam	
6	<i>C. inaequalis</i> O'Brien	We	RSA*	
7	<i>C. junodii</i> P.Beauv.	R	RSA*	
8	<i>C. labiatus</i> R.A.Dyer	We	RSA*	
9	<i>C. montanus</i> R.A.Dyer	We	RSA*	
	<i>Haemanthus</i> L. (3 species)			
10	<i>H. albiflos</i> Jacq.	We	RSA*	
11	<i>H. humilis</i> Jacq. subsp. <i>humilis</i>	W	RSA*	
12	<i>H. paucifolius</i> Snijman & A.E.van Wyk	We	RSA*	
	ASPHODELACEAE (5 genera, 50 taxa, 47 species)			
	<i>Aloe</i> L. (18 species)			
13	<i>A. arborescens</i> Mill. subsp. <i>mzimnyi</i> Van Jaarsv. & A.E.van Wyk	R	RSA*	
14	<i>A. catengiana</i> Reynolds	We	Nam	
15	<i>A. challisii</i> Van Jaarsv. & A.E.van Wyk	R	RSA*	Lm
16	<i>A. corallina</i> I.Verd.	We	Nam	
17	<i>A. dabenorisana</i> Van Jaarsv.	We	RSA*	
18	<i>A. dewinteri</i> Giess	We	Nam*	
19	<i>A. haemanthifolia</i> A.Berger & Marloth	We	RSA*	
20	<i>A. hardyi</i> Glen	R	RSA*	
21	<i>A. kouebokkeveldensis</i> Van Jaarsv. & A.B.Low	R	RSA*	
22	<i>A. meyeri</i> Van Jaarsv.	We	RSA, Nam	
23	<i>A. mutabilis</i> Pillans	We	RSA	
24	<i>A. nubigena</i> Groenew.	We	RSA*	Lm
25	<i>A. omavandae</i> Van Jaarsv.	R	Nam*	
26	<i>A. pavelkae</i> Van Jaarsv., Swanepoel, A.E.van Wyk & Lavranos	R	Nam*	
27	<i>A. pictifolia</i> D.S.Hardy	R	RSA*	
28	<i>A. reynoldsii</i> Letty	R	RSA*	
29	<i>A. soutpansbergensis</i> I.Verd.	R	RSA*	Lm
30	<i>A. thompsoniae</i> Groenew.	R	RSA*	



TABLE 10.1 (continued)—Check list of obligate and near-obligate cremnophilous taxa (220 taxa, 203 species)

No.	Taxon	Cremonophilous growth form	Degree of cliff occupation	Weight class
		See 9.1.2 for explanation of the symbols below	*** = strictly obligate cremnophyte, displaying cliff-adapted features ** = obligate cremnophyte * = predominantly on cliffs (80%)	light = < 50 g medium = 51–500 g heavy = >500 g
	Bulbine Wolf (10 taxa)			
31	<i>B. cremonophila</i> Van Jaarsv.	A:S:Lper:R:C:Lp (eg)	***	light
32	<i>B. latifolia</i> (L.f.) Schult. & Schult.f. var. <i>curvata</i> Van Jaarsv.	E:F:P:R:So:Lp (eg)	***	medium
33	<i>B. meiringii</i> Van Jaarsv.	A:S:Lper:R:C:Lp (eg) (vb)	***	light
34	<i>B. natalensis</i> Baker	A:S:Lper:R:So:La	**	medium
35	<i>B. pendens</i> G.Will. & Baijnath	A:S:Lar:D:(vb) (eg)	***	light
36	<i>B. ramosa</i> Van Jaarsv.	A:S:Lper:R:C:La (vb)	**	light–medium
37	<i>B. retinens</i> Van Jaarsv. & S.A.Hammer	A:S:Lper:R:C:La (vb)	**	light–medium
38	<i>B. rupicola</i> G.Will.	A:S:Lper:R:C:La (vb)	**	light
39	<i>B. suurbergensis</i> Van Jaarsv. & A.E.van Wyk	E:F:P:R:C:Ar (vb)	***	medium
40	<i>B. thomasiae</i> Van Jaarsv.	A:S:Lper:R:C:Lp (eg) (vb)	***	light–medium
	Gasteria Duval (9 taxa)			
41	<i>G. batesiana</i> G.D.Rowley var. <i>batesiana</i>	A:S:Lper:R:C:La (vb)	***	medium
42	<i>G. batesiana</i> G.D.Rowley var. <i>dolomitica</i> Van Jaarsv. & A.E.van Wyk	A:S:Lper:R:C:La (vb)	***	medium
43	<i>G. croucheri</i> (Hook.f.) Baker subsp. <i>pendulifolia</i> (Van Jaarsv.) Zonn.	A:S:Lper:R:C:Lp (vb) (eg)	***	medium-heavy
44	<i>G. doreniae</i> Van Jaarsv. & A.E.van Wyk	A:S:Lper:R:C:La (vb)	**	light–medium
45	<i>G. glauca</i> Van Jaarsv.	A:S:Lper:R:C:La (vb) (rd) (r)	***	light–medium
46	<i>G. glomerata</i> Van Jaarsv.	A:S:Lper:R:C:La (vb) (rd) (r)	***	light–medium
47	<i>G. pillansii</i> Kensit var. <i>ernesti-ruschii</i> (Dinter & Von Poelln.) Van Jaarsv.	A:S:Lper:R:C:La (vb)	*	light–medium
48	<i>G. rawlinsonii</i> Oberm.	E:F:P:R:C:Rls (eg)	***	medium-heavy
49	<i>G. tukhelensis</i> Van Jaarsv.	A:S:Lper:R:C:La (vb)	**	medium-heavy
	Haworthia Duval (12 taxa)			
50	<i>H. angustifolia</i> Haw. var. <i>baylissii</i> (C.L.Scott) M.B.Bayer	A:S:Lper:R:C:La (vb)	***	light
51	<i>H. attenuata</i> (Haw.) Haw. var. <i>attenuata</i>	A:S:Lper:R:C:La (vb)	**	light–medium
52	<i>H. cymbiformis</i> (Haw.) Duval var. <i>ramosa</i> (G.G.Sm.) M.B.Bayer	A:S:Lper:R:C:La (vb)	**	light–medium
53	<i>H. cymbiformis</i> (Haw.) Duval var. <i>setulifera</i> (Poelln.) M.B.Bayer	A:S:Lper:R:C:La (vb)	**	light–medium
54	<i>H. glabrata</i> (Salm-Dyck) Baker	A:S:Lper:R:C:La (vb)	**	light–medium
55	<i>H. gracilis</i> Poelln. var. <i>picturata</i> M.B.Bayer	A:S:Lper:R:C:La (vb)	***	light–medium
56	<i>H. marumiana</i> Uitewaal var. <i>batesiana</i> (Uitewaal) M.B.Bayer	A:S:Lper:R:C:La (vb)	***	light–medium
57	<i>H. marumiana</i> Uitewaal var. <i>marumiana</i>	A:S:Lper:R:C:La (vb)	**	light–medium
58	<i>H. mirabilis</i> (Haw.) Haw. var. <i>consanguinea</i> M.B.Bayer	A:S:Lper:R:C:La (vb)	**	light–medium
59	<i>H. scabra</i> Haw. var. <i>starkiana</i> (Poelln.) M.B.Bayer	A:S:Lper:R:C:La (vb)	**	medium
60	<i>H. turgida</i> Haw. var. <i>turgida</i>	A:S:Lper:R:C:La (vb)	**	light–medium
61	<i>H. zantmeriana</i> Poelln.	A:S:Lper:R:C:La (vb)	**	light–medium
	Trachyandra Kunth (1 species)			
62	<i>T. tabularis</i> (Baker) Oberm.	A:S:Lper:R:C:Lp	***	medium



TABLE 10.1 (continued)—Check list of obligate and near-obligate cremnophilous taxa (220 taxa, 203 species)

No.	Taxon	Vegetative dispersal backup	Geology	Aspect
	Bulbine Wolf (10 taxa)			
31	<i>B. cremnophila</i> Van Jaarsv.	dividing or proliferating clusters	sandstone	N, S, E, W
32	<i>B. latifolia</i> (L.f.) Schult. & Schult.f. var. <i>curvata</i> Van Jaarsv.	solitary	sandstone	N, S, E, W
33	<i>B. meiringii</i> Van Jaarsv.	dividing or proliferating clusters	sandstone	S
34	<i>B. natalensis</i> Baker	solitary	sandstone, mudstone	S
35	<i>B. pendens</i> G.Will. & Baijnath	dividing or proliferating clusters	quartz	S, E
36	<i>B. ramosa</i> Van Jaarsv.	dividing or proliferating clusters	sandstone	S
37	<i>B. retinens</i> Van Jaarsv. & S.A.Hammer	dividing or proliferating clusters	sandstone	S, W, E, N
38	<i>B. rupicola</i> G.Will.	dividing or proliferating clusters	sandstone	S, W
39	<i>B. suurbergensis</i> Van Jaarsv. & A.E.van Wyk	dividing or proliferating clusters	sandstone	S, E, W
40	<i>B. thomasiae</i> Van Jaarsv.	dividing or proliferating clusters	mudstone	S
	Gasteria Duval (9 taxa)			
41	<i>G. batesiana</i> G.D.Rowley var. <i>batesiana</i>	proliferating clusters and leaf stolons	sandstone	S
42	<i>G. batesiana</i> G.D.Rowley var. <i>dolomitica</i> Van Jaarsv. & A.E.van Wyk	proliferating clusters and leaf stolons	dolomite	S
43	<i>G. croucheri</i> (Hook.f.) Baker subsp. <i>pendulifolia</i> (Van Jaarsv.) Zonn.	proliferating clusters and leaf stolons	sandstone	S
44	<i>G. doreeniae</i> Van Jaarsv. & A.E.van Wyk	proliferating clusters and leaf stolons	sandstone	S, W
45	<i>G. glauca</i> Van Jaarsv.	proliferating clusters and leaf stolons	sandstone	S, E
46	<i>G. glomerata</i> Van Jaarsv.	proliferating clusters and leaf stolons	sandstone	S
47	<i>G. pillansii</i> Kensit var. <i>ernesti-ruschii</i> (Dinter & Von Poelln.) Van Jaarsv.	proliferating clusters and leaf stolons	sandstone	S
48	<i>G. rawlinsonii</i> Oberm.	dividing or proliferating clusters	sandstone	S
49	<i>G. tukhelensis</i> Van Jaarsv.	proliferating clusters and leaf stolons	mudstone	S
	Haworthia Duval (12 taxa)			
50	<i>H. angustifolia</i> Haw. var. <i>baylissii</i> (C.L.Scott) M.B.Bayer	dividing or proliferating clusters	sandstone	S
51	<i>H. attenuata</i> (Haw.) Haw. var. <i>attenuata</i>	dividing or proliferating clusters	Enon Conglomerate	W, E
52	<i>H. cymbiformis</i> (Haw.) Duval var. <i>ramosa</i> (G.G.Sm.) M.B.Bayer	dividing or proliferating clusters	mudstone	S
53	<i>H. cymbiformis</i> (Haw.) Duval var. <i>setulifera</i> (Poelln.) M.B.Bayer	dividing or proliferating clusters	mudstone	S
54	<i>H. glabrata</i> (Salm-Dyck) Baker	dividing or proliferating clusters	shale	N
55	<i>H. gracilis</i> Poelln. var. <i>picturata</i> M.B.Bayer	dividing or proliferating clusters	sandstone	S
56	<i>H. marumiana</i> Uitewaal var. <i>batesiana</i> (Uitewaal) M.B.Bayer	dividing or proliferating clusters	shale	S
57	<i>H. marumiana</i> Uitewaal var. <i>marumiana</i>	dividing or proliferating clusters	sandstone	S
58	<i>H. mirabilis</i> (Haw.) Haw. var. <i>consanguinea</i> M.B.Bayer	dividing or proliferating clusters	sandstone	S
59	<i>H. scabra</i> Haw. var. <i>starkiana</i> (Poelln.) M.B.Bayer	dividing or proliferating clusters	sandstone	N, E
60	<i>H. turgida</i> Haw. var. <i>turgida</i>	dividing or proliferating clusters	sandstone	S
61	<i>H. zantmeriana</i> Poelln.	dividing or proliferating clusters	sandstone	S
	Trachyandra Kunth (1 species)			
62	<i>T. tabularis</i> (Baker) Oberm.	dividing or proliferating clusters	sandstone	S



TABLE 10.1 (continued)—Check list of obligate and near-obligate cremnophilous taxa (220 taxa, 203 species)

No.	Taxon	Altitude (m)	Rainfall (mm per annum)	Rainfall seasonality	Deciduousness
				S = summer W = winter W/S = any time of year	E = evergreen SA = summer-aestivating SD = summer-deciduous WD = winter-deciduous
Bulbine Wolf (10 taxa)					
31	<i>B. cremnophila</i> Van Jaarsv.	400–1000	400–500	W/S	E
32	<i>B. latifolia</i> (L.f.) Schult. & Schult.f. var. <i>curvata</i> Van Jaarsv.	250–500	400–500	W/S	E
33	<i>B. meiringii</i> Van Jaarsv.	500–800	200–300	W/S	E
34	<i>B. natalensis</i> Baker	35–600	400–500	W/S	E
35	<i>B. pendens</i> G.Will. & Baijnath	300–800	75–150	W	SD
36	<i>B. ramosa</i> Van Jaarsv.	400–600	200–300	W/S	E
37	<i>B. retinens</i> Van Jaarsv. & S.A.Hammer	500–800	300–400	W/S	E
38	<i>B. rupicola</i> G.Will.	500–800	300–400	W/S	E
39	<i>B. suurbergensis</i> Van Jaarsv. & A.E.van Wyk	400–600	400–500	W/S	E
40	<i>B. thomasiae</i> Van Jaarsv.	200–800	500–600	S	E
Gasteria Duval (9 taxa)					
41	<i>G. batesiana</i> G.D.Rowley var. <i>batesiana</i>	300–800	500–600	S	E
42	<i>G. batesiana</i> G.D.Rowley var. <i>dolomitica</i> Van Jaarsv. & A.E.van Wyk	450–600	400–600	S	E
43	<i>G. croucheri</i> (Hook.f.) Baker subsp. <i>pendulifolia</i> (Van Jaarsv.) Zonn.	100–400	1000–1250	S	E
44	<i>G. doreniae</i> Van Jaarsv. & A.E.van Wyk	350–500	400–500	W/S	E
45	<i>G. glauca</i> Van Jaarsv.	400–800	500–600	W/S	E
46	<i>G. glomerata</i> Van Jaarsv.	400–700	300–400	W/S	E
47	<i>G. pillansii</i> Kensit var. <i>ernesti-ruschii</i> (Dinter & Von Poelln.) Van Jaarsv.	400–600	150–200	W	E
48	<i>G. rawlinsonii</i> Oberm.	300–700	200–300	W/S	E
49	<i>G. tukhelensis</i> Van Jaarsv.	350–400	500–700	S	E
Haworthia Duval (12 taxa)					
50	<i>H. angustifolia</i> Haw. var. <i>baylissii</i> (C.L.Scott) M.B.Bayer	400–500	400–500	W/S	E
51	<i>H. attenuata</i> (Haw.) Haw. var. <i>attenuata</i>	400	300–400	S	E
52	<i>H. cymbiformis</i> (Haw.) Duval var. <i>ramosa</i> (G.G.Sm.) M.B.Bayer	400–500	250–400	W/S	E
53	<i>H. cymbiformis</i> (Haw.) Duval var. <i>setulifera</i> (Poelln.) M.B.Bayer	400–1500	800–1250	W/S	E
54	<i>H. glabrata</i> (Salm-Dyck) Baker	500–1000	800–1250	S	E
55	<i>H. gracilis</i> Poelln. var. <i>picturata</i> M.B.Bayer	400–1000	300–400	W/S	E
56	<i>H. marumiana</i> Uitewaal var. <i>batesiana</i> (Uitewaal) M.B.Bayer	500–1500	300–400	W/S	E
57	<i>H. marumiana</i> Uitewaal var. <i>marumiana</i>	300–1000	300–400	W/S	E
58	<i>H. mirabilis</i> (Haw.) Haw. var. <i>consanguinea</i> M.B.Bayer	1000–1500	600–800	W/S	E
59	<i>H. scabra</i> Haw. var. <i>starkiana</i> (Poelln.) M.B.Bayer	100–1500	200–300	W/S	E
60	<i>H. turgida</i> Haw. var. <i>turgida</i>	500–1500	250–500	W/S	E
61	<i>H. zantmeriana</i> Poelln.	600–1500	250–400	W/S	E
Trachyandra Kunth (1 species)					
62	<i>T. tabularis</i> (Baker) Oberm.	500–900	2000–3000	W	E



TABLE 10.1 (continued)—Check list of obligate and near-obligate cremnophilous taxa (220 taxa, 203 species)

No.	Taxon	Fog	Biomes	Pollination
		*** = regular fog ** = occasional fog * = little fog – = no fog	IOCB = Indian Ocean Coastal Belt	
	Bulbine Wolf (10 taxa)			
31	<i>B. cremnophila</i> Van Jaarsv.	–	Albany Thicket	insect
32	<i>B. latifolia</i> (L.f.) Schult. & Schult.f. var. <i>curvata</i> Van Jaarsv.	–	Albany Thicket	insect
33	<i>B. meiringii</i> Van Jaarsv.	–	Albany Thicket	insect
34	<i>B. natalensis</i> Baker	–	Succulent Karoo	insect
35	<i>B. pendens</i> G.Will. & Baijnath	**	Succulent Karoo	insect
36	<i>B. ramosa</i> Van Jaarsv.	–	Succulent Karoo	insect
37	<i>B. retinens</i> Van Jaarsv. & S.A.Hammer	–	Albany Thicket	insect
38	<i>B. rupicola</i> G.Will.	–	Albany Thicket	insect
39	<i>B. suurbergensis</i> Van Jaarsv. & A.E.van Wyk	–	Albany Thicket	insect
40	<i>B. thomasiae</i> Van Jaarsv.	–	Savanna	insect
	Gasteria Duval (9 taxa)			
41	<i>G. batesiana</i> G.D.Rowley var. <i>batesiana</i>	–	Savanna	bird
42	<i>G. batesiana</i> G.D.Rowley var. <i>dolomitica</i> Van Jaarsv. & A.E.van Wyk	–	Savanna	bird
43	<i>G. croucheri</i> (Hook.f.) Baker subsp. <i>pendulifolia</i> (Van Jaarsv.) Zonn.	–	IOCB	bird
44	<i>G. doreniae</i> Van Jaarsv. & A.E.van Wyk	–	Albany Thicket	bird
45	<i>G. glauca</i> Van Jaarsv.	–	Albany Thicket	bird
46	<i>G. glomerata</i> Van Jaarsv.	–	Albany Thicket	bird
47	<i>G. pillansii</i> Kensit var. <i>ernesti-ruschii</i> (Dinter & Von Poelln.) Van Jaarsv.	****	Succulent Karoo	bird
48	<i>G. rawlinsonii</i> Oberm.	–	Albany Thicket	bird
49	<i>G. tukhelensis</i> Van Jaarsv.	–	Savanna	bird
	Haworthia Duval (12 taxa)			
50	<i>H. angustifolia</i> Haw. var. <i>baylissii</i> (C.L.Scott) M.B.Bayer	–	Albany Thicket	insect
51	<i>H. attenuata</i> (Haw.) Haw. var. <i>attenuata</i>	–	Albany Thicket	insect
52	<i>H. cymbiformis</i> (Haw.) Duval var. <i>ramosa</i> (G.G.Sm.) M.B.Bayer	–	Albany Thicket	insect
53	<i>H. cymbiformis</i> (Haw.) Duval var. <i>setulifera</i> (Poelln.) M.B.Bayer	–	Savanna	insect
54	<i>H. glabrata</i> (Salm-Dyck) Baker	–	Savanna	insect
55	<i>H. gracilis</i> Poelln. var. <i>picturata</i> M.B.Bayer	–	Albany Thicket	insect
56	<i>H. marumiana</i> Uitewaal var. <i>batesiana</i> (Uitewaal) M.B.Bayer	–	Albany Thicket	insect
57	<i>H. marumiana</i> Uitewaal var. <i>marumiana</i>	–	Albany Thicket	insect
58	<i>H. mirabilis</i> (Haw.) Haw. var. <i>consanguinea</i> M.B.Bayer	–	Fynbos	insect
59	<i>H. scabra</i> Haw. var. <i>starkiana</i> (Poelln.) M.B.Bayer	–	Succulent Karoo	insect
60	<i>H. turgida</i> Haw. var. <i>turgida</i>	–	Albany Thicket	insect
61	<i>H. zantmeriana</i> Poelln.	–	Albany Thicket	insect
	Trachyandra Kunth (1 species)			
62	<i>T. tabularis</i> (Baker) Oberm.	**	Fynbos	insect



TABLE 10.1 (continued)—Check list of obligate and near-obligate cremnophilous taxa (220 taxa, 203 species)

No.	Taxon	Seed dispersal	Conservation status	Light requirements
			LC = Least Concern NT = Not Threatened VU = Vulnerable	BL = bright light DS = dappled shade FS = full sun
	Bulbine Wolf (10 taxa)			
31	<i>B. cremnophila</i> Van Jaarsv.	wind	LC	BL, DS
32	<i>B. latifolia</i> (L.f.) Schult. & Schult.f. var. <i>curvata</i> Van Jaarsv.	wind	LC	FS, BL
33	<i>B. meiringii</i> Van Jaarsv.	wind	LC	FS, BL
34	<i>B. natalensis</i> Baker	wind	LC	BL, DS
35	<i>B. pendens</i> G.Will. & Baijnath	wind	LC	BL, DS
36	<i>B. ramosa</i> Van Jaarsv.	wind	LC	FS, BL
37	<i>B. retinens</i> Van Jaarsv. & S.A.Hammer	wind	LC	FS, BL
38	<i>B. rupicola</i> G.Will.	wind	LC	BL, DS
39	<i>B. suurbergensis</i> Van Jaarsv. & A.E.van Wyk	wind	LC	BL, DS
40	<i>B. thomasiae</i> Van Jaarsv.	wind	LC	BL, DS
	Gasteria Duval (9 taxa)			
41	<i>G. batesiana</i> G.D.Rowley var. <i>batesiana</i>	wind	NT	BL, DS
42	<i>G. batesiana</i> G.D.Rowley var. <i>dolomitica</i> Van Jaarsv. & A.E.van Wyk	wind	VU	BL, DS
43	<i>G. croucheri</i> (Hook.f.) Baker subsp. <i>pendulifolia</i> (Van Jaarsv.) Zonn.	wind	VU	BL, DS
44	<i>G. doreeniae</i> Van Jaarsv. & A.E.van Wyk	wind	LC	BL, DS
45	<i>G. glauca</i> Van Jaarsv.	wind	LC	BL, DS
46	<i>G. glomerata</i> Van Jaarsv.	wind	LC	BL, DS
47	<i>G. pillansii</i> Kensit var. <i>ernesti-ruschii</i> (Dinter & Von Poelln.) Van Jaarsv.	wind	LC	BL, DS
48	<i>G. rawlinsonii</i> Oberm.	wind	LC	BL, DS
49	<i>G. tukhelensis</i> Van Jaarsv.	wind	LC	BL, DS
	Haworthia Duval (12 taxa)			
50	<i>H. angustifolia</i> Haw. var. <i>baylissii</i> (C.L.Scott) M.B.Bayer	wind	LC	BL, DS
51	<i>H. attenuata</i> (Haw.) Haw. var. <i>attenuata</i>	wind	LC	FS
52	<i>H. cymbiformis</i> (Haw.) Duval var. <i>ramosa</i> (G.G.Sm.) M.B.Bayer	wind	LC	BL, DS
53	<i>H. cymbiformis</i> (Haw.) Duval var. <i>setulifera</i> (Poelln.) M.B.Bayer	wind	LC	BL, DS
54	<i>H. glabrata</i> (Salm-Dyck) Baker	wind	LC	FS
55	<i>H. gracilis</i> Poelln. var. <i>picturata</i> M.B.Bayer	wind	LC	BL, DS
56	<i>H. marumiana</i> Uitewaal var. <i>batesiana</i> (Uitewaal) M.B.Bayer	wind	LC	BL, DS
57	<i>H. marumiana</i> Uitewaal var. <i>marumiana</i>	wind	LC	BL, DS
58	<i>H. mirabilis</i> (Haw.) Haw. var. <i>consanguinea</i> M.B.Bayer	wind	LC	BL, DS
59	<i>H. scabra</i> Haw. var. <i>starkiana</i> (Poelln.) M.B.Bayer	wind	LC	FS
60	<i>H. turgida</i> Haw. var. <i>turgida</i>	wind	LC	FS
61	<i>H. zantmeriana</i> Poelln.	wind	LC	BL, DS
	Trachyandra Kunth (1 species)			
62	<i>T. tabularis</i> (Baker) Oberm.	wind	LC	FS, BL, DS



TABLE 10.1 (continued)—Check list of obligate and near-obligate cremnophilous taxa (220 taxa, 203 species)

No.	Taxon	Rich flowering	Reduction in armament	Cliff habitat
		*** = rich ** = exposed * = insignificant	*** = margin without teeth ** = margin with smaller teeth * = no significant change, same as other non-cremnophytes	C = coastal R = river E = escarpment M = mountain I = inselberg
	Bulbine Wolf (10 taxa)			
31	<i>B. cremnophila</i> Van Jaarsv.	**	*	R, M
32	<i>B. latifolia</i> (L.f.) Schult. & Schult.f. var. <i>curvata</i> Van Jaarsv.	**	*	R, M
33	<i>B. meiringii</i> Van Jaarsv.	**	*	R, M
34	<i>B. natalensis</i> Baker	**	*	R, M
35	<i>B. pendens</i> G.Will. & Baijnath	**	*	R, M
36	<i>B. ramosa</i> Van Jaarsv.	**	*	R, M
37	<i>B. retinens</i> Van Jaarsv. & S.A.Hammer	**	*	R, M
38	<i>B. rupicola</i> G.Will.	**	*	R, M
39	<i>B. suurbergensis</i> Van Jaarsv. & A.E.van Wyk	**	*	R, M
40	<i>B. thomasiae</i> Van Jaarsv.	**	*	R
	Gasteria Duval (9 taxa)			
41	<i>G. batesiana</i> G.D.Rowley var. <i>batesiana</i>	**	*	R
42	<i>G. batesiana</i> G.D.Rowley var. <i>dolomitica</i> Van Jaarsv. & A.E.van Wyk	**	*	R
43	<i>G. croucheri</i> (Hook.f.) Baker subsp. <i>pendulifolia</i> (Van Jaarsv.) Zonn.	**	*	R
44	<i>G. doreeniae</i> Van Jaarsv. & A.E.van Wyk	**	*	R, M
45	<i>G. glauca</i> Van Jaarsv.	***	*	R, M
46	<i>G. glomerata</i> Van Jaarsv.	***	*	R, M
47	<i>G. pillansii</i> Kensit var. <i>ernesti-ruschii</i> (Dinter & Von Poelln.) Van Jaarsv.	**	*	R, M
48	<i>G. rawlinsonii</i> Oberm.	**	*	R, M
49	<i>G. tukhelensis</i> Van Jaarsv.	**	*	R
	Haworthia Duval (12 taxa)			
50	<i>H. angustifolia</i> Haw. var. <i>baylissii</i> (C.L.Scott) M.B.Bayer	*	*	R, M
51	<i>H. attenuata</i> (Haw.) Haw. var. <i>attenuata</i>	*	*	R
52	<i>H. cymbiformis</i> (Haw.) Duval var. <i>ramosa</i> (G.G.Sm.) M.B.Bayer	*	*	R
53	<i>H. cymbiformis</i> (Haw.) Duval var. <i>setulifera</i> (Poelln.) M.B.Bayer	*	*	R
54	<i>H. glabrata</i> (Salm-Dyck) Baker	*	*	R
55	<i>H. gracilis</i> Poelln. var. <i>picturata</i> M.B.Bayer	*	*	R, M
56	<i>H. marumiana</i> Uitewaal var. <i>batesiana</i> (Uitewaal) M.B.Bayer	*	***	E
57	<i>H. marumiana</i> Uitewaal var. <i>marumiana</i>	*	*	R, M
58	<i>H. mirabilis</i> (Haw.) Haw. var. <i>consanguinea</i> M.B.Bayer	*	*	R, M
59	<i>H. scabra</i> Haw. var. <i>starkiana</i> (Poelln.) M.B.Bayer	*	*	R, M
60	<i>H. turgida</i> Haw. var. <i>turgida</i>	*	*	R, M
61	<i>H. zantmeriana</i> Poelln.	*	*	R, M
	Trachyandra Kunth (1 species)			
62	<i>T. tabularis</i> (Baker) Oberm.	*	*	M



TABLE 10.1 (continued)—Check list of obligate and near-obligate cremnophilous taxa (220 taxa, 203 species)

No.	Taxon	Occurrence	Endemism	Windows
		W = widespread We = widespread but endemic to its vegetation region R = restricted	* = endemic Bots = Botswana Les = Lesotho Moz = Mozambique Nam = Namibia RSA = South Africa Swaz = Swaziland	Lm = on leaf margin Mw = micro-windows O = other
	Bulbine Wolf (10 taxa)			
31	<i>B. cremnophila</i> Van Jaarsv.	R	RSA*	
32	<i>B. latifolia</i> (L.f.) Schult. & Schult.f. var. <i>curvata</i> Van Jaarsv.	R	RSA*	
33	<i>B. meiringii</i> Van Jaarsv.	R	RSA*	O
34	<i>B. natalensis</i> Baker	We	RSA*	O
35	<i>B. pendens</i> G.Will. & Baijnath	R	RSA*	O
36	<i>B. ramosa</i> Van Jaarsv.	R	RSA*	O
37	<i>B. retinens</i> Van Jaarsv. & S.A.Hammer	R	RSA*	O
38	<i>B. rupicola</i> G.Will.	We	RSA*	O
39	<i>B. suurbergensis</i> Van Jaarsv. & A.E.van Wyk	R	RSA*	O
40	<i>B. thomasiae</i> Van Jaarsv.	R	RSA*	O
	Gasteria Duval (9 taxa)			
41	<i>G. batesiana</i> G.D.Rowley var. <i>batesiana</i>	We	RSA, Swaz	
42	<i>G. batesiana</i> G.D.Rowley var. <i>dolomitica</i> Van Jaarsv. & A.E.van Wyk	R	RSA*	
43	<i>G. croucheri</i> (Hook.f.) Baker subsp. <i>pendulifolia</i> (Van Jaarsv.) Zonn.	R	RSA*	
44	<i>G. doreniae</i> Van Jaarsv. & A.E.van Wyk	R	RSA*	
45	<i>G. glauca</i> Van Jaarsv.	R	RSA*	
46	<i>G. glomerata</i> Van Jaarsv.	R	RSA*	
47	<i>G. pillansii</i> Kensit var. <i>ernesti-ruschii</i> (Dinter & Von Poelln.) Van Jaarsv.	R	RSA, Nam	
48	<i>G. rawlinsonii</i> Oberm.	We	RSA*	
49	<i>G. tukhelensis</i> Van Jaarsv.	R	RSA*	
	Haworthia Duval (12 taxa)			
50	<i>H. angustifolia</i> Haw. var. <i>baylissii</i> (C.L.Scott) M.B.Bayer	R	RSA*	
51	<i>H. attenuata</i> (Haw.) Haw. var. <i>attenuata</i>	R	RSA*	
52	<i>H. cymbiformis</i> (Haw.) Duval var. <i>ramosa</i> (G.G.Sm.) M.B.Bayer	R	RSA*	Mw, O
53	<i>H. cymbiformis</i> (Haw.) Duval var. <i>setulifera</i> (Poelln.) M.B.Bayer	We	RSA*	Mw, O
54	<i>H. glabrata</i> (Salm-Dyck) Baker	R	RSA*	
55	<i>H. gracilis</i> Poelln. var. <i>picturata</i> M.B.Bayer	R	RSA*	Mw, O
56	<i>H. marumiana</i> Uitewaal var. <i>batesiana</i> (Uitewaal) M.B.Bayer	We	RSA*	O
57	<i>H. marumiana</i> Uitewaal var. <i>marumiana</i>	We	RSA*	
58	<i>H. mirabilis</i> (Haw.) Haw. var. <i>consanguinea</i> M.B.Bayer	We	RSA*	Mw, O
59	<i>H. scabra</i> Haw. var. <i>starkiana</i> (Poelln.) M.B.Bayer	We	RSA*	
60	<i>H. turgida</i> Haw. var. <i>turgida</i>	We	RSA*	Mw, O
61	<i>H. zantmeriana</i> Poelln.	We	RSA*	O
	Trachyandra Kunth (1 species)			
62	<i>T. tabularis</i> (Baker) Oberm.	R	RSA*	



TABLE 10.1 (continued)—Check list of obligate and near-obligate cremnophilous taxa (220 taxa, 203 species)

No.	Taxon	Cremonophilous growth form	Degree of cliff occupation	Weight class
		See 9.1.2 for explanation of the symbols below	*** = strictly obligate cremnophyte, displaying cliff-adapted features ** = obligate cremnophyte * = predominantly on cliffs (80%)	light = < 50 g medium = 51–500 g heavy = >500 g
	HYACINTHACEAE (5 genera, 18 taxa)			
	<i>Albica</i> L. (6 species)			
63	<i>A. batteniana</i> Hilliard & B.L.Burt	A:B:Lper:C:La (e) (vb) (r)	**	medium-heavy
64	<i>A. cremnophila</i> Van Jaarsv. & A.E.van Wyk	A:B:Lper:C:Lp (e) (vb) (eg)	***	medium
65	<i>A. crudenii</i> Archibald	A:B:D:C:Lp (e) (vb) (eg)	***	light
66	<i>A. kirstenii</i> (J.C.Manning & Goldblatt) J.C.Manning & Goldblatt	A:B:D:C:Lp (e) (vb)	**	light
67	<i>A. shawii</i> Baker	A:B:Lper:C:Lp (vb) (eg)	**	light
68	<i>A. thermanum</i> Van Jaarsv.	A:B:Lper:C:Lp (e) (vb) (eg)	***	medium
	<i>Drimia</i> Jacq. (5 species)			
69	<i>D. cremnophila</i> Van Jaarsv.	A:B:Lper:C:Lp (e) (vb)	***	light-medium
70	<i>D. flagellaris</i> T.J.Edwards, D.Styles & N.R.Crouch	A:B:Lper:C:Lp (e) (vb)	***	medium
71	<i>D. loedolffiae</i> Van Jaarsv.	A:B:Lper:C:Lp (e) (vb)	***	medium
72	<i>D. mzimvubuensis</i> Van Jaarsv.	A:B:Lper:C:Lp (e) (vb)	***	light-medium
73	<i>D. uniflora</i> J.C.Manning & Goldblatt	A:B:Lper:C:La (vb)	*	light
	<i>Ledebouria</i> Roth (3 species)			
74	<i>L. concolor</i> (Baker) Jessop	A:B:Lper:C:La (e) (vb) (rd)	**	medium
75	<i>L. cremnophila</i> S.Venter & Van Jaarsv.	A:B:Lper:C:La (e) (vb)	***	medium
76	<i>L. venteri</i> Van Jaarsv. & A.E.van Wyk	A:B:Lper:C:La (e) (vb)	*	medium
	<i>Ornithogalum</i> L. (3 taxa)			
77	<i>O. juncifolium</i> Jacq. var. <i>emsii</i> Van Jaarsv. & A.E.van Wyk	A:B:Lper:C:La (e) (vb)	***	light
78	<i>O. longibracteatum</i> Jacq.	A:B:Lper:C:La: (e) (vb)	**	medium
79	<i>O. pendens</i> Van Jaarsv.	A:B:D:C:Lp: (vb)	***	light
	<i>Schizobasis</i> Baker (1 species)			
80	<i>S. intricata</i> (Baker) Baker	A:B:D:C:La (e) (vb)	**	light-medium
	DICOTYLEDONS (10 families, 140 taxa)			
	ASCLEPIADACEAE (3 genera, 4 species)			
	<i>Huernia</i> R.Br. (1 species)			
81	<i>H. pendula</i> E.A.Bruce	E:Ex:P:St (vb) (eg)	***	light-medium
	<i>Lavrania</i> Plowes (1 species)			
82	<i>L. haagnerae</i> Plowes	E:Ex:De:St (vb)	***	medium-heavy
	<i>Tromotriche</i> Haw. (2 species)			
83	<i>T. baylissii</i> (L.C.Leach) Bruyns	E:Ex:P:Ss (vb) (eg)	***	light-medium
84	<i>T. choanatha</i> (Lavranos & H.Hall) Bruyns	E:Ex:P:Ss (vb) (eg)	***	light-medium
	ASTERACEAE (3 genera, 10 taxa)			
	<i>Kleinia</i> Mill. (1 species)			
85	<i>K. galpinii</i> Hook.f.	A:S:Lper:R:C:La (vb) (r)	**	medium
	<i>Othonna</i> L. (4 species)			
86	<i>O. armiana</i> Van Jaarsv.	A:S:Lar:D:Ca:La: (r)	***	light-medium
87	<i>O. capensis</i> L.H.Bailey	E:F:P:El:S:E: (vb)	**	light-medium
88	<i>O. cremnophila</i> B.Nord. & Van Jaarsv.	E:F:As:S/H:Ca:D	***	medium
89	<i>O. triplinervia</i> DC.	E:F:As:S/H:Ca:Ev	***	medium



TABLE 10.1 (continued)—Check list of obligate and near-obligate cremnophilous taxa (220 taxa, 203 species)

No.	Taxon	Vegetative dispersal backup	Geology	Aspect
HYACINTHACEAE (5 genera, 18 taxa)				
<i>Albuca</i> L. (6 species)				
63	<i>A. batteniana</i> Hilliard & B.L.Burt	dividing or proliferating clusters	mudstone	S
64	<i>A. cremnophila</i> Van Jaarsv. & A.E.van Wyk	dividing or proliferating clusters	sandstone	S
65	<i>A. crudenii</i> Archibald	dividing or proliferating clusters	sandstone	S
66	<i>A. kirstenii</i> (J.C.Manning & Goldblatt) J.C.Manning & Goldblatt	dividing or proliferating clusters	sandstone	E
67	<i>A. shawii</i> Baker	dividing or proliferating clusters	sandstone, shale	S
68	<i>A. thermanum</i> Van Jaarsv.	dividing or proliferating clusters	sandstone	S
<i>Drimia</i> Jacq. (5 species)				
69	<i>D. cremnophila</i> Van Jaarsv.	proliferating clusters and bulb scale proliferation	shale	S
70	<i>D. flagellaris</i> T.J.Edwards, D.Styles & N.R.Crouch	proliferating clusters and bulb scale proliferation	sandstone	S, E
71	<i>D. loedolffiae</i> Van Jaarsv.	dividing or proliferating clusters	shale	W, E, S
72	<i>D. mzimvubuensis</i> Van Jaarsv.	proliferating clusters and bulb scale proliferation	shale	S
73	<i>D. uniflora</i> J.C.Manning & Goldblatt	dividing or proliferating clusters	sandstone	S, E
<i>Ledebouria</i> Roth (3 species)				
74	<i>L. concolor</i> (Baker) Jessop	dividing or proliferating clusters	sandstone	S
75	<i>L. cremnophila</i> S.Venter & Van Jaarsv.	dividing or proliferating clusters	quartz	S
76	<i>L. venteri</i> Van Jaarsv. & A.E.van Wyk	dividing or proliferating clusters	sandstone	E, W, S
<i>Ornithogalum</i> L. (3 taxa)				
77	<i>O. juncifolium</i> Jacq. var. <i>emsii</i> Van Jaarsv. & A.E.van Wyk	dividing or proliferating clusters and bulbils	shale	S
78	<i>O. longibracteatum</i> Jacq.	dividing or proliferating clusters and bulbils	sandstone, shale	N, W, E, S
79	<i>O. pendens</i> Van Jaarsv.	dividing or proliferating clusters	sandstone	S
<i>Schizobasis</i> Baker (1 species)				
80	<i>S. intricata</i> (Baker) Baker	dividing or proliferating clusters	sandstone, quartz	S
DICOTYLEDONS (10 families, 140 taxa)				
ASCLEPIADACEAE (3 genera, 4 species)				
<i>Huernia</i> R.Br. (1 species)				
81	<i>H. pendula</i> E.A.Bruce	active growth and rooting	shale	S
<i>Lavrania</i> Plowes (1 species)				
82	<i>L. haagnerae</i> Plowes	active growth and rooting	dolomite	S
<i>Tromotriche</i> Haw. (2 species)				
83	<i>T. baylissii</i> (L.C.Leach) Bruyns	active growth and rooting	sandstone	S
84	<i>T. choanatha</i> (Lavranos & H.Hall) Bruyns	active growth and rooting	sandstone	S
ASTERACEAE (3 genera, 10 taxa)				
<i>Kleinia</i> Mill. (1 species)				
85	<i>K. galpinii</i> Hook.f.	dividing or proliferating clusters	sandstone	E, N
<i>Othonna</i> L. (4 species)				
86	<i>O. armiana</i> Van Jaarsv.	solitary	diabase	S
87	<i>O. capensis</i> L.H.Bailey	active growth and rooting	sandstone	S
88	<i>O. cremnophila</i> B.Nord. & Van Jaarsv.	solitary	quartz	S
89	<i>O. triplinervia</i> DC.	active growth and rooting	sandstone	S



TABLE 10.1 (continued)—Check list of obligate and near-obligate cremnophilous taxa (220 taxa, 203 species)

No.	Taxon	Altitude (m)	Rainfall (mm per annum)	Rainfall seasonality	Deciduousness
				S = summer W = winter W/S = any time of year	E = evergreen SA = summer-aestivating SD = summer-deciduous WD = winter-deciduous
HYACINTHACEAE (5 genera, 18 taxa)					
<i>Albucca</i> L. (6 species)					
63	<i>A. batteniana</i> Hilliard & B.L.Burt	25–800	700–800	S	E
64	<i>A. cremnophila</i> Van Jaarsv. & A.E.van Wyk	300–600	200–300	W/S	E
65	<i>A. crudenii</i> Archibald	350–400	400–600	W/S	SD
66	<i>A. kirstenii</i> (J.C.Manning & Goldblatt) J.C.Manning & Goldblatt	200–300	300–400	W/S	SD
67	<i>A. shawii</i> Baker	533–2400	800–1500	S	WD
68	<i>A. thermanum</i> Van Jaarsv.	400–800	200–300	W/S	E
<i>Drimia</i> Jacq. (5 species)					
69	<i>D. cremnophila</i> Van Jaarsv.	50–600	800–1000	S	WD
70	<i>D. flagellaris</i> T.J.Edwards, D.Styles & N.R.Crouch	250–800	100–1250	S	E
71	<i>D. loedolffiae</i> Van Jaarsv.	300–500	600–1250	S	E
72	<i>D. mzimvubuensis</i> Van Jaarsv.	300–500	600–1250	S	E
73	<i>D. uniflora</i> J.C.Manning & Goldblatt	500–3000	100–1250	W/S	E
<i>Ledebouria</i> Roth (3 species)					
74	<i>L. concolor</i> (Baker) Jessop	300–800	300–500	S	E
75	<i>L. cremnophila</i> S.Venter & Van Jaarsv.	400–600	500–700	S	E
76	<i>L. venteri</i> Van Jaarsv. & A.E.van Wyk	600–800	300–400	S/W	E
<i>Ornithogalum</i> L. (3 taxa)					
77	<i>O. juncifolium</i> Jacq. var. <i>emsii</i> Van Jaarsv. & A.E.van Wyk	500–600	300–400	W/S	E
78	<i>O. longibracteatum</i> Jacq.	300–500	300–1000	W/S	E
79	<i>O. pendens</i> Van Jaarsv.	400–500	100–250	W	SD
<i>Schizobasis</i> Baker (1 species)					
80	<i>S. intricata</i> (Baker) Baker	250–2000	800–1000	W/S	WD
DICOTYLEDONS (10 families, 140 taxa)					
ASCLEPIADACEAE (3 genera, 4 species)					
<i>Huernia</i> R.Br. (1 species)					
81	<i>H. pendula</i> E.A.Bruce	400–800	300–800	S	E
<i>Lavrania</i> Plowes (1 species)					
82	<i>L. haagnerae</i> Plowes	700–900	50–150	S	E
<i>Tromotriche</i> Haw. (2 species)					
83	<i>T. baylissii</i> (L.C.Leach) Bruyns	250–900	200–300	W/S	E
84	<i>T. choanantha</i> (Lavranos & H.Hall) Bruyns	400–600	200–300	W/S	E
ASTERACEAE (3 genera, 10 taxa)					
<i>Kleinia</i> Mill. (1 species)					
85	<i>K. galpinii</i> Hook.f.	600–1525	1250–2000	S	E
<i>Othonna</i> L. (4 species)					
86	<i>O. armiana</i> Van Jaarsv.	800–900	100–150	W	SD
87	<i>O. capensis</i> L.H.Bailey	20–1220	300–500	W/S	E
88	<i>O. cremnophila</i> B.Nord. & Van Jaarsv.	600–1000	75–150	W	SD
89	<i>O. triplinervia</i> DC.	400–700	300–500	W/S	E



TABLE 10.1 (continued)—Check list of obligate and near-obligate cremnophilous taxa (220 taxa, 203 species)

No.	Taxon	Fog	Biomes	Pollination
		*** = regular fog ** = occasional fog * = little fog – = no fog	IOCB = Indian Ocean Coastal Belt	
HYACINTHACEAE (5 genera, 18 taxa)				
<i>Albica</i> L. (6 species)				
63	<i>A. batteniana</i> Hilliard & B.L.Burtt	–	Albany Thicket	insect
64	<i>A. cremnophila</i> Van Jaarsv. & A.E.van Wyk	–	Albany Thicket	insect
65	<i>A. crudenii</i> Archibald	–	Albany Thicket	insect
66	<i>A. kirstenii</i> (J.C.Manning & Goldblatt) J.C.Manning & Goldblatt	–	Albany Thicket	insect
67	<i>A. shawii</i> Baker	–	Grassland	insect
68	<i>A. thermanum</i> Van Jaarsv.	–	Succulent Karoo	insect
<i>Drimia</i> Jacq. (5 species)				
69	<i>D. cremnophila</i> Van Jaarsv.	–	Savanna	insect
70	<i>D. flagellaris</i> T.J.Edwards, D.Styles & N.R.Crouch	–	IOCB	insect
71	<i>D. loedolffiae</i> Van Jaarsv.	–	Savanna	insect
72	<i>D. mzimvubuensis</i> Van Jaarsv.	–	Savanna	insect
73	<i>D. uniflora</i> J.C.Manning & Goldblatt	**	Fynbos, Savanna, Succulent Karoo, Albany Thicket, Nama-Karoo, Grassland	insect
<i>Ledebouria</i> Roth (3 species)				
74	<i>L. concolor</i> (Baker) Jessop	–	Albany Thicket	insect
75	<i>L. cremnophila</i> S.Venter & Van Jaarsv.	–	Savanna	insect
76	<i>L. venterii</i> Van Jaarsv. & A.E.van Wyk	–	Albany Thicket	insect
<i>Ornithogalum</i> L. (3 taxa)				
77	<i>O. juncifolium</i> Jacq. var. <i>emsii</i> Van Jaarsv. & A.E.van Wyk	–	Albany Thicket	insect
78	<i>O. longibracteatum</i> Jacq.	–	Albany Thicket	insect
79	<i>O. pendens</i> Van Jaarsv.	**	Succulent Karoo	insect
<i>Schizobasis</i> Baker (1 species)				
80	<i>S. intricata</i> (Baker) Baker	–	Savanna	insect
DICOTYLEDONS (10 families, 140 taxa)				
ASCLEPIADACEAE (3 genera, 4 species)				
<i>Huernia</i> R.Br. (1 species)				
81	<i>H. pendula</i> E.A.Bruce	–	Savanna	insect
<i>Lavrana</i> Plowes (1 species)				
82	<i>L. haagnerae</i> Plowes	–	Desert	insect
<i>Tromotriche</i> Haw. (2 species)				
83	<i>T. baylissii</i> (L.C.Leach) Bruyns	–	Albany Thicket	insect
84	<i>T. choanantha</i> (Lavranos & H.Hall) Bruyns	–	Albany Thicket	insect
ASTERACEAE (3 genera, 10 taxa)				
<i>Kleinia</i> Mill. (1 species)				
85	<i>K. galpinii</i> Hook.f.	–	Grassland	insect
<i>Othonna</i> L. (4 species)				
86	<i>O. armiana</i> Van Jaarsv.	–	Succulent Karoo	insect
87	<i>O. capensis</i> L.H.Bailey	–	Albany Thicket	insect
88	<i>O. cremnophila</i> B.Nord. & Van Jaarsv.	–	Succulent Karoo	insect
89	<i>O. triplinervia</i> DC.	–	Albany Thicket	insect



TABLE 10.1 (continued)—Check list of obligate and near-obligate cremnophilous taxa (220 taxa, 203 species)

No.	Taxon	Seed dispersal	Conservation status	Light requirements
			LC = Least Concern NT = Not Threatened VU = Vulnerable	BL = bright light DS = dappled shade FS = full sun
HYACINTHACEAE (5 genera, 18 taxa)				
<i>Albuca</i> L. (6 species)				
63	<i>A. batteniana</i> Hilliard & B.L.Burt	wind	LC	FS, BL, DS
64	<i>A. cremnophila</i> Van Jaarsv. & A.E.van Wyk	wind	LC	FS, BL, DS
65	<i>A. crudenii</i> Archibald	wind	LC	BL, DS
66	<i>A. kirstenii</i> (J.C.Manning & Goldblatt) J.C.Manning & Goldblatt	wind	LC	FS, BL, DS
67	<i>A. shawii</i> Baker	wind	LC	BL, DS
68	<i>A. thermanum</i> Van Jaarsv.	wind	LC	FS, BL, DS
<i>Drimia</i> Jacq. (5 species)				
69	<i>D. cremnophila</i> Van Jaarsv.	wind	LC	BL, DS
70	<i>D. flagellaris</i> T.J.Edwards, D.Styles & N.R.Crouch	wind	LC	FS, BL, DS
71	<i>D. loedolffiae</i> Van Jaarsv.	wind	LC	BL, DS
72	<i>D. mzimvubuensis</i> Van Jaarsv.	wind	LC	BL, DS
73	<i>D. uniflora</i> J.C.Manning & Goldblatt	wind	LC	BL
<i>Ledebouria</i> Roth (3 species)				
74	<i>L. concolor</i> (Baker) Jessop	autochory	LC	FS, BL, DS
75	<i>L. cremnophila</i> S.Venter & Van Jaarsv.	autochory	LC	BL, DS
76	<i>L. venteri</i> Van Jaarsv. & A.E.van Wyk	autochory	LC	FS, BL, DS
<i>Ornithogalum</i> L. (3 taxa)				
77	<i>O. juncifolium</i> Jacq. var. <i>emsii</i> Van Jaarsv. & A.E.van Wyk	wind	LC	FS, BL, DS
78	<i>O. longibracteatum</i> Jacq.	wind	LC	FS, BL, DS
79	<i>O. pendens</i> Van Jaarsv.	wind	LC	BL, DS
<i>Schizobasis</i> Baker (1 species)				
80	<i>S. intricata</i> (Baker) Baker	wind	LC	FS, BL, DS
DICOTYLEDONS (10 families, 140 taxa)				
ASCLEPIADACEAE (3 genera, 4 species)				
<i>Huernia</i> R.Br. (1 species)				
81	<i>H. pendula</i> E.A.Bruce	wind	LC	FS, BL, DS
<i>Lavrania</i> Plowes (1 species)				
82	<i>L. haagnerae</i> Plowes	wind	LC	FS, BL
<i>Tromotriche</i> Haw. (2 species)				
83	<i>T. baylissii</i> (L.C.Leach) Bruyns	wind	LC	BL, DS
84	<i>T. choanatha</i> (Lavranos & H.Hall) Bruyns	wind	LC	BL, DS
ASTERACEAE (3 genera, 10 taxa)				
<i>Kleinia</i> Mill. (1 species)				
85	<i>K. galpinii</i> Hook.f.	wind	LC	FS
<i>Othonna</i> L. (4 species)				
86	<i>O. armiana</i> Van Jaarsv.	wind	LC	FS
87	<i>O. capensis</i> L.H.Bailey	wind	LC	FS
88	<i>O. cremnophila</i> B.Nord. & Van Jaarsv.	wind	LC	FS
89	<i>O. triplinervia</i> DC.	wind	LC	FS, BL



TABLE 10.1 (continued)—Check list of obligate and near-obligate cremnophilous taxa (220 taxa, 203 species)

No.	Taxon	Rich flowering	Reduction in armament	Cliff habitat
		*** = rich ** = exposed * = insignificant	*** = margin without teeth ** = margin with smaller teeth * = no significant change, same as other non-cremnophytes	C = coastal R = river E = escarpment M = mountain I = inselberg
HYACINTHACEAE (5 genera, 18 taxa)				
<i>Albuca</i> L. (6 species)				
63	<i>A. batteniana</i> Hilliard & B.L.Burt	***	*	C
64	<i>A. cremnophila</i> Van Jaarsv. & A.E.van Wyk	**	*	R, M
65	<i>A. crudenii</i> Archibald	**	*	R, M
66	<i>A. kirstenii</i> (J.C.Manning & Goldblatt) J.C.Manning & Goldblatt	**	*	R
67	<i>A. shawii</i> Baker	**	*	R, M
68	<i>A. thermanum</i> Van Jaarsv.	**	*	R, M
<i>Drimia</i> Jacq. (5 species)				
69	<i>D. cremnophila</i> Van Jaarsv.	*	*	R
70	<i>D. flagellaris</i> T.J.Edwards, D.Styles & N.R.Crouch	*	*	R
71	<i>D. loedolffiae</i> Van Jaarsv.	*	*	R
72	<i>D. mzimvubuensis</i> Van Jaarsv.	*	*	R
73	<i>D. uniflora</i> J.C.Manning & Goldblatt	*	*	R, M
<i>Ledebouria</i> Roth (3 species)				
74	<i>L. concolor</i> (Baker) Jessop	*	*	R, M
75	<i>L. cremnophila</i> S.Venter & Van Jaarsv.	*	*	R, M
76	<i>L. venteri</i> Van Jaarsv. & A.E.van Wyk	*	*	R, M
<i>Ornithogalum</i> L. (3 taxa)				
77	<i>O. juncifolium</i> Jacq. var. <i>emsii</i> Van Jaarsv. & A.E.van Wyk	**	*	R
78	<i>O. longibracteatum</i> Jacq.	**	*	R, M, C
79	<i>O. pendens</i> Van Jaarsv.	**	*	R
<i>Schizobasis</i> Baker (1 species)				
80	<i>S. intricata</i> (Baker) Baker	*	*	R
DICOTYLEDONS (10 families, 140 taxa)				
ASCLEPIADACEAE (3 genera, 4 species)				
<i>Huernia</i> R.Br. (1 species)				
81	<i>H. pendula</i> E.A.Bruce	**	*	R
<i>Lavrana</i> Plowes (1 species)				
82	<i>L. haagnerae</i> Plowes	**	*	R, M
<i>Tromotriche</i> Haw. (2 species)				
83	<i>T. baylissii</i> (L.C.Leach) Bruyns	**	*	R, M
84	<i>T. choanatha</i> (Lavranos & H.Hall) Bruyns	**	*	R, M
ASTERACEAE (3 genera, 10 taxa)				
<i>Kleinia</i> Mill. (1 species)				
85	<i>K. galpinii</i> Hook.f.	***	*	E, M
<i>Othonna</i> L. (4 species)				
86	<i>O. armiana</i> Van Jaarsv.	***	*	M, I
87	<i>O. capensis</i> L.H.Bailey	**	*	E, R
88	<i>O. cremnophila</i> B.Nord. & Van Jaarsv.	**	*	M
89	<i>O. triplinervia</i> DC.	**	*	R



TABLE 10.1 (continued)—Check list of obligate and near-obligate cremnophilous taxa (220 taxa, 203 species)

No.	Taxon	Occurrence	Endemism	Windows
		W = widespread We = widespread but endemic to its vegetation region R = restricted	* = endemic Bots = Botswana Les = Lesotho Moz = Mozambique Nam = Namibia RSA = South Africa Swaz = Swaziland	Lm = on leaf margin Mw = micro-windows O = other
HYACINTHACEAE (5 genera, 18 taxa)				
<i>Albucca</i> L. (6 species)				
63	<i>A. batteniana</i> Hilliard & B.L.Burt	We	RSA*	
64	<i>A. cremnophila</i> Van Jaarsv. & A.E.van Wyk	We	RSA*	O
65	<i>A. crudenii</i> Archibald	R	RSA*	
66	<i>A. kirstenii</i> (J.C.Manning & Goldblatt) J.C.Manning & Goldblatt	We	RSA*	
67	<i>A. shawii</i> Baker	W	RSA*	
68	<i>A. thermanum</i> Van Jaarsv.	R	RSA*	
<i>Drimia</i> Jacq. (5 species)				
69	<i>D. cremnophila</i> Van Jaarsv.	We	RSA*	
70	<i>D. flagellaris</i> T.J.Edwards, D.Styles & N.R.Crouch	We	RSA*	O
71	<i>D. loedolffiae</i> Van Jaarsv.	We	RSA*	O
72	<i>D. mzimvubuensis</i> Van Jaarsv.	R	RSA*	O
73	<i>D. uniflora</i> J.C.Manning & Goldblatt	W	RSA, Swaz	
<i>Ledebouria</i> Roth (3 species)				
74	<i>L. concolor</i> (Baker) Jessop	We	RSA*	
75	<i>L. cremnophila</i> S.Venter & Van Jaarsv.	R	RSA*	
76	<i>L. venteri</i> Van Jaarsv. & A.E.van Wyk	We	RSA*	
<i>Ornithogalum</i> L. (3 taxa)				
77	<i>O. juncifolium</i> Jacq. var. <i>emsii</i> Van Jaarsv. & A.E.van Wyk	R	RSA*	
78	<i>O. longibracteatum</i> Jacq.	W	RSA*	
79	<i>O. pendens</i> Van Jaarsv.	R	RSA*	
<i>Schizobasis</i> Baker (1 species)				
80	<i>S. intricata</i> (Baker) Baker	W	RSA, Swaz, Bots	
DICOTYLEDONS (10 families, 140 taxa)				
ASCLEPIADACEAE (3 genera, 4 species)				
<i>Huernia</i> R.Br. (1 species)				
81	<i>H. pendula</i> E.A.Bruce	We	RSA*	
<i>Lavrana</i> Plowes (1 species)				
82	<i>L. haagnerae</i> Plowes	We	Nam*	
<i>Tromotriche</i> Haw. (2 species)				
83	<i>T. baylissii</i> (L.C.Leach) Bruyns	We	RSA*	
84	<i>T. choanatha</i> (Lavranos & H.Hall) Bruyns	We	RSA*	
ASTERACEAE (3 genera, 10 taxa)				
<i>Kleinia</i> Mill. (1 species)				
85	<i>K. galpinii</i> Hook.f.	We	RSA*	
<i>Othonna</i> L. (4 species)				
86	<i>O. armiana</i> Van Jaarsv.	R	RSA*	
87	<i>O. capensis</i> L.H.Bailey	W	RSA*	
88	<i>O. cremnophila</i> B.Nord. & Van Jaarsv.	R	RSA*	
89	<i>O. triplinervia</i> DC.	We	RSA*	



TABLE 10.1 (continued)—Check list of obligate and near-obligate cremnophilous taxa (220 taxa, 203 species)

No.	Taxon	Cremonophilous growth form	Degree of cliff occupation	Weight class
		See 9.1.2 for explanation of the symbols below	*** = strictly obligate cremnophyte, displaying cliff-adapted features ** = obligate cremnophyte * = predominantly on cliffs (80%)	light = < 50 g medium = 51–500 g heavy = >500 g
	Senecio L. (5 taxa)			
90	<i>S. medley-woodii</i> Hutch.	E:F:As:S/H:Es (vb)	***	medium
91	<i>S. muirii</i> L.Bolus	E:F:P:Els:(vb) (eg)	***	medium
92	<i>S. pondoensis</i> Van Jaarsv. & A.E.van Wyk	E:F:As:S/H:Es (vb)	***	medium
93	<i>S. serpens</i> G.D.Rowley	E:F:As:S/H:Es (vb)	**	medium
94	<i>S. talinoides</i> Sch.Bip. subsp. <i>talinoides</i>	E:F:As:S/H:Es (vb)	**	medium
	CACTACEAE (1 taxon)			
	Rhipsalis Gaertn. (1 taxon)			
95	<i>R. baccifera</i> (J.Mill.) Stearn subsp. <i>mauritiana</i> (D.C.) Barthlott	E:Ex:P:St (vb) (eg)	***	medium
	CRASSULACEAE (4 genera, 66 taxa)			
	Adromischus Lem. (10 taxa, 8 species)			
96	<i>A. cristatus</i> (Haw.) Lem. var. <i>mzimvubuensis</i> Van Jaarsv.	A:S:Lper:Lc:Ts (vb)	**	light-medium
97	<i>A. cristatus</i> (Haw.) Lem. var. <i>schonlandii</i> (E.Phillips) Toelken	A:S:Lper:Lc:Ts (vb)	***	light-medium
98	<i>A. cristatus</i> (Haw.) Lem. var. <i>zeyheri</i> (Harv.) Toelken	E:F:P:Els (vb)	***	light-medium
99	<i>A. diabolicus</i> Toelken	A:S:Lper:Lc:Ts (vb)	***	light-medium
100	<i>A. fallax</i> Toelken	E:F:As:S/H:Es (vb)	**	light-medium
101	<i>A. leucophyllus</i> Uitewaal	E:F:P:Els (vb)	**	light
102	<i>A. liebenbergii</i> Hutchison subsp. <i>orientalis</i> Van Jaarsv.	E:F:S/H:As:Es (vb)	**	light-medium
103	<i>A. schuldianus</i> (Poelln.) Poelln. subsp. <i>brandbergensis</i> B.Nord. & Van Jaarsv.	A:S:Lper:Lc:Ca (vb)	**	light
104	<i>A. subdistichus</i> Makin ex Bruyns	E:F:P:Els E (vb)	**	light
105	<i>A. umbraticola</i> C.A.Sm. subsp. <i>ramosus</i> Toelken	A:S:Lper:Lc:Ts (vb)	**	light
	Cotyledon L. (4 taxa)			
106	<i>C. barbeyi</i> Schweinf. var. A	E:F:As:S/H:Es (vb)	**	light-medium
107	<i>C. eliseae</i> Van Jaarsv.	E:F:As:S/H:Es: (vb)	***	light-medium
108	<i>C. pendens</i> Van Jaarsv.	E:F:P:Els (eg) (vb) (r)	***	light-medium
109	<i>C. tomentosa</i> Harv. subsp. <i>tomentosa</i>	E:F:As:S/H:Es (vb)	***	light-medium
	Crassula L. (38 taxa)			
110	<i>C. alba</i> Forssk. var. <i>pallida</i> Toelken	A:S:Lper:R:C:La (vb)	**	light-medium
111	<i>C. atropurpurea</i> (Harv.) D.Dietr. var. <i>anomala</i> (Schönland & Baker f.) Toelken	E:F:As:S/H:Es (vb)	**	light
112	<i>C. aurisbergensis</i> G.Will.	A:S:Lper:R:C:La (vb)	***	light
113	<i>C. badspoortense</i> Van Jaarsv.	E:F:P:Els: (vb)	***	light-medium
114	<i>C. brachystachya</i> Toelken	A:S:Lper:R:C:La (vb)	***	light
115	<i>C. capitella</i> Thunb. subsp. <i>thyrsiflora</i> (Thunb.) Toelken	A:S:Lper:R:C:La (vb)	**	light
116	<i>C. cremonophila</i> Van Jaarsv. & A.E.van Wyk	A:S:Lper:R:C:La (vb) (rd) (r)	***	light



TABLE 10.1 (continued)—Check list of obligate and near-obligate cremnophilous taxa (220 taxa, 203 species)

No.	Taxon	Vegetative dispersal backup	Geology	Aspect
	Senecio L. (5 taxa)			
90	<i>S. medley-woodii</i> Hutch.	dividing or proliferating clusters	sandstone, shale	S, N, W, E
91	<i>S. muiirii</i> L.Bolus	active growth and rooting	sandstone, shale	S
92	<i>S. pondoensis</i> Van Jaarsv. & A.E.van Wyk	active growth and rooting	sandstone	S
93	<i>S. serpens</i> G.D.Rowley	active growth and rooting	sandstone	S, E, N, W
94	<i>S. talinoides</i> Sch.Bip. subsp. <i>talinoides</i>	active growth and rooting	sandstone, shale	S
	CACTACEAE (1 taxon)			
	Rhipsalis Gaertn. (1 taxon)			
95	<i>R. baccifera</i> (J.Mill.) Stearn subsp. <i>mauritiana</i> (D.C.) Barthlott	active growth and rooting	sandstone	S
	CRASSULACEAE (4 genera, 66 taxa)			
	Adromischus Lem. (10 taxa, 8 species)			
96	<i>A. cristatus</i> (Haw.) Lem. var. <i>mzimvubuensis</i> Van Jaarsv.	proliferating clusters and leaf stolons	shale	N, W, E
97	<i>A. cristatus</i> (Haw.) Lem. var. <i>schonlandii</i> (E.Phillips) Toelken	proliferating clusters and leaf stolons	sandstone	N, W, E
98	<i>A. cristatus</i> (Haw.) Lem. var. <i>zeyheri</i> (Harv.) Toelken	proliferating clusters and leaf stolons	sandstone	S
99	<i>A. diabolicus</i> Toelken	proliferating clusters and leaf stolons	quartz	S
100	<i>A. fallax</i> Toelken	proliferating clusters and leaf stolons	shale	S
101	<i>A. leucophyllus</i> Uitewaal	proliferating clusters and leaf stolons	sandstone	S, W, E
102	<i>A. liebenbergii</i> Hutchison subsp. <i>orientalis</i> Van Jaarsv.	proliferating clusters and leaf stolons	shale	N, S, E
103	<i>A. schuldianus</i> (Poelln.) Poelln. subsp. <i>brandbergensis</i> B.Nord. & Van Jaarsv.	proliferating clusters and leaf stolons	granite	S
104	<i>A. subdistichus</i> Makin ex Bruyns	proliferating clusters and leaf stolons	sandstone	S
105	<i>A. umbraticola</i> C.A.Sm. subsp. <i>ramosus</i> Toelken	proliferating clusters and leaf stolons	sandstone	N, E
	Cotyledon L. (4 taxa)			
106	<i>C. barbeyi</i> Schweinf. var. A	solitary	sandstone	W
107	<i>C. eliseae</i> Van Jaarsv.	solitary	sandstone	S
108	<i>C. pendens</i> Van Jaarsv.	active growth and rooting	shale	S
109	<i>C. tomentosa</i> Harv. subsp. <i>tomentosa</i>	solitary	sandstone	N, S, E, W
	Crassula L. (38 taxa)			
110	<i>C. alba</i> Forssk. var. <i>pallida</i> Toelken	dividing or proliferating clusters	sandstone	N, E
111	<i>C. atropurpurea</i> (Harv.) D.Dietr. var. <i>anomala</i> (Schönland & Baker f.) Toelken	proliferating clusters and leaf stolons	sandstone	N, S, E, W
112	<i>C. aurusbergensis</i> G.Will.	proliferating clusters and leaf stolons	sandstone	S
113	<i>C. badspootense</i> Van Jaarsv.	solitary	sandstone	S
114	<i>C. brachystachya</i> Toelken	proliferating clusters and leaf stolons	sandstone	S
115	<i>C. capitella</i> Thunb. subsp. <i>thyrsiflora</i> (Thunb.) Toelken	proliferating clusters and leaf stolons	sandstone	S
116	<i>C. cremnophila</i> Van Jaarsv. & A.E.van Wyk	proliferating clusters and leaf stolons	sandstone	S



TABLE 10.1 (continued)—Check list of obligate and near-obligate cremnophilous taxa (220 taxa, 203 species)

No.	Taxon	Altitude (m)	Rainfall (mm per annum)	Rainfall seasonality	Deciduousness
				S = summer W = winter W/S = any time of year	E = evergreen SA = summer-aestivating SD = summer-deciduous WD = winter-deciduous
	Senecio L. (5 taxa)				
90	<i>S. medley-woodii</i> Hutch.	460–800	1000–1250	S	E
91	<i>S. muiirii</i> L.Bolus	300–800	300–400	W/S	E
92	<i>S. pondoensis</i> Van Jaarsv. & A.E.van Wyk	200–250	1000–1250	S	E
93	<i>S. serpens</i> G.D.Rowley	400–1800	100–1250	W	E
94	<i>S. talinoides</i> Sch.Bip. subsp. <i>talinoides</i>	300–1000	500–700	WS	E
	CACTACEAE (1 taxon)				
	Rhipsalis Gaertn. (1 taxon)				
95	<i>R. baccifera</i> (J.Mill.) Stearn subsp. <i>mauritiana</i> (D.C.) Barthlott	100–1750	1000–1250	S	E
	CRASSULACEAE (4 genera, 66 taxa)				
	Adromischus Lem. (10 taxa, 8 species)				
96	<i>A. cristatus</i> (Haw.) Lem. var. <i>mzimvubuensis</i> Van Jaarsv.	460–800	400–700	S	E
97	<i>A. cristatus</i> (Haw.) Lem. var. <i>schonlandii</i> (E.Phillips) Toelken	100–1500	300–400	S/W	E
98	<i>A. cristatus</i> (Haw.) Lem. var. <i>zeyheri</i> (Harv.) Toelken	50–800	300–700	S/W	E
99	<i>A. diabolicus</i> Toelken	300–800	50–100	S/W	E
100	<i>A. fallax</i> Toelken	800–1500	300–400	S	E
101	<i>A. leucophyllus</i> Uitewaal	500–1000	300–400	W/S	E
102	<i>A. liebenbergii</i> Hutchison subsp. <i>orientalis</i> Van Jaarsv.	300–800	600–1000	S	E
103	<i>A. schuldianus</i> (Poelln.) Poelln. subsp. <i>brandbergensis</i> B.Nord. & Van Jaarsv.	500–2200	200–300	S	E
104	<i>A. subdistichus</i> Makin ex Bruyns	500–2000	300–400	W/S	E
105	<i>A. umbraticola</i> C.A.Sm. subsp. <i>ramosus</i> Toelken	1500–1700	600–800	S	E
	Cotyledon L. (4 taxa)				
106	<i>C. barbeyi</i> Schweinf. var. A	400–600	350–400	S	E
107	<i>C. eliseae</i> Van Jaarsv.	200–300	300–400	W/S	E
108	<i>C. pendens</i> Van Jaarsv.	300–400	1000–1250	S	E
109	<i>C. tomentosa</i> Harv. subsp. <i>tomentosa</i>	300–700	300–400	W/S	E
	Crassula L. (38 taxa)				
110	<i>C. alba</i> Forssk. var. <i>pallida</i> Toelken	400–2000	1000–1500	S	E
111	<i>C. atropurpurea</i> (Harv.) D.Dietr. var. <i>anomala</i> (Schönland & Baker f.) Toelken	800–2000	450–800	W	E
112	<i>C. aurusbergensis</i> G.Will.	900–1050	50–75	W	E
113	<i>C. badspoortense</i> Van Jaarsv.	500–800	250–300	W/S	E
114	<i>C. brachystachya</i> Toelken	1300–2000	200–400	W/S	E
115	<i>C. capitella</i> Thunb. subsp. <i>thyrsiflora</i> (Thunb.) Toelken	300–1000	200–300	W/S	E
116	<i>C. cremnophila</i> Van Jaarsv. & A.E.van Wyk	500–800	200–300	W/S	E



TABLE 10.1 (continued)—Check list of obligate and near-obligate cremnophilous taxa (220 taxa, 203 species)

No.	Taxon	Fog	Biomes	Pollination
		*** = regular fog ** = occasional fog * = little fog – = no fog	IOCB = Indian Ocean Coastal Belt	
	Senecio L. (5 taxa)			
90	<i>S. medley-woodii</i> Hutch.	–	Savanna	insect
91	<i>S. muiirii</i> L.Bolus	–	Albany Thicket	insect
92	<i>S. pondoensis</i> Van Jaarsv. & A.E.van Wyk	–	IOCB	insect
93	<i>S. serpens</i> G.D.Rowley	–	Fynbos	insect
94	<i>S. talinoides</i> Sch.Bip. subsp. <i>talinoides</i>	–	Savanna	insect
	CACTACEAE (1 taxon)			
	Rhipsalis Gaertn. (1 taxon)			
95	<i>R. baccifera</i> (J.Mill.) Stearn subsp. <i>mauritiana</i> (D.C.) Barthlott	–	IOCB	insect
	CRASSULACEAE (4 genera, 66 taxa)			
	Adromischus Lem. (10 taxa, 8 species)			
96	<i>A. cristatus</i> (Haw.) Lem. var. <i>mzimvubuensis</i> Van Jaarsv.	–	Savanna	insect
97	<i>A. cristatus</i> (Haw.) Lem. var. <i>schonlandii</i> (E.Phillips) Toelken	–	Albany Thicket	insect
98	<i>A. cristatus</i> (Haw.) Lem. var. <i>zeyheri</i> (Harv.) Toelken	–	Albany Thicket	insect
99	<i>A. diabolicus</i> Toelken	**	Desert	insect
100	<i>A. fallax</i> Toelken	*	Albany Thicket	insect
101	<i>A. leucophyllus</i> Uitewaal	–	Succulent Karoo	insect
102	<i>A. liebenbergii</i> Hutchison subsp. <i>orientalis</i> Van Jaarsv.	–	Savanna	insect
103	<i>A. schuldianus</i> (Poelln.) Poelln. subsp. <i>brandbergensis</i> B.Nord. & Van Jaarsv.	–	Desert	insect
104	<i>A. subdistichus</i> Makin ex Bruyns	–	Albany Thicket	insect
105	<i>A. umbraticola</i> C.A.Sm. subsp. <i>ramosus</i> Toelken	–	Savanna	insect
	Cotyledon L. (4 taxa)			
106	<i>C. barbeyi</i> Schweinf. var. A	–	Savanna	bird
107	<i>C. eliseae</i> Van Jaarsv.	–	Albany Thicket	bird
108	<i>C. pendens</i> Van Jaarsv.	–	Savanna	bird
109	<i>C. tomentosa</i> Harv. subsp. <i>tomentosa</i>	–	Albany Thicket	bird
	Crassula L. (38 taxa)			
110	<i>C. alba</i> Forssk. var. <i>pallida</i> Toelken	–	Grassland	insect
111	<i>C. atropurpurea</i> (Harv.) D.Dietr. var. <i>anomala</i> (Schönland & Baker f.) Toelken	–	Albany Thicket	insect
112	<i>C. aurusbergensis</i> G.Will.	–	Succulent Karoo	insect
113	<i>C. badspoortense</i> Van Jaarsv.	–	Succulent Karoo	insect
114	<i>C. brachystachya</i> Toelken	–	Succulent Karoo	insect
115	<i>C. capitella</i> Thunb. subsp. <i>thyrsiflora</i> (Thunb.) Toelken	–	Thicket	insect
116	<i>C. cremnophila</i> Van Jaarsv. & A.E.van Wyk	–	Albany Thicket	insect



TABLE 10.1 (continued)—Check list of obligate and near-obligate cremnophilous taxa (220 taxa, 203 species)

No.	Taxon	Seed dispersal	Conservation status	Light requirements
			LC = Least Concern NT = Not Threatened VU = Vulnerable	BL = bright light DS = dappled shade FS = full sun
	Senecio L. (5 taxa)			
90	<i>S. medley-woodii</i> Hutch.	wind	LC	FS, BL, DS
91	<i>S. muiirii</i> L.Bolus	wind	LC	FS, BL, DS
92	<i>S. pondoensis</i> Van Jaarsv. & A.E.van Wyk	wind	LC	FS, BL
93	<i>S. serpens</i> G.D.Rowley	wind	LC	FS
94	<i>S. talinoides</i> Sch.Bip. subsp. <i>talinoides</i>	wind	LC	FS
	CACTACEAE (1 taxon)			
	Rhipsalis Gaertn. (1 taxon)			
95	<i>R. baccifera</i> (J.Mill.) Stearn subsp. <i>mauritiana</i> (D.C.) Barthlott	bird	LC	FS, BL, DS
	CRASSULACEAE (4 genera, 66 taxa)			
	Adromischus Lem. (10 taxa, 8 species)			
96	<i>A. cristatus</i> (Haw.) Lem. var. <i>mzimvubuensis</i> Van Jaarsv.	wind	LC	FS, BL
97	<i>A. cristatus</i> (Haw.) Lem. var. <i>schonlandii</i> (E.Phillips) Toelken	wind	LC	FS, BL
98	<i>A. cristatus</i> (Haw.) Lem. var. <i>zeyheri</i> (Harv.) Toelken	wind	LC	FS, BL
99	<i>A. diabolicus</i> Toelken	wind	LC	FS, BL
100	<i>A. fallax</i> Toelken	wind	LC	FS, BL
101	<i>A. leucophyllus</i> Uitewaal	wind	LC	FS, BL
102	<i>A. liebenbergii</i> Hutchison subsp. <i>orientalis</i> Van Jaarsv.	wind	LC	FS, BL
103	<i>A. schuldianus</i> (Poelln.) Poelln. subsp. <i>brandbergensis</i> B.Nord. & Van Jaarsv.	wind	LC	FS, BL
104	<i>A. subdistichus</i> Makin ex Bruyns	wind	LC	FS, BL
105	<i>A. umbraticola</i> C.A.Sm. subsp. <i>ramosus</i> Toelken	wind	LC	FS, BL
	Cotyledon L. (4 taxa)			
106	<i>C. barbeyi</i> Schweinf. var. A	wind	LC	FS, BL
107	<i>C. eliseae</i> Van Jaarsv.	wind	LC	FS, BL
108	<i>C. pendens</i> Van Jaarsv.	wind	LC	FS, BL
109	<i>C. tomentosa</i> Harv. subsp. <i>tomentosa</i>	wind	LC	FS, BL
	Crassula L. (38 taxa)			
110	<i>C. alba</i> Forssk. var. <i>pallida</i> Toelken	wind	LC	FS, BL
111	<i>C. atropurpurea</i> (Harv.) D.Dietr. var. <i>anomala</i> (Schönland & Baker f.) Toelken	wind	LC	FS, BL
112	<i>C. aurusbergensis</i> G.Will.	wind	LC	FS, BL
113	<i>C. badspoortense</i> Van Jaarsv.	wind	LC	FS, BL
114	<i>C. brachystachya</i> Toelken	wind	LC	FS, BL
115	<i>C. capitella</i> Thunb. subsp. <i>thyrsiflora</i> (Thunb.) Toelken	wind	LC	FS, BL
116	<i>C. cremnophila</i> Van Jaarsv. & A.E.van Wyk	wind	LC	BL, DS



TABLE 10.1 (continued)—Check list of obligate and near-obligate cremnophilous taxa (220 taxa, 203 species)

No.	Taxon	Rich flowering	Reduction in armament	Cliff habitat
		*** = rich ** = exposed * = insignificant	*** = margin without teeth ** = margin with smaller teeth * = no significant change, same as other non-cremnophytes	C = coastal R = river E = escarpment M = mountain I = inselberg
	Senecio L. (5 taxa)			
90	<i>S. medley-woodii</i> Hutch.	***	*	R
91	<i>S. muirii</i> L.Bolus	*	*	R
92	<i>S. pondoensis</i> Van Jaarsv. & A.E.van Wyk	*	*	R
93	<i>S. serpens</i> G.D.Rowley	*	*	M
94	<i>S. talinoides</i> Sch.Bip. subsp. <i>talinoides</i>	*	*	R
	CACTACEAE (1 taxon)			
	Rhipsalis Gaertn. (1 taxon)			
95	<i>R. baccifera</i> (J.Mill.) Stearn subsp. <i>mauritiana</i> (D.C.) Barthlott	*	*	R
	CRASSULACEAE (4 genera, 66 taxa)			
	Adromischus Lem. (10 taxa, 8 species)			
96	<i>A. cristatus</i> (Haw.) Lem. var. <i>mzimvubuensis</i> Van Jaarsv.	*	*	R
97	<i>A. cristatus</i> (Haw.) Lem. var. <i>schonlandii</i> (E.Phillips) Toelken	*	*	R
98	<i>A. cristatus</i> (Haw.) Lem. var. <i>zeyheri</i> (Harv.) Toelken	*	*	R
99	<i>A. diabolicus</i> Toelken	*	*	R, M
100	<i>A. fallax</i> Toelken	*	*	E
101	<i>A. leucophyllus</i> Uitewaal	*	*	R, M
102	<i>A. liebenbergii</i> Hutchison subsp. <i>orientalis</i> Van Jaarsv.	*	*	R
103	<i>A. schuldianus</i> (Poelln.) Poelln. subsp. <i>brandbergensis</i> B.Nord. & Van Jaarsv.	*	*	I
104	<i>A. subdistichus</i> Makin ex Bruyns	*	*	M, R
105	<i>A. umbraticola</i> C.A.Sm. subsp. <i>ramosus</i> Toelken	*	*	R, M
	Cotyledon L. (4 taxa)			
106	<i>C. barbeyi</i> Schweinf. var. A	**	*	R, M
107	<i>C. eliseae</i> Van Jaarsv.	***	*	R
108	<i>C. pendens</i> Van Jaarsv.	**	*	R
109	<i>C. tomentosa</i> Harv. subsp. <i>tomentosa</i>	***	*	R
	Crassula L. (38 taxa)			
110	<i>C. alba</i> Forssk. var. <i>pallida</i> Toelken	**	*	E
111	<i>C. atropurpurea</i> (Harv.) D.Dietr. var. <i>anomala</i> (Schönland & Baker f.) Toelken	**	*	M
112	<i>C. aurusbergensis</i> G.Will.	**	*	I
113	<i>C. badspoortense</i> Van Jaarsv.	**	*	R, M
114	<i>C. brachystachya</i> Toelken	**	*	M
115	<i>C. capitella</i> Thunb. subsp. <i>thyrsiflora</i> (Thunb.) Toelken	**	*	R
116	<i>C. cremnophila</i> Van Jaarsv. & A.E.van Wyk	***	*	R, M



TABLE 10.1 (continued)—Check list of obligate and near-obligate cremnophilous taxa (220 taxa, 203 species)

No.	Taxon	Occurrence	Endemism	Windows
		W = widespread We = widespread but endemic to its vegetation region R = restricted	* = endemic Bots = Botswana Les = Lesotho Moz = Mozambique Nam = Namibia RSA = South Africa Swaz = Swaziland	Lm = on leaf margin Mw = micro-windows O = other
	Senecio L. (5 taxa)			
90	<i>S. medley-woodii</i> Hutch.	We	RSA*	
91	<i>S. muiirii</i> L.Bolus	We	RSA*	O
92	<i>S. pondoensis</i> Van Jaarsv. & A.E.van Wyk	R	RSA*	O
93	<i>S. serpens</i> G.D.Rowley	We	RSA*	O
94	<i>S. talinoides</i> Sch.Bip. subsp. <i>talinoides</i>	We	RSA*	O
	CACTACEAE (1 taxon)			
	Rhipsalis Gaertn. (1 taxon)			
95	<i>R. baccifera</i> (J.Mill.) Stearn subsp. <i>mauritiana</i> (D.C.) Barthlott	W	RSA	
	CRASSULACEAE (4 genera, 66 taxa)			
	Adromischus Lem. (10 taxa, 8 species)			
96	<i>A. cristatus</i> (Haw.) Lem. var. <i>mzimvubuensis</i> Van Jaarsv.	We	RSA*	
97	<i>A. cristatus</i> (Haw.) Lem. var. <i>schonlandii</i> (E.Phillips) Toelken	We	RSA*	
98	<i>A. cristatus</i> (Haw.) Lem. var. <i>zeyheri</i> (Harv.) Toelken	W	RSA*	
99	<i>A. diabolicus</i> Toelken	We	RSA*	
100	<i>A. fallax</i> Toelken	We	RSA*	
101	<i>A. leucophyllus</i> Uitewaal	We	RSA*	
102	<i>A. liebenbergii</i> Hutchison subsp. <i>orientalis</i> Van Jaarsv.	We	RSA*	
103	<i>A. schuldianus</i> (Poelln.) Poelln. subsp. <i>brandbergensis</i> B.Nord. & Van Jaarsv.	R	Nam*	O
104	<i>A. subdistichus</i> Makin ex Bruyns	We	RSA*	
105	<i>A. umbraticola</i> C.A.Sm. subsp. <i>ramosus</i> Toelken	W	RSA*	
	Cotyledon L. (4 taxa)			
106	<i>C. barbeyi</i> Schweinf. var. A	R	RSA*	
107	<i>C. eliseae</i> Van Jaarsv.	R	RSA*	
108	<i>C. pendens</i> Van Jaarsv.	We	RSA*	
109	<i>C. tomentosa</i> Harv. subsp. <i>tomentosa</i>	We	RSA*	
	Crassula L. (38 taxa)			
110	<i>C. alba</i> Forssk. var. <i>pallida</i> Toelken	We	RSA, Swaz	
111	<i>C. atropurpurea</i> (Harv.) D.Dietr. var. <i>anomala</i> (Schönland & Baker f.) Toelken	We	RSA*	
112	<i>C. aurusbergensis</i> G.Will.	R	Nam*	
113	<i>C. badspootense</i> Van Jaarsv.	We	RSA*	
114	<i>C. brachystachya</i> Toelken	We	RSA*	
115	<i>C. capitella</i> Thunb. subsp. <i>thyrsiflora</i> (Thunb.) Toelken	We	RSA*	
116	<i>C. cremnophila</i> Van Jaarsv. & A.E.van Wyk	R	RSA*	



TABLE 10.1 (continued)—Check list of obligate and near-obligate cremnophilous taxa (220 taxa, 203 species)

No.	Taxon	Cremonophilous growth form	Degree of cliff occupation	Weight class
		See 9.1.2 for explanation of the symbols below	*** = strictly obligate cremnophyte, displaying cliff-adapted features ** = obligate cremnophyte * = predominantly on cliffs (80%)	light = < 50 g medium = 51–500 g heavy = >500 g
117	<i>Crassula cymbiformis</i> Toelken	A:S:Lper:R:C:La (vb)	***	light
118	<i>C. exilis</i> Harv. subsp. <i>cooperi</i> (Regel) Toelken	A:S:Lper:R:C:La (vb)	**	light
119	<i>C. exilis</i> Harv. subsp. <i>exilis</i>	A:S:Lper:R:C:La (vb)	**	light
120	<i>C. exilis</i> Harv. subsp. <i>sedifolia</i> (N.E.Br.) Toelken	A:S:Lper:R:C:La (vb)	**	light
121	<i>C. expansa</i> Dryand. subsp. <i>fragilis</i> (Baker) Toelken	E:F:P:El:s (vb)	*	light
122	<i>C. foveata</i> Van Jaarsv.	A:S:Lper:R:C:La (vb)	*	light
123	<i>C. intermedia</i> Schönland	A:S:Lper:R:C:La (vb)	**	light
124	<i>C. lanuginosa</i> Harv. var. <i>lanuginosa</i>	E:F:P:El:s (vb)	**	light
125	<i>C. montana</i> Thunb. subsp. <i>montana</i>	A:S:Lper:R:C:La (vb)	***	light
126	<i>C. montana</i> Thunb. subsp. <i>quadrangularis</i> (Schönland) Toelken	A:S:Lper:R:C:La (vb)	***	light
127	<i>C. nemorosa</i> (Eckl. & Zeyh.) Endl. ex Walp.	A:S:Lar:D (vb)	*	light
128	<i>C. orbicularis</i> L.	A:S:Lper:R:C:La (vb)	*	light
129	<i>C. peculiaris</i> (Toelken) Toelken & Wickens	E:F:P:El:s (vb)	**	light
130	<i>C. pellucida</i> L. subsp. <i>spongiosa</i> Toelken	E:F:P:El:s (vb)	***	light
131	<i>C. perforata</i> Thunb. subsp. <i>kougaensis</i> Van Jaarsv. & A.E.van Wyk	E:F:P:El:s (vb) (eg)	***	light
132	<i>C. perforata</i> Thunb. subsp. <i>perforata</i>	E:F:P:El:s (vb)	*	light-medium
133	<i>C. pseudohemisphaerica</i> Friedrich	A:S:Lper:R:C:La (vb)	**	light
134	<i>C. pubescens</i> Thunb. subsp. <i>rattrayi</i> (Schönland & Baker f.) Toelken	A:S:Lper:Lc:Ts (vb)	**	light
135	<i>C. rupestris</i> Thunb. subsp. <i>marnieriana</i> (H.E.Huber & H.Jacobsen) Toelken	E:F:P:El:s (vb)	***	light-medium
136	<i>C. rupestris</i> Thunb. subsp. <i>rupestris</i>	E:F:P:El:s (vb)	**	light-medium
137	<i>C. sediflora</i> (Eckl. & Zeyh.) Endl. & Walp var. <i>sediflora</i>	E:F:P:El:s (vb)	**	light
138	<i>C. sericea</i> Schönland var. <i>sericea</i>	A:S:Lper:Lc:Ts (vb)	**	light
139	<i>C. setulosa</i> Harv. var. <i>jenkinsii</i> Schönland	A:S:Lper:R:C:La: (vb)	*	light
140	<i>C. setulosa</i> Harv. var. <i>longiciliata</i> Toelken	A:S:Lper:R:C:La (vb)	**	light
141	<i>C. setulosa</i> Harv. var. <i>setulosa</i>	A:S:Lper:R:C:La: (vb)	*	light
142	<i>C. sladenii</i> Schönland	E:F:P:El:s (vb) (e)	***	medium
143	<i>C. smithii</i> Van Jaarsv., D.G.A.Styles & G.McDonald	A:S:Lper:R:C:La (vb)	*	light-medium
144	<i>C. socialis</i> Schönland	A:S:Lper:R:C:La (vb)	**	light
145	<i>C. streyi</i> Toelken	E:F:As:S/H:Es (vb)	*	medium
146	<i>C. tabularis</i> Dinter	A:S:Lper:R:C:La (vb)	*	light
147	<i>C. tomentosa</i> Thunb. var. <i>glabrifolia</i> (Harv.) Toelken	A:S:Lper:R:C:La (vb) (r)	**	light



TABLE 10.1 (continued)—Check list of obligate and near-obligate cremnophilous taxa (220 taxa, 203 species)

No.	Taxon	Vegetative dispersal backup	Geology	Aspect
117	<i>Crassula cymbiformis</i> Toelken	proliferating clusters and leaf stolons	sandstone, quartz	S
118	<i>C. exilis</i> Harv. subsp. <i>cooperi</i> (Regel) Toelken	proliferating clusters and leaf stolons	shale	S
119	<i>C. exilis</i> Harv. subsp. <i>exilis</i>	proliferating clusters and leaf stolons	quartz	S
120	<i>C. exilis</i> Harv. subsp. <i>sedifolia</i> (N.E.Br.) Toelken	proliferating clusters and leaf stolons	quartz	S
121	<i>C. expansa</i> Dryand. subsp. <i>fragilis</i> (Baker) Toelken	proliferating clusters and leaf stolons	sandstone	S
122	<i>C. foveata</i> Van Jaarsv.	proliferating clusters and leaf stolons	shale	N, E, S, W
123	<i>C. intermedia</i> Schönland	proliferating clusters and leaf stolons	sandstone	S
124	<i>C. lanuginosa</i> Harv. var. <i>lanuginosa</i>	proliferating clusters and leaf stolons	shale	S
125	<i>C. montana</i> Thunb. subsp. <i>montana</i>	proliferating clusters and leaf stolons	sandstone	S
126	<i>C. montana</i> Thunb. subsp. <i>quadrangularis</i> (Schönland) Toelken	proliferating clusters and leaf stolons	sandstone	S
127	<i>C. nemorosa</i> (Eckl. & Zeyh.) Endl. ex Walp.	proliferating clusters and leaf stolons	shale, sandstone	S
128	<i>C. orbicularis</i> L.	proliferating clusters and leaf stolons	shale, sandstone	S
129	<i>C. peculiaris</i> (Toelken) Toelken & Wickens	proliferating clusters and leaf stolons	sandstone	S
130	<i>C. pellucida</i> L. subsp. <i>spongiosa</i> Toelken	active growth and rooting	sandstone	S
131	<i>C. perforata</i> Thunb. subsp. <i>kougaensis</i> Van Jaarsv. & A.E.van Wyk	active growth and rooting	sandstone, shale	S, E, W, N
132	<i>C. perforata</i> Thunb. subsp. <i>perforata</i>	active growth and rooting	sandstone	S, E, W, N
133	<i>C. pseudohemisphaerica</i> Friedrich	proliferating clusters and leaf stolons	sandstone, shale	S
134	<i>C. pubescens</i> Thunb. subsp. <i>rattrayi</i> (Schönland & Baker f.) Toelken	proliferating clusters and leaf stolons	shale	S
135	<i>C. rupestris</i> Thunb. subsp. <i>marnieriana</i> (H.E.Huber & H.Jacobsen) Toelken	active growth and rooting	sandstone	S, E, N, W
136	<i>C. rupestris</i> Thunb. subsp. <i>rupestris</i>	active growth and rooting	shale, sandstone	N, E
137	<i>C. sediflora</i> (Eckl. & Zeyh.) Endl. & Walp var. <i>sediflora</i>	active growth and rooting	sandstone	S, E
138	<i>C. sericea</i> Schönland var. <i>sericea</i>	active growth and rooting	quartz	S, E
139	<i>C. setulosa</i> Harv. var. <i>jenkinsii</i> Schönland	proliferating clusters and inflorescence propagules	quartz	N, W, E
140	<i>C. setulosa</i> Harv. var. <i>longiciliata</i> Toelken	proliferating clusters and inflorescence propagules	sandstone	N, W, E
141	<i>C. setulosa</i> Harv. var. <i>setulosa</i>	proliferating clusters and inflorescence propagules	sandstone, basalt	N, W, E
142	<i>C. sladenii</i> Schönland	active growth and rooting	dolomite, sandstone	S, E
143	<i>C. smithii</i> Van Jaarsv., D.G.A.Styles & G.McDonald	dividing or proliferating clusters	sandstone	S
144	<i>C. socialis</i> Schönland	proliferating clusters and leaf stolons	shale	S
145	<i>C. streyi</i> Toelken	dividing or proliferating clusters	sandstone	S, E, W
146	<i>C. tabularis</i> Dinter	proliferating clusters and leaf stolons	sandstone, mudstone	S
147	<i>C. tomentosa</i> Thunb. var. <i>glabrifolia</i> (Harv.) Toelken	proliferating clusters and leaf stolons	sandstone	S



TABLE 10.1 (continued)—Check list of obligate and near-obligate cremnophilous taxa (220 taxa, 203 species)

No.	Taxon	Altitude (m)	Rainfall (mm per annum)	Rainfall seasonality	Deciduousness
				S = summer W = winter W/S = any time of year	E = evergreen SA = summer-aestivating SD = summer-deciduous WD = winter-deciduous
117	<i>Crassula cymbiformis</i> Toelken	1000–1750	700–800	S	E
118	<i>C. exilis</i> Harv. subsp. <i>cooperi</i> (Regel) Toelken	900–1500	500–1000	S	E
119	<i>C. exilis</i> Harv. subsp. <i>exilis</i>	900–1100	100–200	W	E
120	<i>C. exilis</i> Harv. subsp. <i>sedifolia</i> (N.E.Br.) Toelken	500–900	200–300	SW	E
121	<i>C. expansa</i> Dryand. subsp. <i>fragilis</i> (Baker) Toelken	50–1800	450–1000	S	E
122	<i>C. foveata</i> Van Jaarsv.	300–800	800–1000	S	E
123	<i>C. intermedia</i> Schönland	50–500	400–1000	S	E
124	<i>C. lanuginosa</i> Harv. var. <i>lanuginosa</i>	1000–3000	200–450	S	E
125	<i>C. montana</i> Thunb. subsp. <i>montana</i>	200–2000	200–300	W/S	E
126	<i>C. montana</i> Thunb. subsp. <i>quadrangularis</i> (Schönland) Toelken	1000–1400	200–300	W/S	E
127	<i>C. nemorosa</i> (Eckl. & Zeyh.) Endl. ex Walp.	200–1800	200–450	W	SD
128	<i>C. orbicularis</i> L.	50–1800	400–1000	W/S	E
129	<i>C. peculiaris</i> (Toelken) Toelken & Wickens	1200–1800	800–2000	W/S	E
130	<i>C. pellucida</i> L. subsp. <i>spongiosa</i> Toelken	800–1600	800–2000	W	E
131	<i>C. perforata</i> Thunb. subsp. <i>kougaensis</i> Van Jaarsv. & A.E.van Wyk	300–800	400–800	W/S	E
132	<i>C. perforata</i> Thunb. subsp. <i>perforata</i>	300–800	400–800	W/S	E
133	<i>C. pseudohemisphaerica</i> Friedrich	50–900	100–300	W	E
134	<i>C. pubescens</i> Thunb. subsp. <i>rattrayi</i> (Schönland & Baker f.) Toelken	800–1500	300–400	W/S	E
135	<i>C. rupestris</i> Thunb. subsp. <i>marnieriana</i> (H.E.Huber & H.Jacobsen) Toelken	800–2000	250–350	W/S	E
136	<i>C. rupestris</i> Thunb. subsp. <i>rupestris</i>	400–700	400–1000	W/S	E
137	<i>C. sediflora</i> (Eckl. & Zeyh.) Endl. & Walp var. <i>sediflora</i>	350–950	700–1000	S	E
138	<i>C. sericea</i> Schönland var. <i>sericea</i>	100–1000	75–250	S	E
139	<i>C. setulosa</i> Harv. var. <i>jenkinsii</i> Schönland	1000–1800	500–1000	S	E
140	<i>C. setulosa</i> Harv. var. <i>longiciliata</i> Toelken	1000–3000	1000–1500	S	E
141	<i>C. setulosa</i> Harv. var. <i>setulosa</i>	200–3000	800–2000	S	E
142	<i>C. sladenii</i> Schönland	500–1100	75–200	W	E
143	<i>C. smithii</i> Van Jaarsv., D.G.A.Styles & G.McDonald	800–1300	700–800	S	E
144	<i>C. socialis</i> Schönland	800–1200	300–400	W/S	E
145	<i>C. streyi</i> Toelken	50–250	800–1000	S	E
146	<i>C. tabularis</i> Dinter	1200–2000	300–400	S	E
147	<i>C. tomentosa</i> Thunb. var. <i>glabrifolia</i> (Harv.) Toelken	400–1700	75–300	W	E



TABLE 10.1 (continued)—Check list of obligate and near-obligate cremnophilous taxa (220 taxa, 203 species)

No.	Taxon	Fog	Biomes	Pollination
		*** = regular fog ** = occasional fog * = little fog – = no fog	IOCB = Indian Ocean Coastal Belt	
117	<i>Crassula cymbiformis</i> Toelken	*	Grassland	insect
118	<i>C. exilis</i> Harv. subsp. <i>cooperi</i> (Regel) Toelken	*	Grassland	insect
119	<i>C. exilis</i> Harv. subsp. <i>exilis</i>	*	Succulent Karoo	insect
120	<i>C. exilis</i> Harv. subsp. <i>sedifolia</i> (N.E.Br.) Toelken	*	Desert	insect
121	<i>C. expansa</i> Dryand. subsp. <i>fragilis</i> (Baker) Toelken	–	Savanna	insect
122	<i>C. foveata</i> Van Jaarsv.	–	Savanna	insect
123	<i>C. intermedia</i> Schönland	–	Albany Thicket	insect
124	<i>C. lanuginosa</i> Harv. var. <i>lanuginosa</i>	–	Grassland	insect
125	<i>C. montana</i> Thunb. subsp. <i>montana</i>	–	Fynbos	insect
126	<i>C. montana</i> Thunb. subsp. <i>quadrangularis</i> (Schönland) Toelken	*	Albany Thicket	insect
127	<i>C. nemorosa</i> (Eckl. & Zeyh.) Endl. ex Walp.	*	Albany Thicket	insect
128	<i>C. orbicularis</i> L.	–	Albany Thicket	insect
129	<i>C. peculiaris</i> (Toelken) Toelken & Wickens	**	Fynbos	insect
130	<i>C. pellucida</i> L. subsp. <i>spongiosa</i> Toelken	**	Fynbos	insect
131	<i>C. perforata</i> Thunb. subsp. <i>kougaensis</i> Van Jaarsv. & A.E.van Wyk	–	Savanna	insect
132	<i>C. perforata</i> Thunb. subsp. <i>perforata</i>	*	Albany Thicket	insect
133	<i>C. pseudohemisphaerica</i> Friedrich	**	Succulent Karoo	insect
134	<i>C. pubescens</i> Thunb. subsp. <i>rattrayi</i> (Schönland & Baker f.) Toelken	*	Albany Thicket	insect
135	<i>C. rupestris</i> Thunb. subsp. <i>marnieriana</i> (H.E.Huber & H.Jacobsen) Toelken	–	Albany Thicket	insect
136	<i>C. rupestris</i> Thunb. subsp. <i>rupestris</i>	–	Fynbos	insect
137	<i>C. sediflora</i> (Eckl. & Zeyh.) Endl. & Walp var. <i>sediflora</i>	*	Grassland	insect
138	<i>C. sericea</i> Schönland var. <i>sericea</i>	**	Succulent Karoo	insect
139	<i>C. setulosa</i> Harv. var. <i>jenkinsii</i> Schönland	*	Grassland	insect
140	<i>C. setulosa</i> Harv. var. <i>longiciliata</i> Toelken	**	Grassland	insect
141	<i>C. setulosa</i> Harv. var. <i>setulosa</i>	**	Grassland	insect
142	<i>C. sladenii</i> Schönland	***	Succulent Karoo	insect
143	<i>C. smithii</i> Van Jaarsv., D.G.A.Styles & G.McDonald	*	Grassland	insect
144	<i>C. socialis</i> Schönland	–	Albany Thicket	insect
145	<i>C. streyi</i> Toelken	–	IOCB	insect
146	<i>C. tabularis</i> Dinter	–	Nama-Karoo	insect
147	<i>C. tomentosa</i> Thunb. var. <i>glabrifolia</i> (Harv.) Toelken	*	Fynbos	insect



TABLE 10.1 (continued)—Check list of obligate and near-obligate cremnophilous taxa (220 taxa, 203 species)

No.	Taxon	Seed dispersal	Conservation status	Light requirements
			LC = Least Concern NT = Not Threatened VU = Vulnerable	BL = bright light DS = dappled shade FS = full sun
117	<i>Crassula cymbiformis</i> Toelken	wind	LC	FS, BL
118	<i>C. exilis</i> Harv. subsp. <i>cooperi</i> (Regel) Toelken	wind	LC	BL, DS
119	<i>C. exilis</i> Harv. subsp. <i>exilis</i>	wind	LC	BL, DS
120	<i>C. exilis</i> Harv. subsp. <i>sedifolia</i> (N.E.Br.) Toelken	wind	LC	BL, DS
121	<i>C. expansa</i> Dryand. subsp. <i>fragilis</i> (Baker) Toelken	wind	LC	BL, DS
122	<i>C. foveata</i> Van Jaarsv.	wind	LC	FS, BL, DS
123	<i>C. intermedia</i> Schönland	wind	LC	BL, DS
124	<i>C. lanuginosa</i> Harv. var. <i>lanuginosa</i>	wind	LC	FS, BL, DS
125	<i>C. montana</i> Thunb. subsp. <i>montana</i>	wind	LC	BL, DS
126	<i>C. montana</i> Thunb. subsp. <i>quadrangularis</i> (Schönland) Toelken	wind	LC	BL, DS
127	<i>C. nemorosa</i> (Eckl. & Zeyh.) Endl. ex Walp.	wind	LC	BL, DS
128	<i>C. orbicularis</i> L.	wind	LC	BL, DS
129	<i>C. peculiaris</i> (Toelken) Toelken & Wickens	wind	LC	BL, DS
130	<i>C. pellucida</i> L. subsp. <i>spongiosa</i> Toelken	wind	LC	BL, DS
131	<i>C. perforata</i> Thunb. subsp. <i>kougaensis</i> Van Jaarsv. & A.E.van Wyk	wind	LC	FS, BL
132	<i>C. perforata</i> Thunb. subsp. <i>perforata</i>	wind	LC	FS, DS, BL
133	<i>C. pseudoemisphaerica</i> Friedrich	wind	LC	BL, DS
134	<i>C. pubescens</i> Thunb. subsp. <i>rattrayi</i> (Schönland & Baker f.) Toelken	wind	LC	FS, BL
135	<i>C. rupestris</i> Thunb. subsp. <i>marnieriana</i> (H.E.Huber & H.Jacobsen) Toelken	wind	LC	FS, BL
136	<i>C. rupestris</i> Thunb. subsp. <i>rupestris</i>	wind	LC	FS, BL
137	<i>C. sediflora</i> (Eckl. & Zeyh.) Endl. & Walp var. <i>sediflora</i>	wind	LC	FS, BL
138	<i>C. sericea</i> Schönland var. <i>sericea</i>	wind	LC	FS, BL
139	<i>C. setulosa</i> Harv. var. <i>jenkinsii</i> Schönland	wind	LC	FS, BL
140	<i>C. setulosa</i> Harv. var. <i>longiciliata</i> Toelken	wind	LC	FS, BL
141	<i>C. setulosa</i> Harv. var. <i>setulosa</i>	wind	LC	FS, BL
142	<i>C. sladenii</i> Schönland	wind	LC	FS, BL
143	<i>C. smithii</i> Van Jaarsv., D.G.A.Styles & G.McDonald	wind	LC	FS, BL
144	<i>C. socialis</i> Schönland	wind	LC	FS, BL
145	<i>C. streyi</i> Toelken	wind	LC	BL, DS
146	<i>C. tabularis</i> Dinter	wind	LC	FS, BL
147	<i>C. tomentosa</i> Thunb. var. <i>glabrifolia</i> (Harv.) Toelken	wind	LC	BL, DS



TABLE 10.1 (continued)—Check list of obligate and near-obligate cremnophilous taxa (220 taxa, 203 species)

No.	Taxon	Rich flowering	Reduction in armament	Cliff habitat
		*** = rich ** = exposed * = insignificant	*** = margin without teeth ** = margin with smaller teeth * = no significant change, same as other non-cremnophytes	C = coastal R = river E = escarpment M = mountain I = inselberg
117	<i>Crassula cymbiformis</i> Toelken	**	*	M
118	<i>C. exilis</i> Harv. subsp. <i>cooperi</i> (Regel) Toelken	**	*	M
119	<i>C. exilis</i> Harv. subsp. <i>exilis</i>	**	*	M
120	<i>C. exilis</i> Harv. subsp. <i>sedifolia</i> (N.E.Br.) Toelken	**	*	M
121	<i>C. expansa</i> Dryand. subsp. <i>fragilis</i> (Baker) Toelken	**	*	R
122	<i>C. foveata</i> Van Jaarsv.	**	*	R
123	<i>C. intermedia</i> Schönland	**	*	R, M
124	<i>C. lanuginosa</i> Harv. var. <i>lanuginosa</i>	**	*	E
125	<i>C. montana</i> Thunb. subsp. <i>montana</i>	**	*	M, R
126	<i>C. montana</i> Thunb. subsp. <i>quadrangularis</i> (Schönland) Toelken	**	*	R
127	<i>C. nemorosa</i> (Eckl. & Zeyh.) Endl. ex Walp.	**	*	M, R
128	<i>C. orbicularis</i> L.	**	*	M, R
129	<i>C. peculiaris</i> (Toelken) Toelken & Wickens	**	*	M
130	<i>C. pellucida</i> L. subsp. <i>spongiosa</i> Toelken	**	*	M
131	<i>C. perforata</i> Thunb. subsp. <i>kougaensis</i> Van Jaarsv. & A.E.van Wyk	**	*	R, M
132	<i>C. perforata</i> Thunb. subsp. <i>perforata</i>	*	*	R
133	<i>C. pseudoemisphaerica</i> Friedrich	**	*	M, R
134	<i>C. pubescens</i> Thunb. subsp. <i>rattrayi</i> (Schönland & Baker f.) Toelken	**	*	E
135	<i>C. rupestris</i> Thunb. subsp. <i>marnieriana</i> (H.E.Huber & H.Jacobsen) Toelken	**	*	R, M
136	<i>C. rupestris</i> Thunb. subsp. <i>rupestris</i>	**	*	M, R
137	<i>C. sediflora</i> (Eckl. & Zeyh.) Endl. & Walp var. <i>sediflora</i>	**	*	M, R
138	<i>C. sericea</i> Schönland var. <i>sericea</i>	**	*	R
139	<i>C. setulosa</i> Harv. var. <i>jenkinsii</i> Schönland	**	*	E, M
140	<i>C. setulosa</i> Harv. var. <i>longiciliata</i> Toelken	**	*	E
141	<i>C. setulosa</i> Harv. var. <i>setulosa</i>	**	*	E, M
142	<i>C. sladenii</i> Schönland	**	*	M, R
143	<i>C. smithii</i> Van Jaarsv., D.G.A.Styles & G.McDonald	**	*	M
144	<i>C. socialis</i> Schönland	**	*	R
145	<i>C. streyi</i> Toelken	**	*	R
146	<i>C. tabularis</i> Dinter	**	*	M
147	<i>C. tomentosa</i> Thunb. var. <i>glabrifolia</i> (Harv.) Toelken	***	*	M, R



TABLE 10.1 (continued)—Check list of obligate and near-obligate cremnophilous taxa (220 taxa, 203 species)

No.	Taxon	Occurrence	Endemism	Windows
		W = widespread We = widespread but endemic to its vegetation region R = restricted	* = endemic Bots = Botswana Les = Lesotho Moz = Mozambique Nam = Namibia RSA = South Africa Swaz = Swaziland	Lm = on leaf margin Mw = micro-windows O = other
117	<i>Crassula cymbiformis</i> Toelken	R	RSA*	
118	<i>C. exilis</i> Harv. subsp. <i>cooperi</i> (Regel) Toelken	We	RSA*	
119	<i>C. exilis</i> Harv. subsp. <i>exilis</i>	We	RSA*	
120	<i>C. exilis</i> Harv. subsp. <i>sedifolia</i> (N.E.Br.) Toelken	We	RSA, Nam	
121	<i>C. expansa</i> Dryand. subsp. <i>fragilis</i> (Baker) Toelken	W	RSA, Swaz, Moz	
122	<i>C. foveata</i> Van Jaarsv.	We	RSA*	
123	<i>C. intermedia</i> Schönland	W	RSA*	
124	<i>C. lanuginosa</i> Harv. var. <i>lanuginosa</i>	We	RSA, Les	
125	<i>C. montana</i> Thunb. subsp. <i>montana</i>	W	RSA*	
126	<i>C. montana</i> Thunb. subsp. <i>quadrangularis</i> (Schönland) Toelken	We	RSA*	
127	<i>C. nemorosa</i> (Eckl. & Zeyh.) Endl. ex Walp.	W	RSA, Nam	
128	<i>C. orbicularis</i> L.	W	RSA*	
129	<i>C. peculiaris</i> (Toelken) Toelken & Wickens	R	RSA*	
130	<i>C. pellucida</i> L. subsp. <i>spongiosa</i> Toelken	We	RSA*	
131	<i>C. perforata</i> Thunb. subsp. <i>kougaensis</i> Van Jaarsv. & A.E.van Wyk	We	RSA*	
132	<i>C. perforata</i> Thunb. subsp. <i>perforata</i>	We	RSA*	
133	<i>C. pseudohemisphaerica</i> Friedrich	We	RSA, Nam	
134	<i>C. pubescens</i> Thunb. subsp. <i>rattrayi</i> (Schönland & Baker f.) Toelken	We	RSA*	
135	<i>C. rupestris</i> Thunb. subsp. <i>marnieriana</i> (H.E.Huber & H.Jacobsen) Toelken	We	RSA*	
136	<i>C. rupestris</i> Thunb. subsp. <i>rupestris</i>	W	RSA*	
137	<i>C. sediflora</i> (Eckl. & Zeyh.) Endl. & Walp var. <i>sediflora</i>	We	RSA*	
138	<i>C. sericea</i> Schönland var. <i>sericea</i>	We	RSA*	
139	<i>C. setulosa</i> Harv. var. <i>jenkinsii</i> Schönland	W	RSA*	
140	<i>C. setulosa</i> Harv. var. <i>longiciliata</i> Toelken	W	RSA*	
141	<i>C. setulosa</i> Harv. var. <i>setulosa</i>	W	RSA, Les, Swaz	
142	<i>C. sladenii</i> Schönland	We	RSA, Nam	
143	<i>C. smithii</i> Van Jaarsv., D.G.A.Styles & G.McDonald	R	RSA*	
144	<i>C. socialis</i> Schönland	We	RSA*	
145	<i>C. streyi</i> Toelken	We	RSA*	
146	<i>C. tabularis</i> Dinter	We	RSA, Nam	
147	<i>C. tomentosa</i> Thunb. var. <i>glabrifolia</i> (Harv.) Toelken	We	RSA*	



TABLE 10.1 (continued)—Check list of obligate and near-obligate cremnophilous taxa (220 taxa, 203 species)

No.	Taxon	Cremonophilous growth form	Degree of cliff occupation	Weight class
		See 9.1.2 for explanation of the symbols below	*** = strictly obligate cremnophyte, displaying cliff-adapted features ** = obligate cremnophyte * = predominantly on cliffs (80%)	light = < 50 g medium = 51–500 g heavy = >500 g
	Tylecodon Toelken (14 taxa)			
148	<i>T. aurusbergensis</i> G.Will. & Van Jaarsv.	E:F:As:S/H:Ca:D (vb)	**	light
149	<i>T. bleckiae</i> G.Will.	E:F:As:S/H:Ca:D (vb)	**	light-medium
150	<i>T. bodleyae</i> Van Jaarsv.	E:F:As:S/H:Ca:D (vb)	**	light-medium
151	<i>T. bruynsii</i> Van Jaarsv. & S.A.Hammer	E:F:As:S/H:Ca:D (vb)	***	light-medium
152	<i>T. buchholzianus</i> (Schuldt. & P.Stephan) Toelken var. <i>fasciculatus</i> G.Will.	E:F:As:S/H:Ca:D (vb)	**	light-medium
153	<i>T. cordiformis</i> G.Will.	E:F:As:S/H:Ca:D (vb) (ft)	**	light
154	<i>T. decipiens</i> Toelken	A:S:Lar:D (vb)	**	light-medium
155	<i>T. ellaphieae</i> Van Jaarsv.	A:S:Lar:D (vb) (ft)	***	light-medium
156	<i>T. longipes</i> Van Jaarsv. & G.Will.	A:S:Lar:D (vb)	***	light-medium
157	<i>T. petrophilus</i> Van Jaarsv. & A.E.van Wyk	A:S:Lar:D (vb)	***	medium
158	<i>T. singularis</i> (R.A.Dyer) Toelken	A:S:Lar:D (ft)	*	light
159	<i>T. sulphureus</i> (Toelken) Toelken var. <i>armianus</i> Van Jaarsv.	E:F:As:S/H:Ca:D (vb)	**	light
160	<i>T. torulosus</i> Toelken	E:F:As:S/H:Ca:D (vb)	***	light-medium
161	<i>T. viridiflorus</i> (Toelken) Toelken	E:F:As:S/H:Ca:D (vb)	**	light-medium
	GERANIACEAE (2 species)			
	Pelargonium L'Her. (2 species)			
162	<i>P. mutans</i> Vorster	E:F:As:S/H:Es (vb)	**	medium
163	<i>P. vanderwaltii</i> Van Jaarsv.	E:F:As:S/H:Es (vb)	**	medium
	GESNERIACEAE (1 species)			
	Streptocarpus Lindl. (1 species)			
164	<i>S. kentaniensis</i> L.L.Britten & Story	A:S:Lper:Lc:Ts (vb)	***	medium
	LAMIACEAE (3 genera, 9 taxa)			
	Aeollanthus Mart. ex Spreng. (2 species)			
165	<i>A. haumannii</i> Van Jaarsv.	E:F:As:S/H:Es (vb)	*	light-medium
166	<i>A. rydingianus</i> Van Jaarsv. & A.E.van Wyk	E:F:AS:S/H:Es (vb)	*	medium
	Plectranthus L'Her. (6 taxa)			
167	<i>P. dolomiticus</i> Codd	E:F:P:Els (vb)	*	light-medium
168	<i>P. ernstii</i> Codd	E:F:As:S/H:Ca:Ev (vb)	***	light-medium
169	<i>P. mutabilis</i> Codd	E:F:P:Els (vb)	**	light-medium
170	<i>P. mzimvubuensis</i> Van Jaarsv.	E:F:As:S/H:Es (vb)	**	medium-heavy
171	<i>P. purpuratus</i> Harv. subsp. <i>purpuratus</i>	E:F:As:S/H:Es (vb)	**	light
172	<i>P. saccatus</i> Benth. subsp. <i>pondoensis</i> Van Jaarsv. & Milstein	E:F:P:Els (vb)	**	medium-heavy
	Tetradenia Benth. (1 species)			
173	<i>T. kaokoensis</i> Van Jaarsv. & A.E.van Wyk	E:F:As:W:D	***	medium



TABLE 10.1 (continued)—Check list of obligate and near-obligate cremnophilous taxa (220 taxa, 203 species)

No.	Taxon	Vegetative dispersal backup	Geology	Aspect
Tylecodon Toelken (14 taxa)				
148	<i>T. aurusbergensis</i> G.Will. & Van Jaarsv.	active growth and rooting	quartz	S
149	<i>T. bleckiae</i> G.Will.	active growth and rooting	sandstone	S
150	<i>T. bodleyae</i> Van Jaarsv.	active growth and rooting	quartz	S, E
151	<i>T. bruynsii</i> Van Jaarsv. & S.A.Hammer	active growth and rooting	quartz	S
152	<i>T. buchholzianus</i> (Schuldt. & P.Stephan) Toelken var. <i>fasciculatus</i> G.Will.	active growth and rooting	quartz	E, S
153	<i>T. cordiformis</i> G.Will.	active growth and rooting	quartz	E
154	<i>T. decipiens</i> Toelken	active growth and rooting	quartz	S
155	<i>T. ellaphieae</i> Van Jaarsv.	active growth and rooting	quartz	S
156	<i>T. longipes</i> Van Jaarsv. & G.Will.	active growth and rooting	quartz	S
157	<i>T. petrophilus</i> Van Jaarsv. & A.E.van Wyk	active growth and rooting	quartz	S
158	<i>T. singularis</i> (R.A.Dyer) Toelken	solitary	dolomite	S
159	<i>T. sulphureus</i> (Toelken) Toelken var. <i>armianus</i> Van Jaarsv.	active growth and rooting	quartz	S
160	<i>T. torulosus</i> Toelken	active growth and rooting	quartz	E
161	<i>T. viridiflorus</i> (Toelken) Toelken	active growth and rooting	quartz	S
GERANIACEAE (2 species)				
Pelargonium L'Her. (2 species)				
162	<i>P. mutans</i> Vorster	active growth and rooting	dolomite, sandstone	S, N
163	<i>P. vanderwaltii</i> Van Jaarsv.	active growth and rooting	granite	S
GESNERIACEAE (1 species)				
Streptocarpus Lindl. (1 species)				
164	<i>S. kentaniensis</i> L.L.Britten & Story	proliferating clusters and leaf stolons	shale	S
LAMIACEAE (3 genera, 9 taxa)				
Aeollanthus Mart. ex Spreng. (2 species)				
165	<i>A. haumannii</i> Van Jaarsv.	active growth and rooting	granite	S
166	<i>A. rydingianus</i> Van Jaarsv. & A.E.van Wyk	active growth and rooting	sandstone	S
Plectranthus L'Her. (6 taxa)				
167	<i>P. dolomiticus</i> Codd	active growth and rooting	dolomite	S, E
168	<i>P. ernstii</i> Codd	active growth and rooting	sandstone	S
169	<i>P. mutabilis</i> Codd	active growth and rooting	sandstone, dolomite	S, E, W
170	<i>P. mzimvubuensis</i> Van Jaarsv.	active growth and rooting	shale	S
171	<i>P. purpuratus</i> Harv. subsp. <i>purpuratus</i>	active growth and rooting	sandstone	S
172	<i>P. saccatus</i> Benth. subsp. <i>pondoensis</i> Van Jaarsv. & Milstein	active growth and rooting	sandstone	S, E
Tetradenia Benth. (1 species)				
173	<i>T. kaokoensis</i> Van Jaarsv. & A.E.van Wyk	solitary	dolomite, sandstone, granite	S, E



TABLE 10.1 (continued)—Check list of obligate and near-obligate cremnophilous taxa (220 taxa, 203 species)

No.	Taxon	Altitude (m)	Rainfall (mm per annum)	Rainfall seasonality	Deciduousness
				S = summer W = winter W/S = any time of year	E = evergreen SA = summer-aestivating SD = summer-deciduous WD = winter-deciduous
Tylecodon Toelken (14 taxa)					
148	<i>T. aurusbergensis</i> G.Will. & Van Jaarsv.	900–1082	50–75	W	SD
149	<i>T. bleckiae</i> G.Will.	600–900	50–150	W	SD
150	<i>T. bodleyae</i> Van Jaarsv.	350–470	50	W	SD
151	<i>T. bruynsii</i> Van Jaarsv. & S.A.Hammer	700–900	50–125	W	SD
152	<i>T. buchholzianus</i> (Schuldt. & P.Stephan) Toelken var. <i>fasciculatus</i> G.Will.	50–700	25–50	W	SD
153	<i>T. cordiformis</i> G.Will.	400–600	50–75	W	SD
154	<i>T. decipiens</i> Toelken	300–480	50–75	W	SD
155	<i>T. ellaphieae</i> Van Jaarsv.	400–1200	50–150	W	SD
156	<i>T. longipes</i> Van Jaarsv. & G.Will.	400–800	50–75	W	SD
157	<i>T. petrophilus</i> Van Jaarsv. & A.E.van Wyk	400–500	100–250	W	SD
158	<i>T. singularis</i> (R.A.Dyer) Toelken	800–1100	50–75	W	SD
159	<i>T. sulphureus</i> (Toelken) Toelken var. <i>armianus</i> Van Jaarsv.	700–1100	50–100	W	SD
160	<i>T. torulosus</i> Toelken	300–500	50–75	W	SD
161	<i>T. viridiflorus</i> (Toelken) Toelken	600–900	50–100	W	SD
GERANIACEAE (2 species)					
Pelargonium L'Her. (2 species)					
162	<i>P. mutans</i> Vorster	400–1000	800–1000	S	E
163	<i>P. vanderwaltii</i> Van Jaarsv.	1800–1900	150–250	S	WD
GESNERIACEAE (1 species)					
Streptocarpus Lindl. (1 species)					
164	<i>S. kentaniensis</i> L.L.Britten & Story	100–200	1000–1250	S	E
LAMIACEAE (3 genera, 9 taxa)					
Aeollanthus Mart. ex Spreng. (2 species)					
165	<i>A. haumannii</i> Van Jaarsv.	1500–1900	150–250	S	E
166	<i>A. rydingianus</i> Van Jaarsv. & A.E.van Wyk	1600	250–300	S	E
Plectranthus L'Her. (6 taxa)					
167	<i>P. dolomiticus</i> Codd	800–1000	500–500	S	E
168	<i>P. ernstii</i> Codd	200–350	1000–1250	S	E
169	<i>P. mutabilis</i> Codd	1000–2230	600–1250	S	E
170	<i>P. mzimvubuensis</i> Van Jaarsv.	300–800	1000–1250	S	E
171	<i>P. purpuratus</i> Harv. subsp. <i>purpuratus</i>	460–795	1000–1250	S	E
172	<i>P. saccatus</i> Benth. subsp. <i>pondoensis</i> Van Jaarsv. & Milstein	300–600	1000–1250	S	E
Tetradenia Benth. (1 species)					
173	<i>T. kaokoensis</i> Van Jaarsv. & A.E.van Wyk	1600–2000	200–250	S	WD



TABLE 10.1 (continued)—Check list of obligate and near-obligate cremnophilous taxa (220 taxa, 203 species)

No.	Taxon	Fog	Biomes	Pollination
		*** = regular fog ** = occasional fog * = little fog – = no fog	IOCB = Indian Ocean Coastal Belt	
	Tylecodon Toelken (14 taxa)			
148	<i>T. aurusbergensis</i> G.Will. & Van Jaarsv.	***	Succulent Karoo	insect
149	<i>T. bleckiae</i> G.Will.	***	Succulent Karoo	insect
150	<i>T. bodleyae</i> Van Jaarsv.	***	Succulent Karoo	insect
151	<i>T. bruynsii</i> Van Jaarsv. & S.A.Hammer	***	Succulent Karoo	insect
152	<i>T. buchholzianus</i> (Schuldt. & P.Stephan) Toelken var. <i>fasciculatus</i> G.Will.	***	Succulent Karoo	insect
153	<i>T. cordiformis</i> G.Will.	***	Succulent Karoo	insect
154	<i>T. decipiens</i> Toelken	***	Succulent Karoo	insect
155	<i>T. ellaphieae</i> Van Jaarsv.	***	Succulent Karoo	insect
156	<i>T. longipes</i> Van Jaarsv. & G.Will.	***	Succulent Karoo	insect
157	<i>T. petrophilus</i> Van Jaarsv. & A.E.van Wyk	**	Succulent Karoo	insect
158	<i>T. singularis</i> (R.A.Dyer) Toelken	***	Succulent Karoo	insect
159	<i>T. sulphureus</i> (Toelken) Toelken var. <i>armianus</i> Van Jaarsv.	*	Desert	insect
160	<i>T. torulosus</i> Toelken	***	Succulent Karoo	insect
161	<i>T. viridiflorus</i> (Toelken) Toelken	***	Succulent Karoo	insect
	GERANIACEAE (2 species)			
	Pelargonium L'Her. (2 species)			
162	<i>P. mutans</i> Vorster	–	Savanna	insect
163	<i>P. vanderwaltii</i> Van Jaarsv.	–	Desert	insect
	GESNERIACEAE (1 species)			
	Streptocarpus Lindl. (1 species)			
164	<i>S. kentaniensis</i> L.L.Britten & Story	–	Savanna	insect
	LAMIACEAE (3 genera, 9 taxa)			
	Aeollanthus Mart. ex Spreng. (2 species)			
165	<i>A. haumannii</i> Van Jaarsv.	*	Desert	insect
166	<i>A. rydingianus</i> Van Jaarsv. & A.E.van Wyk	*	Savanna	insect
	Plectranthus L'Her. (6 taxa)			
167	<i>P. dolomiticus</i> Codd	–	Savanna	insect
168	<i>P. ernstii</i> Codd	*	IOCB	insect
169	<i>P. mutabilis</i> Codd	*	Savanna	insect
170	<i>P. mzimvubuensis</i> Van Jaarsv.	–	Savanna	insect
171	<i>P. purpuratus</i> Harv. subsp. <i>purpuratus</i>	*	IOCB	insect
172	<i>P. saccatus</i> Benth. subsp. <i>pondoensis</i> Van Jaarsv. & Milstein	–	IOCB	insect
	Tetradenia Benth. (1 species)			
173	<i>T. kaokoensis</i> Van Jaarsv. & A.E.van Wyk	*	Desert	insect



TABLE 10.1 (continued)—Check list of obligate and near-obligate cremnophilous taxa (220 taxa, 203 species)

No.	Taxon	Seed dispersal	Conservation status	Light requirements
			LC = Least Concern NT = Not Threatened VU = Vulnerable	BL = bright light DS = dappled shade FS = full sun
Tylecodon Toelken (14 taxa)				
148	<i>T. aurusbergensis</i> G.Will. & Van Jaarsv.	wind	LC	BL, DS
149	<i>T. bleckiae</i> G.Will.	wind	LC	BL, DS
150	<i>T. bodleyae</i> Van Jaarsv.	wind	LC	BL, DS
151	<i>T. bruynsii</i> Van Jaarsv. & S.A.Hammer	wind	LC	BL
152	<i>T. buchholzianus</i> (Schuldt. & P.Stephan) Toelken var. <i>fasciculatus</i> G.Will.	wind	LC	BL, DS
153	<i>T. cordiformis</i> G.Will.	wind	LC	BL, DS
154	<i>T. decipiens</i> Toelken	wind	LC	BL, DS
155	<i>T. ellaphieae</i> Van Jaarsv.	wind	LC	BL, DS
156	<i>T. longipes</i> Van Jaarsv. & G.Will.	wind	LC	BL, DS
157	<i>T. petrophilus</i> Van Jaarsv. & A.E.van Wyk	wind	LC	BL, DS
158	<i>T. singularis</i> (R.A.Dyer) Toelken	wind	LC	BL, DS
159	<i>T. sulphureus</i> (Toelken) Toelken var. <i>armianus</i> Van Jaarsv.	wind	LC	BL, DS
160	<i>T. torulosus</i> Toelken	wind	LC	BL, DS
161	<i>T. viridiflorus</i> (Toelken) Toelken	wind	LC	BL, DS
GERANIACEAE (2 species)				
Pelargonium L'Her. (2 species)				
162	<i>P. mutans</i> Vorster	wind	LC	FS, BL, DS
163	<i>P. vanderwaltii</i> Van Jaarsv.	wind	LC	FS, BL
GESNERIACEAE (1 species)				
Streptocarpus Lindl. (1 species)				
164	<i>S. kentaniensis</i> L.L.Britten & Story	wind	LC	BL, DS
LAMIACEAE (3 genera, 9 taxa)				
Aeollanthus Mart. ex Spreng. (2 species)				
165	<i>A. haumannii</i> Van Jaarsv.	autochory	LC	BL, DS
166	<i>A. rydingianus</i> Van Jaarsv. & A.E.van Wyk	autochory	LC	BL, DS
Plectranthus L'Her. (6 taxa)				
167	<i>P. dolomiticus</i> Codd	autochory	LC	BL, DS
168	<i>P. ernstii</i> Codd	autochory	LC	BL, DS
169	<i>P. mutabilis</i> Codd	autochory	LC	BL, DS
170	<i>P. mzimvubuensis</i> Van Jaarsv.	autochory	LC	BL, DS
171	<i>P. purpuratus</i> Harv. subsp. <i>purpuratus</i>	autochory	LC	BL, DS
172	<i>P. saccatus</i> Benth. subsp. <i>pondoensis</i> Van Jaarsv. & Milstein	autochory	LC	BL, DS
Tetradenia Benth. (1 species)				
173	<i>T. kaokoensis</i> Van Jaarsv. & A.E.van Wyk	wind	LC	FS, BL, DS



TABLE 10.1 (continued)—Check list of obligate and near-obligate cremnophilous taxa (220 taxa, 203 species)

No.	Taxon	Rich flowering	Reduction in armament	Cliff habitat
		*** = rich ** = exposed * = insignificant	*** = margin without teeth ** = margin with smaller teeth * = no significant change, same as other non-cremnophytes	C = coastal R = river E = escarpment M = mountain I = inselberg
	Tylecodon Toelken (14 taxa)			
148	<i>T. aurusbergensis</i> G.Will. & Van Jaarsv.	**	*	I
149	<i>T. bleckiae</i> G.Will.	**	*	M
150	<i>T. bodleyae</i> Van Jaarsv.	**	*	M
151	<i>T. bruynsii</i> Van Jaarsv. & S.A.Hammer	**	*	R
152	<i>T. buchholzianus</i> (Schuldt. & P.Stephan) Toelken var. <i>fasciculatus</i> G.Will.	**	*	M
153	<i>T. cordiformis</i> G.Will.	**	*	M
154	<i>T. decipiens</i> Toelken	**	*	R
155	<i>T. ellaphieae</i> Van Jaarsv.	***	*	M
156	<i>T. longipes</i> Van Jaarsv. & G.Will.	**	*	R
157	<i>T. petrophilus</i> Van Jaarsv. & A.E.van Wyk	**	*	R
158	<i>T. singularis</i> (R.A.Dyer) Toelken	**	*	M
159	<i>T. sulphureus</i> (Toelken) Toelken var. <i>armianus</i> Van Jaarsv.	**	*	R, I
160	<i>T. torulosus</i> Toelken	**	*	R, M
161	<i>T. viridiflorus</i> (Toelken) Toelken	**	*	M
	GERANIACEAE (2 species)			
	Pelargonium L'Her. (2 species)			
162	<i>P. mutans</i> Vorster	**	*	R, M
163	<i>P. vanderwaltii</i> Van Jaarsv.	**	*	I
	GESNERIACEAE (1 species)			
	Streptocarpus Lindl. (1 species)			
164	<i>S. kentaniensis</i> L.L.Britten & Story	**	*	R
	LAMIACEAE (3 genera, 9 taxa)			
	Aeollanthus Mart. ex Spreng. (2 species)			
165	<i>A. haumannii</i> Van Jaarsv.	**	*	I
166	<i>A. rydingianus</i> Van Jaarsv. & A.E.van Wyk	**	*	E
	Plectranthus L'Her. (6 taxa)			
167	<i>P. dolomiticus</i> Codd	**	*	R
168	<i>P. ernstii</i> Codd	**	*	R
169	<i>P. mutabilis</i> Codd	**	*	M, R
170	<i>P. mzimvubuensis</i> Van Jaarsv.	**	*	R
171	<i>P. purpuratus</i> Harv. subsp. <i>purpuratus</i>	**	*	M, R
172	<i>P. saccatus</i> Benth. subsp. <i>pondoensis</i> Van Jaarsv. & Milstein	**	*	R, M
	Tetradenia Benth. (1 species)			
173	<i>T. kaokoensis</i> Van Jaarsv. & A.E.van Wyk	***	*	E



TABLE 10.1 (continued)—Check list of obligate and near-obligate cremnophilous taxa (220 taxa, 203 species)

No.	Taxon	Occurrence	Endemism	Windows
		W = widespread We = widespread but endemic to its vegetation region R = restricted	* = endemic Bots = Botswana Les = Lesotho Moz = Mozambique Nam = Namibia RSA = South Africa Swaz = Swaziland	Lm = on leaf margin Mw = micro-windows O = other
	Tylecodon Toelken (14 taxa)			
148	<i>T. aurusbergensis</i> G.Will. & Van Jaarsv.	R	Nam*	
149	<i>T. bleckiae</i> G.Will.	R	RSA, Nam	
150	<i>T. bodleyae</i> Van Jaarsv.	R	RSA*	
151	<i>T. bruynsii</i> Van Jaarsv. & S.A.Hammer	R	Nam*	
152	<i>T. buchholzianus</i> (Schuldt. & P.Stephan) Toelken var. <i>fasciculatus</i> G.Will.	R	RSA*	
153	<i>T. cordiformis</i> G.Will.	R	RSA*	
154	<i>T. decipiens</i> Toelken	R	RSA*	
155	<i>T. ellaphieae</i> Van Jaarsv.	R	RSA*	
156	<i>T. longipes</i> Van Jaarsv. & G.Will.	R	RSA*	
157	<i>T. petrophilus</i> Van Jaarsv. & A.E.van Wyk	R	RSA*	
158	<i>T. singularis</i> (R.A.Dyer) Toelken	We	Nam*	
159	<i>T. sulphureus</i> (Toelken) Toelken var. <i>armianus</i> Van Jaarsv.	We	RSA*	
160	<i>T. torulosus</i> Toelken	R	RSA*	
161	<i>T. viridiflorus</i> (Toelken) Toelken	We	RSA*	
	GERANIACEAE (2 species)			
	Pelargonium L'Her. (2 species)			
162	<i>P. mutans</i> Vorster	We	RSA*	
163	<i>P. vanderwaltii</i> Van Jaarsv.	R	Nam*	
	GESNERIACEAE (1 species)			
	Streptocarpus Lindl. (1 species)			
164	<i>S. kentaniensis</i> L.L.Britten & Story	We	RSA*	
	LAMIACEAE (3 genera, 9 taxa)			
	Aeollanthus Mart. ex Spreng. (2 species)			
165	<i>A. haumannii</i> Van Jaarsv.	R	Nam*	
166	<i>A. rydingianus</i> Van Jaarsv. & A.E.van Wyk	R	Nam*	
	Plectranthus L'Her. (6 taxa)			
167	<i>P. dolomiticus</i> Codd	R	RSA*	
168	<i>P. ernstii</i> Codd	We	RSA*	
169	<i>P. mutabilis</i> Codd	W	RSA*	
170	<i>P. mzimvubuensis</i> Van Jaarsv.	R	RSA*	
171	<i>P. purpuratus</i> Harv. subsp. <i>purpuratus</i>	We	RSA*	
172	<i>P. saccatus</i> Benth. subsp. <i>pondoensis</i> Van Jaarsv. & Milstein	We	RSA*	
	Tetradenia Benth. (1 species)			
173	<i>T. kaokoensis</i> Van Jaarsv. & A.E.van Wyk	We	Nam*	



TABLE 10.1 (continued)—Check list of obligate and near-obligate cremnophilous taxa (220 taxa, 203 species)

No.	Taxon	Cremonophilous growth form	Degree of cliff occupation	Weight class
		See 9.1.2 for explanation of the symbols below	*** = strictly obligate cremnophyte, displaying cliff-adapted features ** = obligate cremnophyte * = predominantly on cliffs (80%)	light = < 50 g medium = 51–500 g heavy = >500 g
	MESEMBRYANTHEMACEAE (12 genera, 45 taxa)			
	<i>Carruanthus</i> (Schwantes) Schwantes (1 species)			
174	<i>C. peersii</i> L.Bolus	E:F:P:Els (vb) (r)	***	light-medium
	Conophytum N.E.Br. (19 taxa)			
175	<i>C. auriflorum</i> Tischer subsp. <i>turbiniforme</i> (Rawe) S.A.Hammer	A:S:Lar:Lf (vb) (r)		light-medium
176	<i>C. bolusiae</i> Schwantes subsp. <i>bolusiae</i>	A:S:Lar:Lf (vb) (r)	***	light-medium
177	<i>C. carpiantum</i> L.Bolus	A:S:Lar:Lf (vb) (r)	***	light-medium
178	<i>C. danielii</i> Pavelka	A:S:Lar:Lf (vb) (ft) (r)	***	light
179	<i>C. ernstii</i> S.A.Hammer subsp. <i>ernstii</i>	A:S:Lar:Lf (vb) (r) (ft)	***	light-medium
180	<i>C. francoiseae</i> (S.A.Hammer) S.A.Hammer	A:S:Lar:Lf (vb) (r)	***	light-medium
181	<i>C. fulleri</i> L.Bolus	A:S:Lar:Lf (vb) (r)	***	light-medium
182	<i>C. hanae</i> Pavelka	A:S:Lar:Lf (vb) (r)	**	light
183	<i>C. luckhoffii</i> Lavis	A:S:Lar:Lf (vb) (r)	**	light
184	<i>C. marginatum</i> Lavis subsp. <i>haramoepense</i> (L.Bolus) S.A.Hammer	A:S:Lar:Lf (vb) (r)	***	light
185	<i>C. marginatum</i> Lavis subsp. <i>littlewoodii</i> (L.Bolus) S.A.Hammer	A:S:Lar:Lf (vb) (r)	***	light
186	<i>C. obscurum</i> N.E.Br. subsp. <i>sponsaliorum</i> (S.A.Hammer) S.A.Hammer	A:S:Lar:Lf (vb) (r)	***	light
187	<i>C. quaesitum</i> (N.E.Br.) N.E.Br. subsp. <i>densipunctum</i> (L.Bolus) S.A.Hammer	A:S:Lar:Lf (vb)	**	light
188	<i>C. quaesitum</i> (N.E.Br.) N.E.Br. subsp. <i>quaesitum</i> var. <i>rostratum</i> (Tischer) S.A.Hammer	A:S:Lar:Lf (vb)	**	light
189	<i>C. ricardianum</i> Loesch & Tischer subsp. <i>ricardianum</i>	A:S:Lar:Lf (vb) (r) (ft)	***	light-medium
190	<i>C. stephanii</i> Schwantes subsp. <i>stephanii</i>	A:S:Lar:Lf (vb) (ft) (r)	***	light
191	<i>C. tantillum</i> N.E.Br. subsp. <i>amicorum</i> S.A.Hammer & Barnhill	A:S:Lar:Lf (vb) (r)	***	light
192	<i>C. taylorianum</i> (Dinter & Schwantes) N.E.Br. subsp. <i>ernianum</i> (Loesch & Tischer) de Boer ex S.A.Hammer	A:S:Lar:Lf (vb) (r)	***	light
193	<i>C. taylorianum</i> (Dinter & Schwantes) N.E.Br. subsp. <i>rosynense</i> S.A.Hammer	A:S:Lar:Lf (vb) (r)	***	light
	Delosperma N.E.Br. emend Lavis (12 taxa)			
194	<i>Delosperma</i> sp. A	E:F:P:Els (vb)	*	light-medium
195	<i>Delosperma</i> sp. B	E:F:P:Els (vb)	**	medium
196	<i>D. esterhuyseniae</i> L.Bolus	E:F:P:Els (vb)	**	light
197	<i>D. knox-daviesii</i> Lavis	E:F:P:Els (vb)	**	light
198	<i>D. laxipetalum</i> L.Bolus	E:F:As:S/H:Es (vb)	**	medium
199	<i>D. nubigenum</i> (Schltr.) L.Bolus	E:F:P:Els (vb)	**	medium
200	<i>D. saxicola</i> Lavis	E:F:P:Els (vb)	***	light-medium
201	<i>D. subpetiolatum</i> L.Bolus	E:F:P:Els (vb)	**	light-medium
202	<i>D. tradescantioides</i> (A.Berger) L.Bolus	E:F:P:Els (vb)	**	medium
203	<i>D. velutinum</i> L.Bolus	E:F:P:Els (vb)	**	medium
204	<i>D. waterbergense</i> L.Bolus	E:F:P:Els (vb)	**	light
205	<i>D. zoutpansbergense</i> L.Bolus	E:F:P:Els (vb)	**	light



TABLE 10.1 (continued)—Check list of obligate and near-obligate cremnophilous taxa (220 taxa, 203 species)

No.	Taxon	Vegetative dispersal backup	Geology	Aspect
	MESEMBRYANTHEMACEAE (12 genera, 45 taxa)			
	<i>Carruanthus</i> (Schwantes) Schwantes (1 species)			
174	<i>C. peersii</i> L.Bolus	active growth and rooting	sandstone	E
	Conophytum N.E.Br. (19 taxa)			
175	<i>C. auriflorum</i> Tischer subsp. <i>turbiniforme</i> (Rawe) S.A.Hammer	dividing or proliferating clusters	quartz	S
176	<i>C. bolusiae</i> Schwantes subsp. <i>bolusiae</i>	dividing or proliferating clusters	quartz	E, S
177	<i>C. carpianum</i> L.Bolus	dividing or proliferating clusters	granite	S
178	<i>C. danielii</i> Pavelka	dividing or proliferating clusters	granite	S
179	<i>C. ernstii</i> S.A.Hammer subsp. <i>ernstii</i>	dividing or proliferating clusters	quartz	S, W
180	<i>C. francoiseae</i> (S.A.Hammer) S.A.Hammer	dividing or proliferating clusters	quartz	E, S
181	<i>C. fulleri</i> L.Bolus	dividing or proliferating clusters	quartz	S
182	<i>C. hanae</i> Pavelka	dividing or proliferating clusters	gneiss	S
183	<i>C. luckhoffii</i> Lavis	dividing or proliferating clusters	sandstone	S
184	<i>C. marginatum</i> Lavis subsp. <i>haramoepense</i> (L.Bolus) S.A.Hammer	dividing or proliferating clusters	quartz	S
185	<i>C. marginatum</i> Lavis subsp. <i>littlewoodii</i> (L.Bolus) S.A.Hammer	dividing or proliferating clusters	quartz	S
186	<i>C. obscurum</i> N.E.Br. subsp. <i>sponsaliorum</i> (S.A.Hammer) S.A.Hammer	dividing or proliferating clusters	quartz	S
187	<i>C. quaesitum</i> (N.E.Br.) N.E.Br. subsp. <i>densipunctum</i> (L.Bolus) S.A.Hammer	dividing or proliferating clusters	quartz	S
188	<i>C. quaesitum</i> (N.E.Br.) N.E.Br. subsp. <i>quaesitum</i> var. <i>rostratum</i> (Tischer) S.A.Hammer	dividing or proliferating clusters	quartz	S
189	<i>C. ricardianum</i> Loesch & Tischer subsp. <i>ricardianum</i>	dividing or proliferating clusters	quartz	S
190	<i>C. stephanii</i> Schwantes subsp. <i>stephanii</i>	dividing or proliferating clusters	quartz	S
191	<i>C. tantillum</i> N.E.Br. subsp. <i>amicorum</i> S.A.Hammer & Barnhill	dividing or proliferating clusters	quartz	S
192	<i>C. taylorianum</i> (Dinter & Schwantes) N.E.Br. subsp. <i>ernianum</i> (Loesch & Tischer) de Boer ex S.A.Hammer	dividing or proliferating clusters	quartz	S
193	<i>C. taylorianum</i> (Dinter & Schwantes) N.E.Br. subsp. <i>rosynense</i> S.A.Hammer	dividing or proliferating clusters	quartz	S
	Delosperma N.E.Br. emend Lavis (12 taxa)			
194	<i>Delosperma</i> sp. A	active growth and rooting	sandstone	S, E, W
195	<i>Delosperma</i> sp. B	active growth and rooting	sandstone	E, S
196	<i>D. esterhuyseniae</i> L.Bolus	active growth and rooting	sandstone	S
197	<i>D. knox-daviesii</i> Lavis	active growth and rooting	quartz	E
198	<i>D. laxipetalum</i> L.Bolus	active growth and rooting	sandstone	E, S
199	<i>D. nubigenum</i> (Schltr.) L.Bolus	active growth and rooting	basalt	N
200	<i>D. saxicola</i> Lavis	active growth and rooting	sandstone	W
201	<i>D. subpetiolatum</i> L.Bolus	active growth and rooting	sandstone	S, E
202	<i>D. tradescantioides</i> (A.Berger) L.Bolus	active growth and rooting	shale	E, W, S
203	<i>D. velutinum</i> L.Bolus	active growth and rooting	sandstone	N
204	<i>D. waterbergense</i> L.Bolus	active growth and rooting	quartz	S
205	<i>D. zoutpansbergense</i> L.Bolus	active growth and rooting	quartz	S



TABLE 10.1 (continued)—Check list of obligate and near-obligate cremnophilous taxa (220 taxa, 203 species)

No.	Taxon	Altitude (m)	Rainfall (mm per annum)	Rainfall seasonality	Deciduousness
				S = summer W = winter W/S = any time of year	E = evergreen SA = summer-aestivating SD = summer-deciduous WD = winter-deciduous
	MESEMBRYANTHEMACEAE (12 genera, 45 taxa)				
	<i>Carruanthus</i> (Schwantes) Schwantes (1 species)				
174	<i>C. peersii</i> L.Bolus	800–1200	200–300	W/S	E
	Conophytum N.E.Br. (19 taxa)				
175	<i>C. auriflorum</i> Tischer subsp. <i>turbiniforme</i> (Rawe) S.A.Hammer	540–860	100–200	W	SA
176	<i>C. bolusiae</i> Schwantes subsp. <i>bolusiae</i>	500–750	50–100	W	SA
177	<i>C. carpiantum</i> L.Bolus	900–1160	50–100	W	SA
178	<i>C. danielii</i> Pavelka	1000–1150	100–200	W	SA
179	<i>C. ernstii</i> S.A.Hammer subsp. <i>ernstii</i>	400–1200	50–100	W	SA
180	<i>C. francoiseae</i> (S.A.Hammer) S.A.Hammer	350–580	50–100	W	SA
181	<i>C. fulleri</i> L.Bolus	980–1150	50–100	W	SA
182	<i>C. hanae</i> Pavelka	1000–1300	100–200	W	SA
183	<i>C. luckhoffii</i> Lavis	100–980	400–500	W	SA
184	<i>C. marginatum</i> Lavis subsp. <i>haramoepense</i> (L.Bolus) S.A.Hammer	940–1200	50–100	W	SA
185	<i>C. marginatum</i> Lavis subsp. <i>littlewoodii</i> (L.Bolus) S.A.Hammer	750–1200	50–100	W	SA
186	<i>C. obscurum</i> N.E.Br. subsp. <i>sponsaliorum</i> (S.A.Hammer) S.A.Hammer	680	50–100	W	SA
187	<i>C. quaesitum</i> (N.E.Br.) N.E.Br. subsp. <i>densipunctum</i> (L.Bolus) S.A.Hammer	1050–1200	25–50	W	SA
188	<i>C. quaesitum</i> (N.E.Br.) N.E.Br. subsp. <i>quaesitum</i> var. <i>rostratum</i> (Tischer) S.A.Hammer	700–1200	50–100	W	SA
189	<i>C. ricardianum</i> Loesch & Tischer subsp. <i>ricardianum</i>	300–900	50–100	W	SA
190	<i>C. stephanii</i> Schwantes subsp. <i>stephanii</i>	600–1169	25–50	W	SA
191	<i>C. tantillum</i> N.E.Br. subsp. <i>amicorum</i> S.A.Hammer & Barnhill	850	150–250	W	SA
192	<i>C. taylorianum</i> (Dinter & Schwantes) N.E.Br. subsp. <i>ernianum</i> (Loesch & Tischer) de Boer ex S.A.Hammer	850–1400	50–200	W	SA
193	<i>C. taylorianum</i> (Dinter & Schwantes) N.E.Br. subsp. <i>rosynense</i> S.A.Hammer	600–1200	50–100	W	SA
	Delosperma N.E.Br. emend Lavis (12 taxa)				
194	<i>Delosperma</i> sp. A	200–250	1000–1250	S	E
195	<i>Delosperma</i> sp. B	150–250	1000–1250	S	E
196	<i>D. esterhuyseniae</i> L.Bolus	400–1200	200–300	W/S	E
197	<i>D. knox-daviesii</i> Lavis	1500	700–800	S	E
198	<i>D. laxipetalum</i> L.Bolus	550–1100	400–500	W/S	E
199	<i>D. nubigenum</i> (Schltr.) L.Bolus	3000–3400	1000–1500	S	E
200	<i>D. saxicola</i> Lavis	50–100	700–800 m	W/S	E
201	<i>D. subpetiolatum</i> L.Bolus	1000–1400	1000–1200	S	E
202	<i>D. tradescantioides</i> (A.Berger) L.Bolus	400–1440	600–800	S	E
203	<i>D. velutinum</i> L.Bolus	100–1530	700–800	S	E
204	<i>D. waterbergense</i> L.Bolus	1500–1800	700–800	S	E
205	<i>D. zoutpansbergense</i> L.Bolus	1500–1730	1250–1500	S	E



TABLE 10.1 (continued)—Check list of obligate and near-obligate cremnophilous taxa (220 taxa, 203 species)

No.	Taxon	Fog	Biomes	Pollination
		*** = regular fog ** = occasional fog * = little fog – = no fog	IOCB = Indian Ocean Coastal Belt	
	MESEMBRYANTHEMACEAE (12 genera, 45 taxa)			
	<i>Carruanthus</i> (Schwantes) Schwantes (1 species)			
174	<i>C. peersii</i> L.Bolus	–	Albany Thicket	insect
	Conophytum N.E.Br. (19 taxa)			
175	<i>C. auriflorum</i> Tischer subsp. <i>turbiniforme</i> (Rawe) S.A.Hammer	***	Succulent Karoo	insect
176	<i>C. bolusiae</i> Schwantes subsp. <i>bolusiae</i>	***	Succulent Karoo	insect
177	<i>C. carpiantum</i> L.Bolus	***	Succulent Karoo	insect
178	<i>C. danielii</i> Pavelka	***	Succulent Karoo	insect
179	<i>C. ernstii</i> S.A.Hammer subsp. <i>ernstii</i>	***	Succulent Karoo	insect
180	<i>C. francoiseae</i> (S.A.Hammer) S.A.Hammer	***	Succulent Karoo	insect
181	<i>C. fulleri</i> L.Bolus	*	Succulent Karoo	insect
182	<i>C. hanae</i> Pavelka	*	Succulent Karoo	insect
183	<i>C. luckhoffii</i> Lavis	**	Fynbos	insect
184	<i>C. marginatum</i> Lavis subsp. <i>haramoepense</i> (L.Bolus) S.A.Hammer	***	Succulent Karoo	insect
185	<i>C. marginatum</i> Lavis subsp. <i>littlewoodii</i> (L.Bolus) S.A.Hammer	***	Succulent Karoo	insect
186	<i>C. obscurum</i> N.E.Br. subsp. <i>sponsaliorum</i> (S.A.Hammer) S.A.Hammer	***	Succulent Karoo	insect
187	<i>C. quaesitum</i> (N.E.Br.) N.E.Br. subsp. <i>densipunctum</i> (L.Bolus) S.A.Hammer	*	Succulent Karoo	insect
188	<i>C. quaesitum</i> (N.E.Br.) N.E.Br. subsp. <i>quaesitum</i> var. <i>rostratum</i> (Tischer) S.A.Hammer	**	Succulent Karoo	insect
189	<i>C. ricardianum</i> Loesch & Tischer subsp. <i>ricardianum</i>	***	Succulent Karoo	insect
190	<i>C. stephanii</i> Schwantes subsp. <i>stephanii</i>	***	Succulent Karoo	insect
191	<i>C. tantillum</i> N.E.Br. subsp. <i>amicorum</i> S.A.Hammer & Barnhill	***	Succulent Karoo	insect
192	<i>C. taylorianum</i> (Dinter & Schwantes) N.E.Br. subsp. <i>ernianum</i> (Loesch & Tischer) de Boer ex S.A.Hammer	***	Succulent Karoo	insect
193	<i>C. taylorianum</i> (Dinter & Schwantes) N.E.Br. subsp. <i>rosynense</i> S.A.Hammer	***	Succulent Karoo	insect
	Delosperma N.E.Br. emend Lavis (12 taxa)			
194	<i>Delosperma</i> sp. A	–	IOCB	insect
195	<i>Delosperma</i> sp. B	–	IOCB	insect
196	<i>D. esterhuyseniae</i> L.Bolus	*	Albany Thicket	insect
197	<i>D. knox-daviesii</i> Lavis	**	Grassland	insect
198	<i>D. laxipetalum</i> L.Bolus	–	Albany Thicket	insect
199	<i>D. nubigenum</i> (Schltr.) L.Bolus	**	Grassland	insect
200	<i>D. saxicola</i> Lavis	*	Fynbos	insect
201	<i>D. subpetiolatum</i> L.Bolus	*	Grassland	insect
202	<i>D. tradescantioides</i> (A.Berger) L.Bolus	–	Savanna	insect
203	<i>D. velutinum</i> L.Bolus	*	Savanna	insect
204	<i>D. waterbergense</i> L.Bolus	*	Grassland	insect
205	<i>D. zoutpansbergense</i> L.Bolus	**	Grassland	insect



TABLE 10.1 (continued)—Check list of obligate and near-obligate cremnophilous taxa (220 taxa, 203 species)

No.	Taxon	Seed dispersal	Conservation status	Light requirements
			LC = Least Concern NT = Not Threatened VU = Vulnerable	BL = bright light DS = dappled shade FS = full sun
	MESEMBRYANTHEMACEAE (12 genera, 45 taxa)			
	<i>Carruanthus</i> (Schwantes) Schwantes (1 species)			
174	<i>C. peersii</i> L.Bolus	water	LC	FS, BL
	<i>Conophytum</i> N.E.Br. (19 taxa)			
175	<i>C. auriflorum</i> Tischer subsp. <i>turbiniforme</i> (Rawe) S.A.Hammer	water	LC	BL
176	<i>C. bolusiae</i> Schwantes subsp. <i>bolusiae</i>	water	LC	BL
177	<i>C. carpianum</i> L.Bolus	water	LC	BL
178	<i>C. danielii</i> Pavelka	water	LC	BL
179	<i>C. ernstii</i> S.A.Hammer subsp. <i>ernstii</i>	water	LC	BL
180	<i>C. francoiseae</i> (S.A.Hammer) S.A.Hammer	water	LC	BL
181	<i>C. fulleri</i> L.Bolus	water	LC	BL
182	<i>C. hanae</i> Pavelka	water	LC	BL
183	<i>C. luckhoffii</i> Lavis	water	LC	BL
184	<i>C. marginatum</i> Lavis subsp. <i>haramoepense</i> (L.Bolus) S.A.Hammer	water	LC	BL
185	<i>C. marginatum</i> Lavis subsp. <i>littlewoodii</i> (L.Bolus) S.A.Hammer	water	LC	BL
186	<i>C. obscurum</i> N.E.Br. subsp. <i>sponsaliorum</i> (S.A.Hammer) S.A.Hammer	water	LC	BL
187	<i>C. quaesitum</i> (N.E.Br.) N.E.Br. subsp. <i>densipunctum</i> (L.Bolus) S.A.Hammer	water	LC	BL
188	<i>C. quaesitum</i> (N.E.Br.) N.E.Br. subsp. <i>quaesitum</i> var. <i>rostratum</i> (Tischer) S.A.Hammer	water	LC	BL
189	<i>C. ricardianum</i> Loesch & Tischer subsp. <i>ricardianum</i>	water	LC	BL
190	<i>C. stephanii</i> Schwantes subsp. <i>stephanii</i>	water	LC	BL
191	<i>C. tantillum</i> N.E.Br. subsp. <i>amicorum</i> S.A.Hammer & Barnhill	water	LC	BL
192	<i>C. taylorianum</i> (Dinter & Schwantes) N.E.Br. subsp. <i>ernianum</i> (Loesch & Tischer) de Boer ex S.A.Hammer	water	LC	BL
193	<i>C. taylorianum</i> (Dinter & Schwantes) N.E.Br. subsp. <i>rosynense</i> S.A.Hammer	water	LC	BL
	<i>Delosperma</i> N.E.Br. emend Lavis (12 taxa)			
194	<i>Delosperma</i> sp. A	water	LC	FS, BL
195	<i>Delosperma</i> sp. B	water	LC	FS, BL
196	<i>D. esterhuyensiae</i> L.Bolus	water	LC	FS, BL
197	<i>D. knox-daviesii</i> Lavis	water	LC	FS, BL
198	<i>D. laxipetalum</i> L.Bolus	water	LC	FS, BL
199	<i>D. nubigenum</i> (Schltr.) L.Bolus	water	LC	FS, BL
200	<i>D. saxicola</i> Lavis	water	LC	FS, BL
201	<i>D. subpetiolatum</i> L.Bolus	water	LC	FS, BL
202	<i>D. tradescantioides</i> (A.Berger) L.Bolus	water	LC	FS, BL
203	<i>D. velutinum</i> L.Bolus	water	LC	FS, BL
204	<i>D. waterbergense</i> L.Bolus	water	LC	FS, BL
205	<i>D. zoutpansbergense</i> L.Bolus	water	LC	FS, BL



TABLE 10.1 (continued)—Check list of obligate and near-obligate cremnophilous taxa (220 taxa, 203 species)

No.	Taxon	Rich flowering	Reduction in armament	Cliff habitat
		*** = rich ** = exposed * = insignificant	*** = margin without teeth ** = margin with smaller teeth * = no significant change, same as other non-cremnophytes	C = coastal R = river E = escarpment M = mountain I = inselberg
	MESEMBRYANTHEMACEAE (12 genera, 45 taxa)			
	<i>Carruanthus</i> (Schwantes) Schwantes (1 species)			
174	<i>C. peersii</i> L.Bolus	***	*	R, M
	Conophytum N.E.Br. (19 taxa)			
175	<i>C. auriflorum</i> Tischer subsp. <i>turbiniforme</i> (Rawe) S.A.Hammer	***	*	E
176	<i>C. bolusiae</i> Schwantes subsp. <i>bolusiae</i>	***	*	M
177	<i>C. carpiantum</i> L.Bolus	***	*	M
178	<i>C. danielii</i> Pavelka	***	*	M
179	<i>C. ernstii</i> S.A.Hammer subsp. <i>ernstii</i>	***	*	M, R
180	<i>C. francoiseae</i> (S.A.Hammer) S.A.Hammer	***	*	M
181	<i>C. fulleri</i> L.Bolus	***	*	M, I
182	<i>C. hanae</i> Pavelka	***	*	M
183	<i>C. luckhoffii</i> Lavis	***	*	M
184	<i>C. marginatum</i> Lavis subsp. <i>haramoepense</i> (L.Bolus) S.A.Hammer	***	*	M
185	<i>C. marginatum</i> Lavis subsp. <i>littlewoodii</i> (L.Bolus) S.A.Hammer	***	*	M
186	<i>C. obscurum</i> N.E.Br. subsp. <i>sponsaliorum</i> (S.A.Hammer) S.A.Hammer	***	*	M
187	<i>C. quaesitum</i> (N.E.Br.) N.E.Br. subsp. <i>densipunctum</i> (L.Bolus) S.A.Hammer	**	*	M
188	<i>C. quaesitum</i> (N.E.Br.) N.E.Br. subsp. <i>quaesitum</i> var. <i>rostratum</i> (Tischer) S.A.Hammer	**	*	M
189	<i>C. ricardianum</i> Loesch & Tischer subsp. <i>ricardianum</i>	***	***	M
190	<i>C. stephanii</i> Schwantes subsp. <i>stephanii</i>	***	*	M
191	<i>C. tantillum</i> N.E.Br. subsp. <i>amicorum</i> S.A.Hammer & Barnhill	***	*	M
192	<i>C. taylorianum</i> (Dinter & Schwantes) N.E.Br. subsp. <i>ernianum</i> (Loesch & Tischer) de Boer ex S.A.Hammer	***	*	M
193	<i>C. taylorianum</i> (Dinter & Schwantes) N.E.Br. subsp. <i>rosynense</i> S.A.Hammer	***	*	M
	Delosperma N.E.Br. emend Lavis (12 taxa)			
194	<i>Delosperma</i> sp. A	***	*	R
195	<i>Delosperma</i> sp. B	**	*	R
196	<i>D. esterhuyensiae</i> L.Bolus	***	*	M, R
197	<i>D. knox-daviesii</i> Lavis	**	*	E
198	<i>D. laxipetalum</i> L.Bolus	**	*	R, M
199	<i>D. nubigenum</i> (Schltr.) L.Bolus	***	*	E
200	<i>D. saxicola</i> Lavis	**	*	C
201	<i>D. subpetiolatum</i> L.Bolus	***	*	E
202	<i>D. tradescantioides</i> (A.Berger) L.Bolus	**	*	R
203	<i>D. velutinum</i> L.Bolus	**	*	R, M
204	<i>D. waterbergense</i> L.Bolus	***	*	M, I
205	<i>D. zoutpansbergense</i> L.Bolus	**	*	M, I



TABLE 10.1 (continued)—Check list of obligate and near-obligate cremnophilous taxa (220 taxa, 203 species)

No.	Taxon	Occurrence	Endemism	Windows
		W = widespread We = widespread but endemic to its vegetation region R = restricted	* = endemic Bots = Botswana Les = Lesotho Moz = Mozambique Nam = Namibia RSA = South Africa Swaz = Swaziland	Lm = on leaf margin Mw = micro-windows O = other
	MESEMBRYANTHEMACEAE (12 genera, 45 taxa)			
	<i>Carruanthus</i> (Schwantes) Schwantes (1 species)			
174	<i>C. peersii</i> L.Bolus	R	RSA*	
	Conophytum N.E.Br. (19 taxa)			
175	<i>C. auriflorum</i> Tischer subsp. <i>turbiniforme</i> (Rawe) S.A.Hammer	R	RSA*	Mw
176	<i>C. bolusiae</i> Schwantes subsp. <i>bolusiae</i>	R	RSA*	Mw
177	<i>C. carpianum</i> L.Bolus	R	RSA*	Mw
178	<i>C. danielii</i> Pavelka	R	RSA*	Mw
179	<i>C. ernstii</i> S.A.Hammer subsp. <i>ernstii</i>	We	RSA*	Mw
180	<i>C. francoiseae</i> (S.A.Hammer) S.A.Hammer	R	RSA*	Mw
181	<i>C. fulleri</i> L.Bolus	We	RSA*	Mw
182	<i>C. hanae</i> Pavelka	We	RSA*	Mw
183	<i>C. luckhoffii</i> Lavis	R	RSA*	Mw
184	<i>C. marginatum</i> Lavis subsp. <i>haramoepense</i> (L.Bolus) S.A.Hammer	We	RSA*	Mw
185	<i>C. marginatum</i> Lavis subsp. <i>littlewoodii</i> (L.Bolus) S.A.Hammer	We	RSA*	Mw
186	<i>C. obscurum</i> N.E.Br. subsp. <i>sponsaliorum</i> (S.A.Hammer) S.A.Hammer	R	RSA*	Mw
187	<i>C. quaesitum</i> (N.E.Br.) N.E.Br. subsp. <i>densipunctum</i> (L.Bolus) S.A.Hammer	We	Nam*	Mw
188	<i>C. quaesitum</i> (N.E.Br.) N.E.Br. subsp. <i>quaesitum</i> var. <i>rostratum</i> (Tischer) S.A.Hammer	We	RSA, Nam	Mw
189	<i>C. ricardianum</i> Loesch & Tischer subsp. <i>ricardianum</i>	R	Nam*	Mw
190	<i>C. stephanii</i> Schwantes subsp. <i>stephanii</i>	We	RSA*	Mw
191	<i>C. tantillum</i> N.E.Br. subsp. <i>amicorum</i> S.A.Hammer & Barnhill	We	RSA*	Mw
192	<i>C. taylorianum</i> (Dinter & Schwantes) N.E.Br. subsp. <i>ernianum</i> (Loesch & Tischer) de Boer ex S.A.Hammer	R	Nam*	Mw
193	<i>C. taylorianum</i> (Dinter & Schwantes) N.E.Br. subsp. <i>rosynense</i> S.A.Hammer	R	RSA*	Mw
	Delosperma N.E.Br. emend Lavis (12 taxa)			
194	<i>Delosperma</i> sp. A	We	RSA*	
195	<i>Delosperma</i> sp. B	R	RSA*	
196	<i>D. esterhuyensiae</i> L.Bolus	We	RSA*	
197	<i>D. knox-daviesii</i> Lavis	We	RSA*	
198	<i>D. laxipetalum</i> L.Bolus	We	RSA*	
199	<i>D. nubigenum</i> (Schltr.) L.Bolus	We	RSA*	
200	<i>D. saxicola</i> Lavis	R	RSA*	
201	<i>D. subpetiolatum</i> L.Bolus	We	RSA*	
202	<i>D. tradescantioides</i> (A.Berger) L.Bolus	We	RSA*	
203	<i>D. velutinum</i> L.Bolus	We	RSA*	
204	<i>D. waterbergense</i> L.Bolus	R	RSA*	
205	<i>D. zoutpansbergense</i> L.Bolus	R	RSA*	



TABLE 10.1 (continued)—Check list of obligate and near-obligate cremnophilous taxa (220 taxa, 203 species)

No.	Taxon	Cremonophilous growth form	Degree of cliff occupation	Weight class
		See 9.1.2 for explanation of the symbols below	*** = strictly obligate cremnophyte, displaying cliff-adapted features ** = obligate cremnophyte * = predominantly on cliffs (80%)	light = < 50 g medium = 51–500 g heavy = >500 g
	<i>Drosanthemum</i> Schwantes (3 species)			
206	<i>D. anemophilum</i> Van Jaarsv. & S.A.Hammer	E:F:As:W:Ev	**	medium
207	<i>D. expersum</i> (N.E.Br.) Schwantes	E:F:P:Els (vb)	***	light
208	<i>D. inornatum</i> (L.Bolus) L.Bolus	E:F:P:Els:D (vb) (eg)	***	light
	<i>Erepsia</i> N.E.Br. (1 species)			
209	<i>E. heteropetala</i> (Haw.) Schwantes	E:F:As:W:Ev	*	light-medium
	<i>Esterhuysenia</i> L.Bolus (1 species)			
210	<i>E. stokoei</i> (L.Bolus) H.E.K.Hartmann	E:F:P:Els (vb)	***	light
	<i>Jensenobotrya</i> A.G.J.Herre (1 species)			
211	<i>J. lossowiana</i> A.G.J.Herre	E:P:F:Els (vb) (ft)	***	heavy
	<i>Lampranthus</i> N.E.Br. (1 species)			
212	<i>L. affinis</i> L.Bolus	E:F:As:W:Ev (r)	**	medium
	<i>Machairophyllum</i> Schwantes (1 species)			
213	<i>M. brevifolium</i> L.Bolus	A:S:Lper:R:C:La (vb) (r)	***	light-medium
	<i>Oscularia</i> Schwantes (1 species)			
214	<i>O. cremnophila</i> Van Jaarsv., Desmet & A.E.van Wyk	E:F:P:Els (vb)	***	medium-heavy
	<i>Ruschia</i> Schwantes (2 species)			
215	<i>R. knysnana</i> (L.Bolus) L.Bolus	E:F:As:W:Ev (vb)	**	light-medium
216	<i>R. promontorii</i> L.Bolus	E:F:P:Els:Ev (vb)	**	light-medium
	<i>Scopelogenia</i> L.Bolus (2 species)			
217	<i>S. bruynsii</i> Klak	E:F:As:W:Ev (vb)	**	medium-heavy
218	<i>S. verruculata</i> (L.) L.Bolus	E:F:As:W:Ev (vb)	***	medium-heavy
	OXALIDACEAE (1 species)			
	<i>Oxalis</i> L. (1 species)			
219	<i>Oxalis pocockiae</i> L.Bolus	A:B:D:C:La (vb)	**	light
	PORTULACACEAE (1 species)			
	<i>Anacampseros</i> L. (1 species)			
220	<i>A. scopata</i> G.Will.	A:S:Lper:Lc:Ca:(vb) (ft)	***	light
	SEMISUCCULENT AND HERBACEOUS OUTGROUPS			
	PEDALIACEAE (outgroup)			
	<i>Dewinteria</i> Van Jaarsv. & A.E.van Wyk			
221	<i>D. petrophila</i> (De Winter) Van Jaarsv. & A.E.van Wyk	E:F:As:S/H:Es (vb) (r) (fn)	***	light-medium
	SCROPHULARIACEAE (outgroup)			
	<i>Stemodiopsis</i> Engl.			
222	<i>S. rivae</i> Engl.	E:F:As:S/H:Es (vb) (fn)	***	light



TABLE 10.1 (continued)—Check list of obligate and near-obligate cremnophilous taxa (220 taxa, 203 species)

No.	Taxon	Vegetative dispersal backup	Geology	Aspect
	Drosanthemum Schwantes (3 species)			
206	<i>D. anemophilum</i> Van Jaarsv. & S.A.Hammer	solitary	sandstone	N
207	<i>D. expersum</i> (N.E.Br.) Schwantes	active growth and rooting	sandstone	S
208	<i>D. inornatum</i> (L.Bolus) L.Bolus	active growth and rooting	dolomite	S
	Erepsia N.E.Br. (1 species)			
209	<i>E. heteropetala</i> (Haw.) Schwantes	active growth and rooting	sandstone	S, E
	Esterhuysenia L.Bolus (1 species)			
210	<i>E. stokoei</i> (L.Bolus) H.E.K.Hartmann	active growth and rooting	sandstone	S
	Jensenobotrya A.G.J.Herre (1 species)			
211	<i>J. lossowiana</i> A.G.J.Herre	active growth and rooting	sandstone	S, W
	Lampranthus N.E.Br. (1 species)			
212	<i>L. affinis</i> L.Bolus	active growth and rooting	sandstone	S, E, W, N
	Machairophyllum Schwantes (1 species)			
213	<i>M. brevifolium</i> L.Bolus	solitary	conglomerate	S
	Oscularia Schwantes (1 species)			
214	<i>O. cremnophila</i> Van Jaarsv., Desmet & A.E.van Wyk	active growth and rooting	sandstone	S
	Ruschia Schwantes (2 species)			
215	<i>R. knysnana</i> (L.Bolus) L.Bolus	solitary	sandstone	W
216	<i>R. promontorii</i> L.Bolus	active growth and rooting	sandstone	E, W, N
	Scopelogenia L.Bolus (2 species)			
217	<i>S. bruynsii</i> Klak	active growth and rooting	sandstone, granite	
218	<i>S. verruculata</i> (L.) L.Bolus	active growth and rooting	sandstone	S, E, W
	OXALIDACEAE (1 species)			
	Oxalis L. (1 species)			
219	<i>Oxalis pocockiae</i> L.Bolus	winged bulbils	sandstone	E, S, W
	PORTULACACEAE (1 species)			
	Anacampseros L. (1 species)			
220	<i>A. scopata</i> G.Will.		quartz	E, S
	SEMISUCCULENT AND HERBACEOUS OUTGROUPS			
	PEDALIACEAE (outgroup)			
	Dewinteria Van Jaarsv. & A.E.van Wyk			
221	<i>D. petrophila</i> (De Winter) Van Jaarsv. & A.E.van Wyk	dual dispersal, autochory and other, seed cloning	granite	S, E
	SCROPHULARIACEAE (outgroup)			
	Stemodiopsis Engl.			
222	<i>S. rivae</i> Engl.	autochory, infructescence bending back	sandstone	S



TABLE 10.1 (continued)—Check list of obligate and near-obligate cremnophilous taxa (220 taxa, 203 species)

No.	Taxon	Altitude (m)	Rainfall (mm per annum)	Rainfall seasonality	Deciduousness
				S = summer W = winter W/S = any time of year	E = evergreen SA = summer-aestivating SD = summer-deciduous WD = winter-deciduous
	Drosanthemum Schwantes (3 species)				
206	<i>D. anemophilum</i> Van Jaarsv. & S.A.Hammer	800–1000	200–300	W/S	E
207	<i>D. expersum</i> (N.E.Br.) Schwantes	1200–2000	1000–1500	W	E
208	<i>D. inornatum</i> (L.Bolus) L.Bolus	800–1100	50–75	W	SD
	Erepsia N.E.Br. (1 species)				
209	<i>E. heteropetala</i> (Haw.) Schwantes	400–1300	1000–1500	W	E
	Esterhuysenia L.Bolus (1 species)				
210	<i>E. stokoei</i> (L.Bolus) H.E.K.Hartmann	800–1500	1000–1500	W	E
	Jensenobotrya A.G.J.Herre (1 species)				
211	<i>J. lossowiana</i> A.G.J.Herre	10–300	15	W	E
	Lampranthus N.E.Br. (1 species)				
212	<i>L. affinis</i> L.Bolus	300–1050	400–500	W/S	E
	Machairophyllum Schwantes (1 species)				
213	<i>M. brevifolium</i> L.Bolus	500–600	200–300	W/S	E
	Oscularia Schwantes (1 species)				
214	<i>O. cremnophila</i> Van Jaarsv., Desmet & A.E.van Wyk	50–100	300–400	W	E
	Ruschia Schwantes (2 species)				
215	<i>R. knysnana</i> (L.Bolus) L.Bolus	50–650	600–700	W/S	E
216	<i>R. promontorii</i> L.Bolus	120–400	300–400	W	E
	Scopelogenia L.Bolus (2 species)				
217	<i>S. bruynsii</i> Klak	800–2000	120–400	W	E
218	<i>S. verruculata</i> (L.) L.Bolus	100–1000	1000–1500	W	E
	OXALIDACEAE (1 species)				
	Oxalis L. (1 species)				
219	<i>Oxalis pocockiae</i> L.Bolus	350–600	750–2000	W	SD
	PORTULACACEAE (1 species)				
	Anacampseros L. (1 species)				
220	<i>A. scopata</i> G.Will.	350–450	25–50	W	E
	SEMISUCCULENT AND HERBACEOUS OUTGROUPS				
	PEDALIACEAE (outgroup)				
	Dewinteria Van Jaarsv. & A.E.van Wyk				
221	<i>D. petrophila</i> (De Winter) Van Jaarsv. & A.E.van Wyk	900–1500	50–150	S	E
	SCROPHULARIACEAE (outgroup)				
	Stemodiopsis Engl.				
222	<i>S. rivae</i> Engl.	400–1675	300–400	S	E



TABLE 10.1 (continued)—Check list of obligate and near-obligate cremnophilous taxa (220 taxa, 203 species)

No.	Taxon	Fog	Biomes	Pollination
		*** = regular fog ** = occasional fog * = little fog – = no fog	IOCB = Indian Ocean Coastal Belt	
	<i>Drosanthemum</i> Schwantes (3 species)			
206	<i>D. anemophilum</i> Van Jaarsv. & S.A.Hammer	–	Succulent Karoo	insect
207	<i>D. expersum</i> (N.E.Br.) Schwantes	**	Fynbos	insect
208	<i>D. inornatum</i> (L.Bolus) L.Bolus	***	Succulent Karoo	insect
	<i>Erepsia</i> N.E.Br. (1 species)			
209	<i>E. heteropetala</i> (Haw.) Schwantes	*	Fynbos	insect
	<i>Esterhuysenia</i> L.Bolus (1 species)			
210	<i>E. stokoei</i> (L.Bolus) H.E.K.Hartmann	*	Fynbos	insect
	<i>Jensenobotrya</i> A.G.J.Herre (1 species)			
211	<i>J. lossowiana</i> A.G.J.Herre	***	Desert	insect
	<i>Lampranthus</i> N.E.Br. (1 species)			
212	<i>L. affinis</i> L.Bolus	–	Albany Thicket	insect
	<i>Machairophyllum</i> Schwantes (1 species)			
213	<i>M. brevifolium</i> L.Bolus	–	Succulent Karoo	insect
	<i>Oscularia</i> Schwantes (1 species)			
214	<i>O. cremnophila</i> Van Jaarsv., Desmet & A.E.van Wyk	***	Fynbos	insect
	<i>Ruschia</i> Schwantes (2 species)			
215	<i>R. knysnana</i> (L.Bolus) L.Bolus	–	Fynbos	insect
216	<i>R. promontorii</i> L.Bolus	**	Fynbos	insect
	<i>Scopelogenia</i> L.Bolus (2 species)			
217	<i>S. bruynsii</i> Klak	*	Succulent Karoo	insect
218	<i>S. verruculata</i> (L.) L.Bolus	*	Fynbos	insect
	OXALIDACEAE (1 species)			
	<i>Oxalis</i> L. (1 species)			
219	<i>Oxalis pocockiae</i> L.Bolus	–	Fynbos	insect
	PORTULACACEAE (1 species)			
	<i>Anacampseros</i> L. (1 species)			
220	<i>A. scopata</i> G.Will.	***	Succulent Karoo	insect
	SEMISUCCULENT AND HERBACEOUS OUTGROUPS			
	PEDALIACEAE (outgroup)			
	<i>Dewinteria</i> Van Jaarsv. & A.E.van Wyk			
221	<i>D. petrophila</i> (De Winter) Van Jaarsv. & A.E.van Wyk	**	Desert	insect
	SCROPHULARIACEAE (outgroup)			
	<i>Stemodiopsis</i> Engl.			
222	<i>S. rivae</i> Engl.	–	Savanna	insect



TABLE 10.1 (continued)—Check list of obligate and near-obligate cremnophilous taxa (220 taxa, 203 species)

No.	Taxon	Seed dispersal	Conservation status	Light requirements
			LC = Least Concern NT = Not Threatened VU = Vulnerable	BL = bright light DS = dappled shade FS = full sun
	Drosanthemum Schwantes (3 species)			
206	<i>D. anemophilum</i> Van Jaarsv. & S.A.Hammer	wind	LC	FS
207	<i>D. expersum</i> (N.E.Br.) Schwantes	water	LC	FS, BL
208	<i>D. inornatum</i> (L.Bolus) L.Bolus	water	LC	FS, BL
	Erepsia N.E.Br. (1 species)			
209	<i>E. heteropetala</i> (Haw.) Schwantes	water	LC	FS, BL
	Esterhuysenia L.Bolus (1 species)			
210	<i>E. stokoei</i> (L.Bolus) H.E.K.Hartmann	water	LC	FS, BL
	Jensenobotrya A.G.J.Herre (1 species)			
211	<i>J. lossowiana</i> A.G.J.Herre	water	LC	FS, BL
	Lampranthus N.E.Br. (1 species)			
212	<i>L. affinis</i> L.Bolus	water	LC	FS, BL
	Machairophyllum Schwantes (1 species)			
213	<i>M. brevifolium</i> L.Bolus	water	LC	FS
	Oscularia Schwantes (1 species)			
214	<i>O. cremnophila</i> Van Jaarsv., Desmet & A.E.van Wyk	water	LC	FS, BL
	Ruschia Schwantes (2 species)			
215	<i>R. knysnana</i> (L.Bolus) L.Bolus	water	LC	FS
216	<i>R. promontorii</i> L.Bolus	water	LC	FS
	Scopelogenia L.Bolus (2 species)			
217	<i>S. bruynsii</i> Klak	water	LC	FS, BL
218	<i>S. verruculata</i> (L.) L.Bolus	wind	LC	FS, BL
	OXALIDACEAE (1 species)			
	Oxalis L. (1 species)			
219	<i>Oxalis pocockiae</i> L.Bolus	wind	LC	FS, BL
	PORTULACACEAE (1 species)			
	Anacampseros L. (1 species)			
220	<i>A. scopata</i> G.Will.	wind	LC	BL, DS
	SEMISUCCULENT AND HERBACEOUS OUTGROUPS			
	PEDALIACEAE (outgroup)			
	Dewinteria Van Jaarsv. & A.E.van Wyk			
221	<i>D. petrophila</i> (De Winter) Van Jaarsv. & A.E.van Wyk	wind & autochory	LC	BL, DS
	SCROPHULARIACEAE (outgroup)			
	Stemodiopsis Engl.			
222	<i>S. rivae</i> Engl.	autochory	LC	FS, DS, BL



TABLE 10.1 (continued)—Check list of obligate and near-obligate cremnophilous taxa (220 taxa, 203 species)

No.	Taxon	Rich flowering	Reduction in armament	Cliff habitat
		*** = rich ** = exposed * = insignificant	*** = margin without teeth ** = margin with smaller teeth * = no significant change, same as other non-cremnophytes	C = coastal R = river E = escarpment M = mountain I = inselberg
	Drosanthemum Schwantes (3 species)			
206	<i>D. anemophilum</i> Van Jaarsv. & S.A.Hammer	**	*	M
207	<i>D. expersum</i> (N.E.Br.) Schwantes	***	*	M
208	<i>D. inornatum</i> (L.Bolus) L.Bolus	*	*	M
	Erepsia N.E.Br. (1 species)			
209	<i>E. heteropetala</i> (Haw.) Schwantes	**	*	M
	Esterhuysenia L.Bolus (1 species)			
210	<i>E. stokoei</i> (L.Bolus) H.E.K.Hartmann	***	*	M
	Jensenobotrya A.G.J.Herre (1 species)			
211	<i>J. lossowiana</i> A.G.J.Herre	**	***	C
	Lampranthus N.E.Br. (1 species)			
212	<i>L. affinis</i> L.Bolus	***	*	R, M
	Machairophyllum Schwantes (1 species)			
213	<i>M. brevifolium</i> L.Bolus	***	*	M
	Oscularia Schwantes (1 species)			
214	<i>O. cremnophila</i> Van Jaarsv., Desmet & A.E.van Wyk	***	*	M
	Ruschia Schwantes (2 species)			
215	<i>R. knysnana</i> (L.Bolus) L.Bolus	**	*	C, M
216	<i>R. promontorii</i> L.Bolus	**	*	C, M
	Scopelogenia L.Bolus (2 species)			
217	<i>S. bruynsii</i> Klak	***	*	M
218	<i>S. verruculata</i> (L.) L.Bolus	***	*	M
	OXALIDACEAE (1 species)			
	Oxalis L. (1 species)			
219	<i>Oxalis pocockiae</i> L.Bolus	**	*	M, C
	PORTULACACEAE (1 species)			
	Anacampseros L. (1 species)			
220	<i>A. scopata</i> G.Will.	*	*	M
	SEMISUCCULENT AND HERBACEOUS OUTGROUPS			
	PEDALIACEAE (outgroup)			
	Dewinteria Van Jaarsv. & A.E.van Wyk			
221	<i>D. petrophila</i> (De Winter) Van Jaarsv. & A.E.van Wyk	***	*	E, M
	SCROPHULARIACEAE (outgroup)			
	Stemodiopsis Engl.			
222	<i>S. rivae</i> Engl.	**	*	M



TABLE 10.1 (continued)—Check list of obligate and near-obligate cremnophilous taxa (220 taxa, 203 species)

No.	Taxon	Occurrence	Endemism	Windows
		W = widespread We = widespread but endemic to its vegetation region R = restricted	* = endemic Bots = Botswana Les = Lesotho Moz = Mozambique Nam = Namibia RSA = South Africa Swaz = Swaziland	Lm = on leaf margin Mw = micro-windows O = other
	Drosanthemum Schwantes (3 species)			
206	<i>D. anemophilum</i> Van Jaarsv. & S.A.Hammer	R	RSA*	
207	<i>D. expersum</i> (N.E.Br.) Schwantes	We	RSA*	
208	<i>D. inornatum</i> (L.Bolus) L.Bolus	R	Nam*	
	Erepsia N.E.Br. (1 species)			
209	<i>E. heteropetala</i> (Haw.) Schwantes	We	RSA*	
	Esterhuysenia L.Bolus (1 species)			
210	<i>E. stokoei</i> (L.Bolus) H.E.K.Hartmann	We	RSA*	
	Jensenobotrya A.G.J.Herre (1 species)			
211	<i>J. lossowiana</i> A.G.J.Herre	R	Nam*	
	Lampranthus N.E.Br. (1 species)			
212	<i>L. affinis</i> L.Bolus	We	RSA*	
	Machairophyllum Schwantes (1 species)			
213	<i>M. brevifolium</i> L.Bolus	We	RSA*	
	Oscularia Schwantes (1 species)			
214	<i>O. cremnophila</i> Van Jaarsv., Desmet & A.E.van Wyk	R	RSA*	
	Ruschia Schwantes (2 species)			
215	<i>R. knysnana</i> (L.Bolus) L.Bolus	We	RSA*	
216	<i>R. promontorii</i> L.Bolus	We	RSA*	
	Scopelogenia L.Bolus (2 species)			
217	<i>S. bruynsii</i> Klak	We	RSA*	
218	<i>S. verruculata</i> (L.) L.Bolus	We	RSA*	
	OXALIDACEAE (1 species)			
	Oxalis L. (1 species)			
219	<i>Oxalis pocockiae</i> L.Bolus	We	RSA*	
	PORTULACACEAE (1 species)			
	Anacampseros L. (1 species)			
220	<i>A. scopata</i> G.Will.	R	RSA*	
	SEMISUCCULENT AND HERBACEOUS OUTGROUPS			
	PEDALIACEAE (outgroup)			
	Dewinteria Van Jaarsv. & A.E.van Wyk			
221	<i>D. petrophila</i> (De Winter) Van Jaarsv. & A.E.van Wyk	We	Nam*	
	SCROPHULARIACEAE (outgroup)			
	Stemodiopsis Engl.			
222	<i>S. rivae</i> Engl.	We	RSA	

CHAPTER 11

GENERAL DISCUSSION AND CONCLUSIONS

11.1 General observations

This study revealed that cliffs in South Africa and Namibia represent a pristine habitat with a uniquely adapted obligate cremnophilous succulent flora. This flora represents 6% of the total succulent flora of the subregion. The cremnophytes are confined to cliffs along the main drainage lines (river systems) and to cliffs along the Great Escarpment, on inselbergs, inland mountain ranges and coastal cliffs. Centres of diversity are located along the larger river systems, notably the Gourits, Gamtoos and Orange Rivers.

The cliffs investigated, showed very few non-succulent obligate cremnophytes among higher plants (with a few exceptions as in the Drakensberg and Western Cape), suggesting that succulence in seasonally dry climates is an essential element for survival on a cliff. Non- or semisucculent species demand modified strategies to ensure their survival, clearly shown by the two semisucculent obligate cremnophytes *Dewinteria petrophila* [221] and *Stemodiopsis rivae* [222] and by others such as members of *Ficus*, used for comparative purposes as an ‘outgroup’. Succulent plants on cliffs display various adaptive morphological features (traits) that vary from highly specialised to subtle. Among them are plants with elongated stems (cliff hangers), shrublets (cliff squatters) and the clustered growth form (cliff huggers). Some cliff huggers also have pendent leaves.

The 220 species of cremnophytes identified in this study belong to 14 families of vascular plants (ferns one species; monocotyledons three families; dicotyledons ten families) (Tables 11.1 and 11.2). Most of these species and infraspecific taxa are local endemics, only a few extending beyond the borders of South Africa and Namibia. Plants encountered represent presumably highly specialised palaeoendemic taxa such as *Gasteria rawlinsonii* [48] and *G. glomerata* [46] as well as more recent, less modified neoendemic taxa such as *Delosperma* spp. About a quarter of the plants documented (51 taxa) were new to science. This shows that not only in South Africa or Namibia, but throughout the world, cliffs represent a pristine but grossly neglected or underrated habitat with a highly specialised flora (Larson *et al.* 2000). If this trend continues, it is foreseen that many more cremnophytes will still be discovered. Further

research should therefore prove worthwhile, not only at the taxonomic and adaptive level, but also relating to the general ecology of cliffs in the subregion and elsewhere.

Cliffs are a habitat not only for obligate cremnophytes, but also for many other succulent plants and biodiversity in general. Cliffs are an important and well-known refuge and habitat for various animals such as chacma baboons (*Papio ursinus*) and rock dassies (*Procavia capensis*), but especially also for birds and they are furthermore a safe haven for many reptiles such as lizards. Humans have also been associated with cliffs throughout the ages (Larson *et al.* 2000). Masada in Israel, surrounded by cliffs, was a well-known mountain refuge and stronghold for the Israelites during Roman occupation in Biblical times.

Caves and cliffs have been used as shelters for hominids throughout the ages. Even today, hikers often find shelter under overhangs at the base of a cliff. The remains of hominid fossils, rock art and stone artefacts are well associated with cliffs and overhangs in South Africa, and there is hardly an overhang without some form of Stone Age tools. Larson *et al.* (2000) proposed the 'Urban cliff hypothesis' according to which humans today are creating their own cliff and cave shelters and refuge sites (houses, buildings and skyscrapers). Just like cremnophytes, we are free from competition and threats from wild animals today and energy can be spent on other matters. We have transformed our ancient habitat into a safe environment, with the focus now on other issues such as crop-growing, medical and other research and occupations involving in the arts.

The cliff as a shelter for hominids in the past created a safe 'stepping stone' for cultural development, for current advancement in science and ultimately for our present relatively safe (compared with past ages) human society. Competition from other species has effectively been removed. However, it was replaced by competition within human society. Man's greatest threat is its numbers, which are out of control; the species has become its own greatest threat. Perhaps we are heading for a cul-de-sac, like some of the highly modified obligate cremnophytes. Has science as a human tool produced the answers? Or is it becoming our greatest threat?

In the study area, cliffs represent a pristine, stable habitat and vital refuge for succulent and bulbous obligate cremnophytes as well as for local flora and biodiversity in general and should therefore be protected globally. This agrees with observations elsewhere in the world that cliffs are ancient, stable habitats (Klötzli 1991; Larson & Kelly 1991; Larson *et al.* 2000).

One of the main questions at the beginning of the study was: ‘Do cremnophytes display a decrease in defence and an increase in cliff-adapted features?’ In theory, cremnophytes should be adapted to grow on a vertical plane—less thorny (mechanical defence), less bitter (chemical defence) and not well camouflaged. Another question was: ‘How is reproduction of cremnophytes affected on the cliff?’

11.2 Main findings of this study

At the onset of this study it was stated that cliffs are one of the least disturbed and least known terrestrial habitats on earth. Also, that the particular nature of cliffs requires a particular adjustment (or shift) of obligate succulent or semisucculent cremnophytes in both morphology and reproduction. This study confirmed that cliffs not only harbour a highly adapted flora, but also provide stable long-term refugia for biodiversity. The cliff-face flora in the study area is diverse, representing various vascular plant families, usually typical for each subregion.

11.2.1 Obligate or near-obligate cremnophytes

This study revealed 220 species and infraspecific taxa (about 6% of region’s more or less 3 500 succulent plant taxa) as being obligate or near-obligate succulent cremnophytes (Table 11.1). Of the 220 cremnophilous taxa, 103 (46%) were strictly obligate (more than 98% confined to the cliff habitat), 94 (43%) were obligate (90–98% confined to the cliff habitat) and 23 (10%) near-obligate cremnophytes (80–90% of population confined to the cliff habitat).

11.2.2 New taxa

Of the 220 taxa, 57 were recorded as new to science and were named by the author or in collaboration with co-authors. The new taxa represent 26% of the total number of cremnophytes documented during the study (see Appendices 1 and 2).

11.2.3 Growth modification traits (morphological adjustment to the cliff habitat)

Growth modification traits identified vary from subtle to very distinct growth forms, and are the result of the cliff habitat (vertical terrain, aspect, high run-off, rainy season and absence of larger herbivores on the cliff). This has resulted not only in adjusted water-storage ability but also in modifications in growth form (stem length, direction of growth and deciduousness) and in adaptations to sun radiation and defence mechanisms.

11.2.3.1 Increase in succulence and other drought-adapted traits

This includes a clear increase in succulence and xeromorphic features (compared to close non-cremnophilous relatives). Leaves of some species tend to be more compact (abbreviated internodes), forming a cylindrical body (*Crassula perforata* subsp. *kougaensis* [131] and *Crassula rupestris* subsp. *marnieriana* [135]) (Table 11.2). This study also revealed that most obligate cremnophilous succulent elements are confined to shady south-facing cliffs where moisture is retained longer (owing to less solar radiation). Although most obligate cremnophytes are evergreen, some do become deciduous during the dry season (Table 11.3).

11.2.3.2 Decrease in size and weight

There is a general reduction in size (compared to close non-cremnophilous relatives). Cremnophytes tend to be more compact and some species display dwarfism (winter-rainfall regions and at higher altitudes), consequently with less weight tax (Tables 11.4, 11.5, 11.6 and 11.7).

11.2.3.3 Adjustment of growth form

Two distinct growth forms were identified—126 taxa with abbreviated stems (representing 57%) and 94 with extended stems (43%). Of the 126 taxa with abbreviated stems, 17 (8% of total) have leaves that become pendent. Of the 94 taxa with extended stems, 55 (26% of all cremnophytes in study area) have pendent stems. If the taxa with pendent elements (leaves or stems) are combined, there are 72 taxa (55 or 25% with pendent stems and 17 or 8% with pendent leaves). The remaining 39 (18%) (extended stems, cliff squatters) are small shrublets (often short) with one exception, *Drosanthemum anemophilum* [206], a spindly shrub (see Table 11.1).

Growth form adaptations to the vertical habitat thus represent three distinct traits. Firstly, compact cluster or mat-forming plants (cliff huggers) are associated with cliffs in the south and also at higher altitudes (above 1000 m) in the north. The second adaptive growth form is represented by dwarf shrublets (cliff squatters), including ascending but reduced shrublets. Thirdly there are the pendent-stemmed cliff hangers, which can be divided into plants with distinct leaf rosettes (aloes and aloe-related), plants with widely spread leaves (*Delosperma*, *Senecio*) and plants with leafless stems (especially of the Asclepiadaceae) (see Table 11.8). Plants on cliffs often show pendent growth as a result of epinasty—there are 26 taxa (12% of total) displaying epinastic growth (see Table 11.8). Cliff huggers, especially the bulbous ones, sometimes have distinctly drooping leaves, which can be attributed to both

gravity and epinastic growth. Bulbous obligate cremnophytes usually have bulbs with epigeous growth. Another trait among the plants with pendent stems is an increase in flexibility (Table 11.9).

11.2.3.4 Leaves and sun radiation

On south-facing aspects the leaves of aloes re-curve, exposing as much surface as possible to the light. Additional adaptations include various windows for maximum penetration of light (Table 11.10). Fewer species were found to be confined to north-facing aspects; plants restricted to this aspect tend to have mitriform rosettes and firm leaves with a grey-green surface.

11.2.3.5 Decrease in defence (armament)

There is furthermore a decrease in armour, especially noticeable in aloes with marginal teeth, which are either absent or highly reduced (Table 11.11). There is also a reduction in the bitterness of the leaf sap in aloes (see Table 11.12). Camouflage of some of these plants also seems to be less obvious (Table 11.13). In *Conophytum* species, there tends to be an increase in fragility (Table 11.14).

11.2.4 Reproductive traits

Reproduction on the cliff includes modifications such as rich flowering and a shift towards wind-dispersed seed. For long-term survival on the cliff face, cremnophytes often display backup mechanisms of reproduction (see Table 11.1). In addition to sexual reproduction, most succulent cremnophytes have a local vegetative dispersal mode. This includes propagules, runners, rooting of stems in clusters, and bulbils. Non-succulent or partially succulent obligate cremnophytes are clearly in a minority. All three species identified in the present study have additional or adjusted dispersal methods such as amphicarpy or autochory. They are the semisucculent *Dewinteria petrophila* [221], the non-succulent *Stemodiopsis rivae* [222] and *Colpias molle*. It is clear that succulence is a great advantage and necessity for the long-term survival of most cremnophytes.

11.2.4.1 Vegetative reproduction

Most succulent cremnophytes have a vegetative dispersal backup. This has been recorded in 193 (89%) taxa. Vegetative dispersal ranges from distinct bulbils to branches rooting where they touch the substrate, or it can simply entail vegetative clustering. Two partially succulent cremnophilous taxa, *Dewinteria petrophila* [221] and *Stemodiopsis rivae* [222], have

additional reproductive backup adaptations, namely amphicarpy or autochory, and they were used for comparative purposes (as outgroups). This proves that succulence is an essential element for survival on the cliff.

11.2.4.2 Rich flowering

The study revealed 32 (15% of total) taxa that produce large, conspicuous flowers in comparison to plant size. This phenomenon, called rich flowering, was first noticed by Snogerup (1971) in obligate cremnophytes in the Mediterranean region—an increase in floral size in comparison to plant size as a strategy for attracting pollinators.

11.2.4.3 Seed dispersal

The seeds of no less than 162 (74%) of the cremnophilous taxa in the study area are dispersed by the wind. This is clearly the majority, making use of wind turbulence so frequently encountered on cliffs. Although there is a shift to dispersal of seed by wind in cremnophilous mesembs (strictly obligate), the seeds of most cremnophilous mesembs are water-dispersed. This includes 42 taxa (19%). There is furthermore an increase in seed size and texture (epidermis tubercled) in *Conophytum*, aiding establishment in crevices. Some species (11 taxa, 5%) disperse their seed locally through a mechanism known as autochory. Animal dispersal plays a minor role as the seeds of only three taxa (not strictly obligate) are dispersed by frugatory birds.

11.2.5 Taxonomic representation

Of the 220 obligate or near-obligate cremnophytes, 79 taxa (36%) are monocotyledons, 140 taxa (64%) are dicotyledons and one species (*Pyrrosia schimperiana* [1]) is a succulent fern (see Table 11.2). Of these, 29 taxa (13%) are succulent bulbous plants and 190 taxa (86%) are more conventional succulent plants. The bulbous component (29 taxa) represents 37% of the monocotyledons. Most (66 taxa, 30%) of the dicotyledons belong to the Crassulaceae, with *Crassula* the largest genus. This is followed by the Mesembryanthemaceae (45 taxa, 20%), Asteraceae (10 taxa, 5%), Lamiaceae (9 taxa, 4%) and Asclepiadaceae (4 taxa, 2%). The remaining five families have two or fewer taxa each. Among the monocotyledons, the Asphodelaceae is the largest group, with 50 members (23%), followed by the Hyacinthaceae (18 taxa, 8%) and Amaryllidaceae (11 taxa, 5%).

Of the 220 taxa, 182 (83%) are endemic to South Africa. The 18 taxa that are endemic to Namibia represent 60% of the 30 cremnophilous taxa found in that country (Tables 11.15, 11.16 and 11.17).

11.2.6 Representation of cremnophytes in the various biomes

The Albany Thicket Biome (mainly Eastern Cape) and Succulent Karoo have the highest representation of cremnophytes, with 58 taxa (26%) each, Savanna 40 taxa (18%), Grassland 25 taxa (11%), Indian Ocean Coastal Belt 11 taxa (4%), Desert 10 taxa (5%) and the Nama-Karoo and Forest one taxon each (see Table 11.1). Although most cliffs are associated with the Drakensberg (Grassland Biome), this part of the Great Escarpment has only 25 obligate cremnophytes. The river valleys below the cliffs of the Great Escarpment (especially the in the southeast and east of the study area) are also well represented. There is a clear concentration of cremnophytes in the Albany Thicket as well as Succulent Karoo Biomes, but these plants are also well represented in the Savanna Biome (Table 11.1).

11.2.7 Representation of cliffs

Cliffs are well represented throughout the mountainous areas of South Africa and Namibia, especially along the Great Escarpment. Riverine or near-riverine cliffs yielded 108 taxa (50%) during the study, Cape Fold Belt and other mountains 72 taxa (33%), followed by the Great Escarpment which yielded 29 taxa (13%), inselbergs five taxa (2%) and coastal cliffs four taxa (2%).

11.3 Conclusions

11.3.1 Adaptation to the cliff habitat

Adaptations of cremnophytes to the cliff-face habitat vary from remarkable, almost evolutionary ‘cul-de-sac’ features to subtle and hardly noticeable differences. Their success rate as obligate cremnophytes is due to their adaptive or evolutionary plasticity. The main driving forces (stress factors) are lack of a regular water supply, the vertical habitat and absence of disturbance. The end result is an array of various succulent life forms shaped by the habitat (environmental variables). The lack of sufficient moisture has resulted in an increase in succulent storage tissue. The response to gravity is either surrendering to this force (cliff hangers) or compact, clustered growth (cliff huggers) or small squat shrublet growth (cliff squatters) close against the cliff face.

Aspect is important and cooler southern aspects have a marked increase in diversity of cremnophilous species (due to a much higher moisture-holding capacity than northern aspects). Northern aspects are more sunny and exposed, with few obligate cremnophytes.

Local environmental conditions also play a major role. For example, some cremnophytes follow regular fog, their distribution clearly tracking the mist belt along the west coast or the mist zone of the eastern Great Escarpment mountains.

The stable and almost disturbance- and predator-free cliff habitat has led to a relaxation of defence features (see Tables 11.14–11.16), resulting in a fragile habit and a lack of distinctive mechanical defences in the plants. The vertical habitat furthermore requires an efficient reproductive system. Apart from effective pollination (rich flowering), vegetative reproductive strategies for long-term survival are common among cremnophytes.

There is also a shift in seed dispersal, with wind the major role player. Most cremnophilous mesembs have rain-dispersed seed but when the light capsules become detached, they can also be dispersed by wind. The cliff-face flora of each region is clearly related to the local (prevailing) flora, suggesting a local derivation for the specialised cremnophytes.

11.3.2 Isolation of the cliff habitat

The cliff-face flora often occurs as isolated islands within the greater landscape. These sites display the same isolation as oceanic islands. In common with islands, there is often an absence of predators, fewer taxa (compared to larger continental land surfaces) and a higher proportion of endemism. Taxa present in such isolated places are often taxonomically distinct (Hooker 1867; Darwin 1872; Wallace 1892; Gulick 1932; Good 1947; Runemark 1970).

Gasteria rawlinsonii [48] in the Baviaanskloof occurs in deep kloofs of the Baviaanskloof and Kouga Mountains. Although in close proximity, each kloof is isolated from the next and often house distinct forms (e.g. in Geelhoutboskloof, Gertsmitkloof). This clearly shows the ‘island isolation effect’ of local gene exchange. Most succulent cremnophytes are exiles to the cliff face. They have a low competitive ability and hence occupy a habitat where other plants perform poorly. Therefore, succulent cremnophytes are specialist and poorly understood taxa, often at a dead end or cul-de-sac should they lose their

cliff-face habitat. Cliffs should be seen as part of a specialised habitat of great evolutionary significance and conservation value within the greater biosphere. Hence cliffs and their biota should be protected by law on a global scale.

11.3.3 Cliffs as refugia

‘He hideth my soul in the cleft of the rock’, ‘Rock of all ages’, ‘Rock of my salvation’—all well-known phrases among Jews and Christians, associating the rock face with a refuge and a stable, safe habitat. Throughout the ages, cliffs have served as refuges and during disasters and climate change they still serve this purpose. Facultative and obligate cremnophytes (succulent and other) from such sites can re-establish on non-cliff terrain when favourable conditions prevail. Cliffs and their associated steep ground are also the habitat of many other organisms. South Africa and Namibia has a rich and diverse obligate succulent cremnophyte flora that is widespread on cliffs throughout the region. Most cremnophytes, however, are associated with river valleys, concentrated in the Albany Thicket and Succulent Karoo Biomes in the south and west. Cliff faces are important stable habitats and often represent ancient refugia of biodiversity.

11.3.4 Cliffs as living laboratories

Owing to their stability and pristine vegetation, cliffs are among the last virgin habitats on earth. They can serve as living laboratories that may throw light not only on the historical past but also on the evolutionary adaptive plasticity of species when under constant long-term stress from a lack of moisture and the challenges of the vertical terrain. The different adaptive structural features that are due to the various environmental variables (latitude, altitude, rainfall aspect, geology) can be studied in detail.

11.3.5 The vertical habitat as a driving force in evolution

Cliffs are extreme habitats with three constant stress factors—aridity, the vertical habitat and the absence of disturbance or predation. These features have led to particular cliff-dependent adaptations. There is a clear increase in structural adaptive ‘fine-tuning’ or local specialisation such as an increase in succulence, pendent features or compact growth coping with gravity, and modifications in reproductive behaviour. There are a general decrease in size (and weight) and an increase in compact cluster forms. Vegetative backup propagules or vegetative proliferation are essential survival elements on the cliff. Semisucculent or non-succulent obligate cremnophytes show specialist reproductive behaviour such as amphicarp or

autocarpy. Their specialised adaptations reveal information on plant behaviour and evolution (morphological and reproductive). Succulence not only enables plants to survive in hyper-arid environments, but it also allows obligate succulent cremnophytes to grow and survive where most plants would perish. The increase in succulence and other xeromorphic features are clearly adaptations to this dry habitat.

Cremnophytes are subject to little competition in the absence of disturbances by megaherbivores and fire. The resultant relaxation in defence and increase in adaptations to a vertical habitat with its variables lead to the conclusion that predation and competition are important driving forces in evolution and in the shaping of plants. Runemark (1970) suggested small isolated populations (as in many cremnophytes) may be in a creative phase (subject to random fixation of non-adaptive characters) as a result of genetic drift. This is well demonstrated in *Gasteria rawlinsonii*: e.g., leaves in a rosette and large marginal teeth (Geelhoutboskloof; in shady conditions) as to populations with leaves remaining distichous and with small marginal teeth (Gertsmitkloof; open shade, and dryer conditions).

Obligate cremnophilous vegetation is still poorly known and requires further research. If almost 20% of the obligate cremnophytes recorded during the present study were new to science, then further research may uncover many more such specialised species on local cliffs as well as in other parts of the world.

11.3.6 Horticultural application and conservation

Most obligate cremnophytes are not only horticulturally appealing, but are also suitable to fill a specialist niche on artificial ‘cliff’ sites such as window sills, roof gardens, steep embankments and vertical walls. Cremnophytes have been successfully used in hanging baskets, flower boxes on window sills and in other containers. Some are also in demand by specialist connoisseur growers. Cremnophytes showing horticultural appeal include many species of *Aloe*, *Bulbine*, *Cyrtanthus*, *Gasteria*, *Haworthia*, *Crassula*, *Conophytum* and *Delosperma* (Van Jaarsveld 1997b, 2006b). Horticultural subjects include all three major growth forms, namely cliff hangers, cliff huggers and cliff squatters. Their local adaptability ensures long-term survival in the artificial cliff environment. Many of these species are already well established in cultivation, their vegetative backup mode and ease of growth further enhancing their popularity in the ‘neo-urban cliff environment’.

TABLE 11.1—Adaptations to the cliff habitat among South African and Namibian cremnophilous succulent and succulent bulbous plants (220 taxa, 41 genera)

Issue	Monocotyledons	Dicotyledons	Ferns	Total of all cremnophytes studied
Numbers	79 taxa (36%)	140 taxa (64%)	1	220 taxa
Bulbous	29 (37% of monocots, 13% of all cremno- phytes)	1	–	30 (13%)
Succulent (bulbous excluded)	50 (63% of monocots, 23% of total)	139 (63% of total)	1	190 (86%)
Pendent stems	14	42	–	56 (25%)
Pendent leaves from cluster	27	1	1	29 (13%)
Abbreviated growth (clustered or short-stemmed)	65	60	1	126 (57%)
Extended stems	14	80	–	94 (43%)
Ascending (decumbent or erect)	65	98	1	164 (75%)
Epinastic growth	21	8	–	29 (13%)
Vegetative backup	72	130	1	203 (92%)
Rich flowering	3	25	–	28 (15%)
Fynbos	3	18	–	21 (10%)
Succulent Karoo	12	46	–	58 (26%)
Nama-Karoo	1	1	–	2 (1%)
Desert	1	10	–	10 (5%)
Grassland	10	15	–	25 (11%)
Savanna	20	18	–	40 (18%)
Forest	–	–	1	1
Albany Thicket	32	26	–	58 (26%)
Indian Ocean Coastal Belt (IOCB)	2	9	–	11 (4%)
Fog trap	–	9 (Succulent Karoo)	–	9 (4%)
Caudiciform	–	15 (14 Succulent Karoo, 1 IOCB)	–	15 (7%)
Strictly obligate cremnophytes	42	61	–	103 (47%)
Quartz/sandstone	62	113	–	175 (80%)
Shale/mudstone	17	21	–	38 (17%)
Dolomite	3	8	–	11 (5%)
Granite	1	8	–	9 (3%)
Conglomerate	1	1	–	2 (1%)
Wind dispersal (seed)	76	86	1	163 (74%)
Water dispersal (seed)	–	44	–	44 (20%)
Avian dispersal (seed)	3	1	–	4 (2%)
Autochory	3	12	–	15 (5%)
Succulents in study region (3 500)	414	3 085	1	220 (6%)
Winter rain	9	54	–	63 (29%)
Summer rain	32	49	1	82 (37%)
All-year-rain	37	31	–	68 (31%)
Light weight	11	58	–	80 (36%)
Light/medium weight	24	48	–	72 (33%)
Medium weight	25	24	1	50 (23%)
Medium weight/heavy	13	6	–	19 (9%)

Issue	Monocotyledons	Dicotyledons	Ferns	Total of all cremnophytes studied
Heavy	5	1	–	6 (3%)
Evergreen	77	98	1	176 (80%)
Winter-deciduous	7	2	–	9 (4%)
Summer-deciduous (or -aestivating)	4	19	–	23 (10%)
Southern aspect	65	119	1	185 (84%)
Strictly southern aspect	39	84	1	124 (56%)
Northern aspect	13	21	–	34 (15%)
Strictly northern aspect	2	3	–	5 (2%)

TABLE 11.2—South African and Namibian cremnophilous succulent and bulbous succulent plants

Group	Number of cremnophilous taxa		
	Total	Succulent	Bulbous succulent
Monocotyledons	79	50	29
Dicotyledons	140	139	1
Ferns	1	1	–
Total	220	190	30

TABLE 11.3—Summer and winter deciduousness among South African and Namibian cremnophilous succulent and bulbous succulent plants

Group	Number of taxa			
	Total	Summer-deciduous	Winter-deciduous	Evergreen
Monocotyledons	79	4	7	68 (31%)
Dicotyledons	140	38	2	100 (46%)
Ferns	1	–	–	1
Total	220	42 (19%)	9 (5%)	169 (77%)

TABLE 11.4—Weight of the 222 obligate succulent and bulbous succulent cremnophytes occurring in the nine biomes (average weight of mature, fully turgid plants)

Biome	Number of taxa					Total
	Light (1–50 g)	Light / medium	Medium (51–500 g)	Medium / heavy	Heavy (> 500 g)	
Fynbos	9	6	2	2	2	21
Succulent Karoo	25	21	9	3	–	58
Albany Thicket	19	22	15	2	–	58
Savanna	4	12	11	7	3	40
Grassland	13	6	5	1	–	25
Forest	–	–	1	–	–	1
Nama-Karoo	1	–	–	–	–	1
Desert	3	2	2	2	1	10
Indian Ocean Coastal Belt	1	2	5	3	–	11

TABLE 11.5—Comparison of plant size between cremnophytes and related non-cremnophytes (groups of closely related taxa separated by thick lines)

Taxon	Size	Cliff habitat	Other habitat	Locality
<i>Cotyledon barbeyi</i>	large shrub 500 mm tall, leaves 150 mm long		×	Hanglip, Waterberg
<i>C. barbeyi</i> var. A [106]	small shrublet up to 100 mm tall, leaves 30–50 mm long	×		Wyllies Poort, cliffs, Soutpansberg
<i>C. tomentosa</i> subsp. <i>ladismithiensis</i>	shrublet, dense rounded growth up to 300 mm tall, hairy but not as markedly tomentose		×	Ladismith
<i>C. tomentosa</i> subsp. <i>tomentosa</i> [109]	compact shrublet up to 150 mm tall, leaves shorter, markedly tomentose	×		Gert Smitskloof, Baviaanskloof
<i>C. pendens</i> [108]	flaccid drooping stems, leaves markedly swollen	×		Bashee River
<i>C. woodii</i>	woody shrub up to 0.7 m, leaves dorsiventrally compressed		×	Kouga Dam
<i>Crassula capitella</i> subsp. <i>thyrsiflora</i>	leaves up to 50 mm long		×	Oudtshoorn, Little Karoo
<i>C. capitella</i> subsp. <i>thyrsiflora</i> (= <i>C. turrita</i>) [115]	leaves dwarf-sized, 5–12 mm long, symmetrically arranged	×		Kouga Dam cliffs
<i>Ornithogalum longibracteatum</i> (rocky outcrop forms) [78]	bulbs 20–50 mm in diameter	×		Bashee River cliff forms
<i>O. longibracteatum</i>	bulbs 100–120 mm in diameter		×	non-cliff, Knysna
<i>Aloe arborescens</i> subsp. <i>arborescens</i>	large rounded shrubs 1–1.5 m tall		×	Swellendam
<i>A. arborescens</i> subsp. <i>mzimnyati</i> [13]	small shrubs 300–500 mm high	×		Buffalo River, near Thukela River
<i>A. meyeri</i> [22]	rosettes 100–150 mm in diameter	×		Rosyntjieberg
<i>A. perfoliata</i>	rosettes 300–450 mm in diameter		×	Du Toit's Kloof
<i>Bulbine latifolia</i> var. <i>latifolia</i>	rosettes 200–300 mm in diameter, leaves broadly ovate-triangular		×	Hankey
<i>B. latifolia</i> var. <i>curvata</i> [32]	rosettes about 100 mm in diameter with linear-lanceolate leaves drawn together	×		Kouga Dam
<i>Gasteria pillansii</i> var. <i>pillansii</i>	rosettes large, leaves ascending, 100–200 × 25–50 mm		×	Clanwilliam Dam
<i>G. pillansii</i> var. <i>ernesti-ruschii</i> [47]	rosettes small, leaves 20–70 mm long, patent	×		Sonberg, southern Namibia
<i>Othonna herrei</i>	erect shrublet 100–150 mm tall		×	Jenkins Kop, Richtersveld
<i>O. armiana</i> [86]	compact, clustered heads up to 20 mm high	×		Rooiberg, Eksteenfontein
<i>O. triplinervia</i> [89]	with caudex, sprawling to decumbent stems up to 500 mm long	×		Kouga Dam
<i>O. triplinervia</i>	erect shrubs 1.5 m tall		×	Hankey

TABLE 11.6—Average leaf dimensions and internode length in cremnophilous and non-cremnophilous forms of *Crassula rupestris* and *C. perforata*

<i>Crassula</i> taxon	Leaf dimensions (mm)	Length of internode (mm)	Stems	Cliff habitat	Flat ground	Specimens examined
<i>C. rupestris</i>	22 × 18 × 5	10	woody		×	<i>Van Jaarsveld 851/96</i>
<i>C. rupestris</i> subsp. <i>marnieriana</i> [135]	5 × 7 × 3.5	2–3	flaccid	×		<i>Van Jaarsveld 17431</i> (Zorgvliet, Ladismith)
<i>C. rupestris</i> subsp. <i>rupestris</i> [136]	10 × 6 × 4	4–5	flaccid	×		<i>Van Jaarsveld 16950</i> (Dwarsrivier)
<i>C. perforata</i>	14 × 21 × 4	10	woody		×	<i>Van Jaarsveld 17119</i> (Kouga Dam)
<i>C. perforata</i> subsp. <i>kougaensis</i> [131]	7 × 7 × 3	3	flaccid	×		<i>Van Jaarsveld 17097</i> (Kouga Dam)
<i>C. perforata</i> subsp. <i>perforata</i> [132]	10 × 8 × 6	5	flaccid	×		<i>Van Jaarsveld 17835</i> (Enon cliffs)

TABLE 11.7—Average size and stem characters of closely related cremnophilous and non-cremnophilous taxa of *Othonna*, *Plectranthus* and *Tylecodon*

<i>Othonna/Plectranthus/Tylecodon</i> taxon	Succulent caudex	Stem length	Erect	Spreading	Stem diameter (mm)	Cremnophilous	Non-cremnophilous
<i>O. armiana</i> [86]	×	25 mm	×	×	3–10, caudex up to 70	×	
<i>O. herrei</i>		150–250 mm	×		15–30		×
<i>O. triplinervia</i> [89] (cliff form)	×	100–200 mm		×	15	×	
<i>O. triplinervia</i>		2–3 m	×		70–80		×
<i>O. cremnophila</i> [88]	×	150–250 mm	×		3.5–9	×	
<i>O. cyclophylla</i>		1.0–1.5 m	×		30		×
<i>P. ernstii</i> [168]	×	50–200 mm		×	35–50	×	
<i>P. strigosus</i>		100–250 mm		×	2–3		×
<i>P. saccatus</i> subsp. <i>pondoensis</i> [172]		1 m		×	4–8	×	
<i>P. saccatus</i> subsp. <i>saccatus</i>		1 m	×		10–25		×
<i>T. buchholzianus</i> var. <i>fasciculatus</i> [152]	×	60–150 mm	×	×	5–8	×	
<i>T. buchholzianus</i> var. <i>buchholzianus</i>	×	300 mm	×		3–6		×
<i>T. cordiformis</i> [153]	×	20–50 mm		×	12	×	
<i>T. bayeri</i>	×	200 mm		×	2		×
<i>T. decipiens</i> [154]	×	40–80 mm		×	10	×	
<i>T. schaeferianus</i>	×	40–80 mm		×	4–5		×

TABLE 11.8—South African and Namibian cremnophilous succulent and bulbous succulent plants with pendent elements (220 taxa, 41 genera)

Pendent element	Number of taxa			
	Mono-cotyledons	Di-cotyledons	Other groups (fern)	Total cremnophytes
Pendent leaves	18	–	–	18 (8%)
Bulbous plants with pendent leaves	11	–	–	11
Cluster-forming succulent plants with pendent leaves (bulbs excluded)	7	–	–	7
Pendent stems	14	41	–	55 (25%)
With rudimentary foliage	–	4	–	4
Foliated stems	–	37	–	37
Apical rosettes	11	–	–	11
Apical rosette extending into leafy stem	3	–	–	3
Epinastic growth	21	8	–	29 (13%)

TABLE 11.9—Stem flexibility among cremnophilous species and their close non-cremnophilous relatives (groups of closely related taxa separated by thick lines)

Taxon	Stem flaccid, decumbent or becoming pendent	Stem sturdy, erect	Creemnophilous	Non-creemnophilous
<i>Gasteria rawlinsonii</i> [48]	×		×	
<i>G. bicolor</i>		×		×
<i>Aloe challisii</i> [15]	×		×	
<i>A. chortolirioides</i>		×		×
<i>Cotyledon pendens</i> [108]	×		×	
<i>C. woodii</i>		×		×
<i>Huernia pendula</i> [81]	×		×	
Most <i>Huernia</i> spp.		×		×
<i>Tromotriche baylissii</i> [83], <i>T. choanantha</i> [84]	×		×	
Most other <i>Tromotriche</i> spp.		×		×
<i>Plectranthus mutabilis</i> [169]	×		×	
<i>P. hadiensis</i>		×		×
<i>P. saccatus</i> subsp. <i>pondoensis</i> [172]	×		×	
<i>P. saccatus</i> subsp. <i>saccatus</i>		×		×
<i>Senecio medley-woodii</i> [90]	×		×	×
<i>S. pyramidatus</i>		×		×

TABLE 11.10—Occurrence of windows in leaves of some cremnophytes (mainly on shady south-facing aspects)

Taxon	Shape and position of windows						
	Lines	Central band	Dots	Margin	Adaxial	Abaxial	Leaf apex
<i>Albuca cremnophila</i> [64]		×				×	
<i>Aloe challisii</i> [15]				×			
<i>Conophytum ernstii</i> subsp. <i>ernstii</i> [179]			×				
<i>C. fulleri</i> [181]							×
<i>C. marginatum</i> var. <i>haramoepense</i> [184]			×				
<i>C. taylorianum</i> subsp. <i>rosynense</i> [193]			×				
<i>Drimia flagellaris</i> [70]	×						
<i>D. loedolffiae</i> [71]	×						
<i>D. mzimvubuensis</i> [72]		×			×		
<i>Haworthia cymbiformis</i> var. <i>setulifera</i> [53]	×				×	×	×
<i>H. gracilis</i> var. <i>picturata</i> [55]	×				×	×	×
<i>H. mirabilis</i> var. <i>consanguinea</i> [58]	×		×	×	×	×	×
<i>Ornithogalum pendens</i> [79]		×				×	
<i>Senecio muiirii</i> [91]	×					×	

TABLE 11.11—Comparison of spine size and distance between spines in related cremnophilous and non-cremnophilous species of *Aloe* (Van Jaarsveld 1981a,b, 1982a,b; Reynolds 1982) (groups of closely related taxa separated by thick lines)

<i>Aloe</i> taxon	Spines		Cremno-philous	Non-cremnophilous	Locality
	Size (mm), texture	Distance apart (mm)			
<i>A. corallina</i> [16]	1 × 1	10	×		Otjiboronbongo, Namibia
<i>A. dewinteri</i> [18]	1 × 1	8–12	×		Sesfontein, Namibia
<i>A. asperifolia</i>	2 × 1.5	10		×	central Namib, Namibia
<i>A. omavandae</i> [25]	1.0–1.5 × 1	10–15	×		Omavanda, Namibia
<i>A. esculenta</i>	2–3 × 2–3	15–20		×	Ondangua, Namibia
<i>A. littoralis</i>	4 × 4	15–20		×	Windhoek, Namibia
<i>A. meyeri</i> [22]	1–2 × 1–2	3–5	×		Rosyntjieberg, Northern Cape
<i>A. dabenorisana</i> [17]	1.5 × 1.5	10	×		Pella, Northern Cape
<i>A. pavelkae</i> [26]	1.5 × 1.5	4–8	×		Kuamsibberg, southern Namibia
<i>A. perfoliata</i>	3 × 3	7–10	×	×	widespread, Western Cape
<i>A. hardyi</i> [20]	2 × 2	15–20	×		Olifants River, Mpumalanga
<i>A. mutabilis</i> [23]	2 × 2	15–25	×		Witpoortjie, Gauteng
<i>A. arborescens</i> subsp. <i>mzimnyati</i> [13]	2 × 2	10	×		Buffalo River, KwaZulu-Natal
<i>A. arborescens</i>	3–5 × 3–5	20	×	×	widespread, Ugi, Eastern Cape
<i>A. pictifolia</i> [27]	1 × 0.5	2–3	×		Kouga Dam, Eastern Cape
<i>A. microstigma</i>	2–4 × 2–4	5–10		×	Worcester, Western Cape
<i>A. nubigena</i> [24]	leaf margin entire	–	×		Graskop, Mpumalanga
<i>A. verecunda</i>	leaves usually with small, soft spines	2–7		×	Witwatersrand, Gauteng

TABLE 11.12—Comparison of bitterness of leaf sap in cremnophilous and related non-cremnophilous species of *Aloe* (Van Jaarsveld 1981a,b, 1982a,b; Reynolds 1982) (groups of closely related taxa separated by thick lines) (0 = not bitter; 1 = slightly bitter to bitter; 2 = distinctly bitter)

<i>Aloe</i> taxon	Leaf sap: rating of bitterness	Cremno-philous	Non-cremno-philous	Locality
<i>A. corallina</i> [16]	1	×		Otjiboronbongo, Namibia
<i>A. dewinteri</i> [18]	1	×		Sesfontein , Namibia
<i>A. asperifolia</i>	2		×	central Namib, Namibia
<i>A. omavandae</i> [25]	1	×		Omavanda, Namibia
<i>A. esculenta</i>	2		×	Ondangua, Namibia
<i>A. littoralis</i>	2		×	Windhoek, Namibia
<i>A. meyeri</i> [22]	1	×		Rosyntjieberg, Northern Cape
<i>A. dabenorisana</i> [17]	1	×		Pella, Northern Cape
<i>A. pavelkae</i> [26]	1	×		Kuamsibberg, southern Namibia
<i>A. perfoliata</i>	2	×	×	widespread, Western Cape
<i>A. hardyi</i> [20]	1	×		Olifants River, Mpumalanga
<i>A. mutabilis</i> [23]	1	×		Witpoortjie, Gauteng
<i>A. arborescens</i> subsp. <i>mzimnyati</i> [13]	1	×		Buffalo River, KwaZulu-Natal
<i>A. arborescens</i>	2	×	×	widespread, Ugi, Eastern Cape
<i>A. pictifolia</i> [27]	1	×		Kouga Dam, Eastern Cape
<i>A. microstigma</i>	2		×	Worcester, Western Cape
<i>A. nubigena</i> [24]	0	×		Graskop, Mpumalanga
<i>A. thompsonii</i> [30]	0	×		Wolkberg, Limpopo
<i>A. soutpansbergensis</i> [29]	0	×		Soutpansberg, Limpopo
<i>A. challisii</i> [15]	0	×		Steenkampsberg, Mpumalanga
<i>A. ecklonis</i>	1		×	garden material
<i>A. reynoldsii</i> [28]	0	×		Bashee River, Eastern Cape
<i>A. kouebokkeveldensis</i> [21]	0	×		Cold Bokkeveld, Western Cape
<i>A. buhrii</i>	0		×	northeast of Vanrhynsdorp, Northern Cape

TABLE 11.13—Leaf colour in cremnophilous species of *Gasteria* and *Ledebouria* and their non-cremnophilous relatives

<i>Gasteria/Ledebouria</i> taxon	Leaves spotted	Leaves immaculate	Leaves glaucous	Cremnophilous	Non-cremnophilous
<i>G. glomerata</i> [46]		×	×	×	
<i>G. baylissiana</i>	×				×
<i>G. glauca</i> [45]		×	×	×	
<i>G. ellaphieae</i>	×				×
<i>G. rawlinsonii</i> [48]		×		×	
<i>G. bicolor</i>	×				×
<i>L. venterii</i> [76]		×		×	
Other <i>Ledebouria</i> spp.	×				×
<i>L. concolor</i> [74]		×		×	

TABLE 11.14—Comparison of plant fragility in related cremnophytes and non-cremnophytes (from Hammer 1993, 2002; Bayer 1999) (groups of closely related taxa separated by thick lines)

Taxon	Armament	Cliff habitat	Other habitat	Locality
<i>Conophytum ricardianum</i> subsp. <i>richardianum</i> [189]	epidermis soft, fragile	×		Sonberg, Namibia
<i>C. wettsteinii</i>	epidermis firm		×	Sonberg, Namibia
<i>Haworthia mirabilis</i> var. <i>consanguinea</i> [58]	leaves soft, fragile, ascending-spreading	×		Dwarswaterskloof, Caledon district
<i>H. mirabilis</i> var. <i>mirabilis</i>	leaves firm, retuse		×	Mierkraal, Bredasdorp
<i>H. cymbiformis</i> var. <i>setulifera</i> [53]	epidermis fragile	×		Bashee River
<i>H. decipiens</i>	leaves firm		×	Prince Albert, Willowmore
<i>H. emelyae</i>	leaves firm		×	Uniondale
<i>H. gracilis</i> var. <i>picturata</i> [55]	leaves fragile	×		Kouga Dam (Hankey)
<i>H. heidelbergensis</i>	leaves firm		×	Heidelberg, Western Cape
<i>H. marumiana</i> var. <i>batesiana</i> [56]	leaves soft, entire	×		Graaff-Reinet
<i>H. marumiana</i> var. <i>dimorpha</i>	leaves firm, spinescent		×	Montagu
<i>H. arachnoidea</i>	leaves firm		×	widespread, succulent karoo
<i>H. glabrata</i> [54]	leaves firm, but more fragile than most in sect. <i>Hexangularis</i>	×		Bashee River
<i>H. attenuata</i>	leaves firm		×	Port Elizabeth
<i>Bulbine latifolia</i> var. <i>latifolia</i>	leaves firm		×	Hankey
<i>B. natalensis</i> [34]	leaves fragile, soft (translucent)	×		Kouga Dam
<i>B. thomasiae</i> [40]	leaves fragile, soft (translucent)	×		Bashee River, Collywobbles
<i>B. suurbergensis</i> [39]	leaves fragile, soft (translucent)	×		Suurberg
<i>Senecio pondoensis</i> [92]	leaves soft, fragile, pruinose	×		Mzamba River
<i>S. talinoides</i>	leaves firm, glaucous		×	widespread, Eastern Cape

TABLE 11.15—South African and Namibian cremnophilous succulent and bulbous succulent plants: ranking of plant families by size (220 taxa, 41 genera)

Family	Number of taxa	Largest genus	Number of species	Number of genera
FERNS				
Polypodiaceae	1	<i>Pyrrrosia</i>	1	1
SEED PLANTS				
Monocotyledons (3 families)	79 (36%)			
Asphodelaceae	50 (23%)	<i>Aloe</i>	18	5
Hyacinthaceae	18 (8%)	<i>Albuca</i>	6	5
Amaryllidaceae	11 (5%)	<i>Cyrtanthus</i>	8	2
Dicotyledons (10 families)	140 (64%)			
Crassulaceae	66 (30%)	<i>Crassula</i>	38	4
Mesembryanthemaceae	45 (20%)	<i>Conophytum</i>	19	11
Asteraceae	10 (5%)	<i>Senecio</i>	5	3
Lamiaceae	9 (4%)	<i>Plectranthus</i>	6	3
Asclepiadaceae	4 (2%)	<i>Tromotriche</i>	2	2
Geraniaceae	2 (1%)	<i>Pelargonium</i>	2	1
Cactaceae	1	<i>Rhipsalis</i>	1	1
Gesneriaceae	1	<i>Streptocarpus</i>	1	1
Oxalidaceae	1	<i>Oxalis</i>	1	1
Portulacaceae	1	<i>Avonia</i>	1	1

TABLE 11.16—Endemism in South African cremnophilous succulent and bulbous succulent plants

Family	Number of taxa	Number of endemic taxa	% endemic taxa	Number of genera
FERNS				
Polypodiaceae	1	–	–	1
SEED PLANTS				
Monocotyledons (3 families)	79 (36%)	67	85%	12
Amaryllidaceae	11 (5%)	10	90%	2
Asphodelaceae	50 (23%)	41	82%	5
Hyacinthaceae	18 (8%)	16	89%	5
Dicotyledons (10 families)	140 (64%)	115	82%	30
Asclepiadaceae	4 (2%)	3	75%	3
Asteraceae	10 (5%)	10	100%	3
Cactaceae	1	–	–	1
Crassulaceae	66 (30%)	51	77%	4
Geraniaceae	2 (1%)	1	50%	1
Gesneriaceae	1	1	100%	1
Lamiaceae	9 (4%)	6	67%	3
Mesembryanthemaceae	45 (20%)	41	91%	12
Oxalidaceae	1	1	100%	1
Portulacaceae	1	1	100%	1
Total	220	182	83%	42

TABLE 11.17—Endemism in Namibian cremnophilous succulent and bulbous succulent plants

Family	Number of taxa	Number of endemic taxa	% endemic taxa	Number of genera
Monocotyledons (2 families)	8	3	38%	3
Amaryllidaceae	1	–	–	1
Asphodelaceae	7	3	43%	2
Dicotyledons (5 families)	22	15	68%	10
Asclepiadaceae	1	1	100%	1
Crassulaceae	11	5	45%	3
Geraniaceae	1	1	100%	1
Lamiaceae	3	3	100%	2
Mesembryanthemaceae	6	5	83%	3
Total	30	18	60%	13

CHAPTER 12

SPECIES TREATMENT (Enumeration of the

220 obligate or near-obligate cremnophilous succulent and bulbous taxa)

FERNS

POLYPODIACEAE

Pyrrosia Mirb.

1. *Pyrrosia schimperiana* (Mett. ex Kuhn) Alston

PYRROSIA Mirb.

1. *Pyrrosia schimperiana* (Mett. ex Kuhn) Alston in Journal of Botany, London 72, Suppl. 2: 8 (1934).

Cremonophyte growth form: Cluster-forming, subpendulous leaves (of medium weight, cliff hugger).

Growth form formula: A:S:Lper:Lc:Ts (p)

Etymology: After Wilhelm Schimper (1804–1878), plant collector in northern Africa and Arabia.

DESCRIPTION AND HABITAT

Cluster-forming semipoikilohydric plant, with creeping rhizome 2 mm in diameter; rhizome scales up to 6 mm long, dense, ovate-cucullate to lanceolate-acuminate, entire. Fronds ascending-spreading, becoming pendent, 150–300 × 17–35 mm, succulent-coriaceous, closely spaced to ascending, often becoming drooping (2–6 mm apart); stipe tomentose (silvery grey to golden hairs), becoming glabrous with age. Lamina linear-lanceolate to linear-obovate, rarely with 1 or 2 lobes; margin entire; adaxial surface tomentose becoming glabrous, abaxial surface remaining densely tomentose (grey to golden stellate hairs); base cuneate; apex acute. Sori rusty brown dots, 1 mm in diameter, evenly spaced (1–2 mm apart) in distal two thirds on abaxial surface, emerging through dense indumentum.

Phenology: Sori produced mainly in summer and spring. Spores dispersed by wind, coinciding with the rainy season.

Habitat and aspect: Sheer south-facing cliffs and rocky embankments, among lichens and other succulent flora. Plants are scattered, firmly rooted in crevices and on ledges. The average daily maximum temperature is about 26°C for summer and 14°C for winter. Rainfall is experienced mainly in summer, 1000–1250 mm per annum.

Altitude: 1400–1600 m.

Associated vegetation: Mosaic of Northern Mistbelt Forest (Forest Biome) and the Sub-Escarpment Savanna Bioregion of the Savanna Biome (Mucina *et al.* 2005).

Associated cremnophytes: *Aeollanthus parvifolius*, *Aloe spicata*, *Cotyledon barbeyi*, *Delosperma leboomboensis*, *Peperomia blanda* and *Plectranthus cylindraceus*.

Geology: Quartzitic sandstone of the Black Reef Formation (Transvaal Supergroup) with many fissures, ledges and crevices ideal for establishment of plants.

DISTRIBUTION

Widespread in Africa and reaches its southernmost limit in Mpumalanga at the Blyde River Canyon (altitude of 1400–1650 m).

RELATED SPECIES

Differs from *Pyrrhosia africana* by its adaxial leaf surface which is densely hairy at first, becoming glabrescent with scattered sori on the lower surface. *Pyrrhosia africana* is an epiphyte occurring in coastal forest of the Eastern Cape and KwaZulu-Natal, with the upper leaf surface subglabrous and the sori clustered on the lower leaf surface. The succulent, semipoikilohydric leaves and dense, hairy surface of *P. schimperiana* are probably an adaptation to its xeric cliff-face habitat.

ADAPTATIONS TO THE CLIFF ENVIRONMENT

Habit: Plants clustered, with creeping rhizome rooting in crevices, with spreading to drooping fronds. Slow-growing, long-lived perennial.

Size and weight: Heads small, of medium weight.

Stem: Creeping rhizome covered in rhizome scales.

Leaves

Orientation: Spreading and drooping, semipoikilohydric, in winter becoming desiccated but recovering after rain. Well adapted to the dry, xeric habitat.

Succulence: Succulent.

Colour and texture: Green, covered with dense tomentum, becoming glabrescent on adaxial surface; lower surface densely hairy and probably contributing to conservation of water.

Age and persistence: Long-lived, perennial.

Armament: None.

Sexual reproduction

Sori: Scattered on lower surface.

Spores

Dispersal: Spores wind-dispersed, germinating in suitable habitats.

Time: Spores released in the rainy season.

Vegetative reproduction: Plants form clusters from short, creeping rhizomes, thus ensuring a hold on the cliff-face habitat. Spreading by means of vegetative growth, proliferating and rooting where the rhizome touches a crevice (vegetative backup).

CONSERVATION STATUS

Classified as of least concern (Raimondo *et al.* 2009). A rare species, but not threatened owing to the safe cliff habitat.

ADDITIONAL NOTES

Horticulture: *Pyrrhosia schimperiana* is a worthwhile introduction to horticulture and thrives in small containers or hanging baskets. It can also be grown on rocky embankments. It is best grown in a loamy, well-drained soil, with ample feeding during the summer growing season. It is recommended for moist savanna or warm subtropical gardens and should be kept in semishade and well watered in summer. Plants can be divided in spring. In regions with frost the plants should be brought indoors in winter.

VOUCHER

Van Jaarsveld 17246 (NBG).

ILLUSTRATIONS AND MAP

Plate 1, Figures 1a–1c, Map 1.

FLOWERING PLANTS

Monocotyledons

AMARYLLIDACEAE

Cyrtanthus Aiton

2. *C. falcatus* R.A.Dyer
3. *C. flammosus* Snijman & Van Jaarsv.
4. *C. flanagani* Baker
5. *C. herrei* (F.M.Leight.) R.A.Dyer
6. *C. inaequalis* O'Brien
7. *C. junodii* P.Beauv.
8. *C. labiatus* R.A.Dyer
9. *C. montanus* R.A.Dyer

Haemanthus L.

10. *H. albiflos* Jacq.
11. *H. humilis* Jacq. subsp. *humilis*
12. *H. paucifolius* Snijman & A.E.van Wyk

CYRTANTHUS Aiton

2. *Cyrtanthus falcatus* R.A.Dyer in *Herbertia* 6: 76, t. 138, fig. 1 (1939).

Cremnophyte growth form: Cluster-forming, epigeous, bulbous, with pendent leaves (of medium weight to heavy, cliff hugger).

Growth form formula: A:B:D:C:Lp (e) (vb) (eg)

Etymology: Latin *falcatus*, sickle-shaped, pertaining to the leaves.

DESCRIPTION AND HABITAT

Deciduous, epigeous, cluster-forming bulbous plants. Bulbs ovoid to globose, up to 80 mm in diameter, sprouting from base, tapering to a neck up to 120 mm long; tunics dense, brown to grey, membranous. Leaves up to 4, linear, up to 350 × 30 mm, leathery, green; apex acute. Scape up to 300 mm long, glaucous, 15 mm in diameter near base and about 10 mm distally, characteristically recurved at the top with a pendent umbel of up to 10 flowers; bracts 4.50 × 12.5 mm, linear-lanceolate, soon withering; pedicels up to 14 mm long. Perianth pendulous, red, zygomorphic, up to 70 mm long; tube up to 40 mm long, throat about 10 mm in diameter; outer surface greenish, buff, red on lobes; lobes reddish, obovate-oblong, the outer up to 25 mm long and 12.5 mm broad, shortly cucullate at throat, inner lobes 13 mm in diameter, slightly retuse at apex. Stamens arising from base of perianth; anthers yellow, dorsifixed. Ovary up to 10 mm long. Capsule and seed not seen.

Phenology: Synanthous, flowering mainly in spring (October–November).

Pollinators: Sunbirds.

Habitat and aspect: Vertical or near-vertical cliffs, from about 1500–2000 m in the Drakensberg midlands. Habitat consists of wooded valleys and mountainous terrain. Plants are firmly rooted in crevices; size often depends on the growing space allowed by the crevice. Average daily maximum temperature is about 25°C and average daily minimum 10–11°C. Winters are colder, with frost and occasional snow. Rainfall occurs mainly in summer and ranges from 1000–1500 mm per annum (mainly thunder showers).

Altitude: 1100–1800 m.

Associated vegetation: Drakensberg Foothill Moist Grassland (Grassland Biome) (Mucina *et al.* 2005).

Associated cremnophytes: At the Nzinga Waterfall, farm Belmont, *Cyrtanthus falcatus* grows together with *Aloe aristata*.

Geology: Mudstone (Emakwezini Formation), Beaufort Group (Karoo Supergroup). Substrate with sufficient ledges, crevices and fissures for establishment of plants.

DISTRIBUTION

Impendle and Underberg districts, central KwaZulu-Natal.

RELATED SPECIES

Cyrtanthus falcatus is not closely related to other *Cyrtanthus* species. It is perhaps nearest to *C. herrei*, another cremnophyte from the winter-rainfall Richtersveld in the Northern Cape and adjacent mountainous parts of Namibia.

ADAPTATIONS TO THE CLIFF ENVIRONMENT

Habit: Plants forming exposed clusters up to 1 m in diameter. Bulbs firmly wedged, habit often drooping, exploiting the vertical cliff-face habitat and absence of disturbance by larger herbivores. A slow-growing, long-lived perennial.

Size and weight: Heads of medium weight to heavy, clusters.

Bulb: Epigeous, ovoid to round, fleshy and tolerant of warm, dry conditions. Its succulent state suggests an adaptation to its xeric habitat.

Leaves

Orientation: Appearing in spring, distichous, vertically orientated, thus minimising exposure to direct sunshine. The leaves are phenotypically adjustable to the vertical habitat and aspect.

Succulence: Leaves are fleshy, an adaptation to the dry habitat.

Colour: Light grey-green, reflecting excessive light.

Age and persistence: Deciduous, leaves withering in autumn, maximising survival on the dry rock face.

Armament and camouflage: Lack of armament or a camouflage defence strategy and the conspicuous clustered habit suggest an adaptation to the safe cliff habitat in the absence of disturbances.

Sexual reproduction

Inflorescence and flowers: Inflorescence a compact, conspicuous umbel of reddish flowers attractive to sunbirds feeding on the nectar. The ascending scape is decurved at the top, a unique feature in *Cyrtanthus*, and the flowers and pedicels are pendent.

Fruit/Seed

Size: Presumably compressed.

Dispersal: Capsule dehiscent, seeds wind-dispersed (anemochory).

Time: Seeds ripening in summer, coinciding with the rainy season.

Vegetative reproduction: *Cyrtanthus falcatus* is a prolific sprouter from the base, forming dense clusters. The many bulbs are a successful vegetative dispersal strategy, with ledges and crevices continuously being populated with clones, ensuring long-term survival on the cliffs.

CONSERVATION STATUS

Classified as rare (Raimondo *et al.* 2009). A local endemic, not threatened owing to the inaccessible cliff habitat.

ADDITIONAL NOTES

Horticulture: Although *Cyrtanthus falcatus* is a slow grower, it does well in cultivation. It is best grown in dappled shade in cool highveld gardens, excellent for steep embankments, gabions or terraforce. It is also well suited to containers. It is ideal for thicket gardens and plants are best grown in containers, on rockeries or window sills. The species is easily grown from seed or division. Outside its habitat it should preferably be grown under controlled conditions in a cool greenhouse. Its very easy growing nature maximises survival rate on the cliff face.

VOUCHER

Van Jaarsveld 18266 (NBG).

ILLUSTRATIONS AND MAP

Plate 2, Figures 2a–2d, Map 2.

3. *Cyrtanthus flammosus* Snijman & Van Jaarsv. in Flowering Plants of Africa 54: 100–103 (1995).

Cremnophyte growth form: Solitary, evergreen, bulbous (of medium weight, cliff squatter).

Growth form formula: A:B:Lper:So:La (r)

Etymology: Latin *flammosus*, like a flame, pertaining to the flowers.

DESCRIPTION AND HABITAT

Bulbs solitary, partially epigeous, 40 × 40 mm, ovate and covered with dry brown papery scales. Roots slightly fleshy. Leaves 2–4, spreading, linear-lanceolate, ascending to recurved, up to 290 × 20 mm, thick-textured, glaucous, tinged reddish brown. Inflorescence single-flowered, ascending-spreading, with a hollow scape up to 170 mm long, glaucous, green. Perianth large, up to 100 mm in diameter. Scape 250 × 8 mm, fruiting capsule solitary, oblong, 70 × 5 mm, tapering slightly from both ends, ascending when dry. Seed black, 15 × 5 mm, flat and wind-dispersed (June, July), lobes becoming recurved, seed pendulous, dislocated by wind, part containing embryo 6 × 5 mm with wing towards one side (aerobatic propeller type).

Phenology: Flowering in late summer and autumn (March). Seeds wind-dispersed.

Habitat and aspect: Mainly south-facing quartzitic sandstone cliff faces overlooking the Kouga River. Plants grow on fairly large inaccessible rocky ledges with sufficient soil substrate. Summers are hot and dry. The average daily maximum temperature is about 27°C and the average daily minimum temperature about 12°C. Winters are cooler but frost is a rarity or absent. Rainfall mainly in summer and winter, about 400–500 mm per annum.

Altitude: 250–500 m.

Associated vegetation: Mainly Gamtoos Thicket of the Albany Thicket Biome (Mucina *et al.* 2005).

Associated cremnophytes: *Adromischus cristatus* var. *schonlandii*, *Cotyledon tomentosa* subsp. *tomentosa*, *Crassula perforata* subsp. *kougaensis*, *Gasteria glomerata*, *Haworthia gracilis* var. *picturata*, *H. viscosa*, *Othonna lobata* and *Plectranthus verticillatus*.

Geology: Quartzitic sandstone (light-coloured and smooth-textured), Peninsula Formation (Cape Supergroup).

DISTRIBUTION

Cyrtanthus flammosus is known only from cliff faces along the lower reaches of the Kouga River (Eastern Cape), being confined to inaccessible spots.

RELATED SPECIES

Related to two non-cremnophytes, *Cyrtanthus guthrieae* (Bredasdorp, Western Cape) and the coastal *C. elatus* (George to Humansdorp, Eastern Cape) and differing from these by its glaucous, leathery leaves and larger, conspicuous flowers. The inflorescence of *C. flammosus* is reduced to a solitary (rarely two), highly conspicuous flower (enriched flowering). This

enriched flowering compensates for the lack of bulbil formation when compared to *C. montanus* and *C. labiatus*. The glaucous, leathery leaves and somewhat exposed bulb covered with dry, papery, purplish grey tunics suggest an adaptation to a hot and arid environment.

ADAPTATIONS TO THE CLIFF ENVIRONMENT

Habit: Plants solitary, with partially epigeous bulbs and spreading leaves, the latter retained in cultivation. A slow-growing, long-lived perennial.

Size and weight: Bulbs of medium size and weight.

Roots: The slightly fleshy roots grow firmly wedged in crevices and soil pockets.

Bulb: The ovate bulb is covered with papery tunics forming a protective cover over the fleshy bulb scales, thus assisting to reduce transpiration and penetration of light. Exposed parts of the bulb are photosynthetically active.

Leaves

Orientation: Ascending-spreading, apically grouped.

Succulence: Leaves fleshy, an adaptation to the dry habitat.

Colour: Glaucous.

Age and persistence: Becoming deciduous from the base.

Armament: Exposed bulbs suggest a reduction in armament in response to the undisturbed cliff habitat in contrast to the surrounding thorny but heavily grazed thicket vegetation.

Sexual reproduction

Inflorescence and flowers: The solitary, large, red flower is very conspicuous (rich flowering), maximising visibility for pollination and compensating for the lack of vegetative reproduction in the vertical cliff environment. It is very possible that the flower is pollinated by the butterfly *Aerpetes tulbaghia* (Table Mountain Beauty), pollinator of similar flowers in the Western and Eastern Cape.

Fruit/Seed

Size: Seed 15×5 mm (solitary lateral wing included), relatively large size ensuring greater establishment on ledges and in crevices.

Dispersal: Dispersed by wind (anemochory). Each seed has a single lateral wing and displays a propeller action in flight, thus maximising its flying ability and ensuring a well-dispersed distance, settling in crevices.

Time: Seeds ripening in autumn and winter, coinciding with winter rainfall. The cooler conditions and moist environment facilitate successful establishment. Germination after 14–21 days.

Vegetative reproduction: Absent.

CONSERVATION STATUS

Although classified as critically rare (Raimondo *et al.* 2009) and a local endemic, it is not threatened.

ADDITIONAL NOTES

Horticulture: Plants thrive in cultivation. Their very easy growing nature maximises their survival rate. *Cyrtanthus flammus* is a slow grower but does well in cultivation, in dappled shade. It is ideal for thicket gardens and plants are best grown in containers, on rockeries and window sills. It is also suitable for establishment in terraforce and gabions. Plants are easily grown from seed and flowering can occur within the third or fourth years. Outside its natural habitat it should preferably be grown under controlled conditions in a greenhouse.

VOUCHER

Van Jaarsveld 17109 (NBG).

ILLUSTRATIONS AND MAP

Plate 3, Figures 3a & 3b, Map 3.

4. *Cyrtanthus flanaganii* Baker in *Flora capensis* 6: 532 (1897).

Cremnophyte growth form: Cluster-forming, bulbous (of medium weight, cliff hugger).

Growth form formula: A:B:D:C:La (vb)

Etymology: After Henry George Flanagan (1861–1919), Eastern Cape farmer and plant collector who collected this species on the Drakensberg.

DESCRIPTION AND HABITAT

Deciduous, semi-epigeous, cluster-forming geophytes. Bulbs ovoid to globose, up to 30 mm in diameter, sprouting from base, tapering to a neck up to 110 mm long; tunics dense, brown, membranous. Leaves up to 4, linear, up to 200 × 19 mm, leathery, lorate, falcate, green, obtuse. Scape up to 200 mm long, compressed; spathe valves (bracts) white with red veins, 50 mm long, 11 mm wide at base; bracts white, 20 mm long, linear-filiform; pedicels up to 25 mm long. Perianth yellow, ascending, trumpet-shaped; tube 46 mm long, 6 mm in diameter at throat; lobes ascending, 15 mm long, the outer 9 mm in diameter and slightly hooded, the 3 inner 8 mm in diameter, not hooded. Stamens not exerted. Ovary 8 mm long, cylindrical-oblong, faintly 3-lobed; style shortly 3-lobed.

Phenology: Synanthous, flowering mainly in December.

Pollinators: Probably sunbirds.

Habitat and aspect: Vertical cliffs on the central Drakensberg Escarpment. Plants firmly rooted in crevices. The average daily maximum temperature is about 16°C and average daily minimum about 4°C. Winters are colder, with frost and regular snow. Rainfall occurs mainly in summer and ranges from 1000–1500 mm per annum.

Altitude: 2750–3000 m.

Associated vegetation: Ukahlamba Basalt Grassland of the Grassland Biome (Mucina *et al.* 2005).

Associated cremnophytes: At Mont-aux-Sources, *Cyrtanthus flanaganii* grows among tufts of grass and other species such as *Crassula lanceolata* subsp. *lanceolata*, *C. sarcocaulis*, *C. setulosa* var. *longiciliata* and *Eucomis schijffii*.

Geology: Basalt.

DISTRIBUTION

Widespread from Barkly East to Mont-aux-Sources in central KwaZulu-Natal.

RELATED SPECIES

Cyrtanthus flanaganii is not closely related to other *Cyrtanthus* species. It is superficially similar to *C. falcatus*, another cremnophyte from the Drakensberg midlands, the latter with larger, reddish flowers.

ADAPTATIONS TO THE CLIFF ENVIRONMENT

Habit: Plants forming exposed clusters up to 300 mm in diameter. The bulbs are firmly wedged in crevices. A slow-growing, long-lived perennial.

Size and weight: Clusters of medium weight.

Bulb: Bulb hypogeous to semi-epigeous, ovoid to round. The leathery, semisucculent leaves suggest an adaptation to the xeric habitat.

Leaves

Orientation: Leaves appearing in spring and are spreading to ascending. They are phenotypically adjustable according to the availability of light.

Succulence: Fleshy, well adapted to the dry habitat.

Colour: Green.

Age and persistence: A deciduous species; leaves withering in autumn, thus maximising survival on the dry rock face.

Armament and camouflage: Lack of a camouflage defence strategy and the conspicuous clustered habit suggest an adaptation to the safe cliff habitat in the absence of disturbances.

Sexual reproduction

Inflorescence and flowers: The inflorescence is a conspicuous compact umbel of yellow sweetly scented flowers.

Fruit/Seed

Dispersal: Capsule dehiscent, seeds with a lateral wing, wind-dispersed.

Time: Seeds ripening in summer, coinciding with the rainy season.

Vegetative reproduction: Bulbs of *Cyrtanthus flanaganii* are prolific from the base and this successful vegetative dispersal strategy ensures that ledges and crevices are continuously being populated with clones, thus ensuring long-term survival on the cliffs.

CONSERVATION STATUS

A Drakensberg endemic, not threatened owing to the inaccessible cliff habitat.

ADDITIONAL NOTES

Horticulture: Plants are easily grown by division or from seed and thrive in cultivation. Its very easy growing nature maximises its survival rate on the cliff face.

VOUCHER

Van Jaarsveld 16989 (NBG).

ILLUSTRATIONS AND MAP

Figures 4a & 4b, Map 4.

5. *Cyrtanthus herrei* (F.M.Leight.) R.A.Dyer in *The Flowering Plants of Africa* 33: t. 1281 (1959).

Cremonophyte growth form: Cluster-forming, bulbous (of medium weight, cliff hugger).

Growth form formula: A:B:Lper:C:La (e) (vb)

Etymology: After Hans Herre (1895–1979), Curator of the Hortus Botanicus at Stellenbosch University Gardens.

DESCRIPTION AND HABITAT

Bulbs large, cluster-forming, obclavate, epigeous, up to 60 mm in diameter. Roots succulent, terete. Leaves synanthous, distichous, lorate, up to 450 × 50 mm, leathery, glaucous; apex

obtuse. Scape up to 400 mm long, glaucous, up to 28-flowered; bracts up to 80×13 mm, linear-lanceolate, soon withering; pedicels up to 40 mm long. Perianth pendulous, reddish, zygomorphic, up to 55 mm long; tube up to 40 mm long, red; lobes yellowish green. Stamens fused to tepals, filaments up to 6 mm long; anthers yellow, dorsifixed. Ovary up to 8 mm long. Capsule 3-loculed, ovoid, 23×10 –14 mm. Seed black, compressed, 10×5 mm.

Phenology: Flowering in late summer and autumn (March–April). Seeds wind-dispersed.

Pollinators: Sunbirds.

Habitat and aspect: Mainly south- and east-facing ledges and crevices of quartzitic sandstone and granite cliff faces. Plants grow on fairly large inaccessible rocky ledges that allow for sufficient soil substrate. The average daily maximum temperature is about 24°C and the average daily minimum about 10°C . Winters are cooler but frost is rare or absent. Rainfall mainly in winter, ranging from 150–250 mm per annum.

Altitude: 400–1500 m.

Associated vegetation: Rosyntjieberg Succulent Shrubland of the Succulent Karoo Biome (Mucina *et al.* 2005).

Associated cremnophytes: On the Rosyntjieberg, plants share their habitat with *Aloe meyeri*, *Othonna cyclophylla*, *Tylecodon buchholzianus* and *T. ellaphieae*.

Geology: Quartzitic sandstone (Stinkfontein Subgroup, Gariiep Supergroup) and granite of the Tatasberg Complex (Cape Granite Suite). Substrate with many ledges, crevices and fissures, providing ample habitat.

DISTRIBUTION

Cyrtanthus herrei is restricted to cliff faces and steep slopes of northern Namaqualand, the Richtersveld (Northern Cape) and adjacent territory in southern Namibia.

RELATED SPECIES

Related to *Cyrtanthus obliquus* from the southeastern Cape which also sometimes occurs on steep slopes and cliffs. It also resembles *C. falcatus* from the Drakensberg, the latter with leaves becoming deciduous in winter and the peduncle characteristically recurved at the top, with a pendent umbel.

ADAPTATIONS TO THE CLIFF ENVIRONMENT

Habit: Plants with clusters of epigeous bulbs and ascending leaves, the latter retained in cultivation. A slow-growing, long-lived perennial.

Size and weight: Bulbs of medium weight.

Roots: Slightly fleshy, wedged in crevices and soil pockets.

Bulb: The obclavate bulb is covered with papery tunics forming a protective cover over the fleshy bulb scales and probably reducing transpiration and penetration of light. Bulb is photosynthetically active.

Leaves

Orientation: Ascending-spreading, apically grouped.

Succulence: The fleshy leaves are an adaptation to the dry habitat.

Colour: Glauous.

Age and persistence: Becoming deciduous from the base.

Armament: The exposed bulbs suggest a reduction in armament in response to the undisturbed cliff habitat in contrast to the surrounding heavily grazed succulent karoo vegetation.

Sexual reproduction

Inflorescence and flowers: The large red and green flowers are conspicuous, maximising visibility for pollination by sunbirds.

Fruit/Seed

Dispersal: Winged seed dispersed by wind, propeller action maximising its flying ability and ensuring a well-dispersed distance, settling in crevices.

Time: Seeds ripening in early winter, coinciding with winter rainfall and cooler conditions ideal for establishment of seedlings. Germination after 14–21 days.

Vegetative reproduction: *Cyrtanthus herrei* is proliferous from the base, forming dense and large colonies that occupy extensive sections of crevices. This successful vegetative dispersal strategy ensures that ledges and crevices are continuously being populated with clones, thus ensuring long-term survival in the cliff environment.

CONSERVATION STATUS

Classified as near threatened (Raimondo *et al.* 2009) in South Africa and as rare in Namibia (Loots 2005). However, often locally abundant on cliffs and not threatened.

ADDITIONAL NOTES

Horticulture: *Cyrtanthus herrei* requires warm, dry conditions and ample winter rainfall. It is best grown in groups in succulent karoo gardens and should do well on steep embankments, gabions, rockeries or in containers (Van Jaarsveld 2000b). *Cyrtanthus herrei* can be grown in partial shade or full sun. Plants are slow-growing but easily established from seed or division and thrive in cultivation. This easy growing nature maximises its survival rate. Keep dry in summer. Grow it in a well-drained, sandy soil mixture.

VOUCHER

Van Jaarsveld 18788 (NBG).

ILLUSTRATIONS AND MAP

Plate 5, Figures 5a–5d, Map 5.

6. *Cyrtanthus inaequalis* O'Brien in *The Gardeners' Chronicle* 37: 261 (1905).

Cremonophyte growth form: Solitary to cluster-forming, bulbous (of medium weight, cliff hugger).

Growth form formula: A:B:Lper:C:La (e) (vb)

Etymology: Latin *inaequalis*, unequal, pertaining to the length of the pedicel.

DESCRIPTION AND HABITAT

Bulb epigeous, globose, 40–70 × 60–80 mm, purplish green, solitary or forming groups, bulbiferous from base; tunics withering papery brown. Leaves synanthous, evergreen, 2 or 3, glaucous, linear-oblongate, leathery, 300–400 × 9–11 mm; apex subacute; upper surface channelled. Scape 400–450 × 14 mm (narrowing to 6.5 mm), glaucous, 3–5-flowered; bracts 65 × 8 mm, triangular-lanceolate, acuminate, soon withering; pedicels 35–48 mm long. Perianth orange-red, zygomorphic, labiate, 75–90 mm long, tubular, curved; tube 3.5 mm diameter at base expanding to 8 mm at throat, infundibuliform; upper lobes 4, linear-lanceolate, forming a hood, lower lobes 2. Stamens fused to tepals, free for 13 mm; anthers yellow, 7 mm long, oblong. Style 72–78 mm long, 3-lobed; ovary oblong-triangular, 6 × 4 mm. Capsule and seed not seen.

Phenology: Flowering in midsummer (January). Seed wind-dispersed.

Habitat and aspect: Confined to east- and west-facing cliffs. Plants grow in crevices and on ledges of the lower and upper slopes, in ample soil. The climate is hot and dry. The average daily maximum temperature is more or less 25°C and average daily minimum about 10°C, with frost absent or a rarity in the habitat. Rainfall occurs in winter and summer (cyclonic cold fronts and thunder showers), 200–300 mm per annum.

Altitude: 800–1200 m.

Associated vegetation: Gamka Thicket of the Albany Thicket Biome (Mucina *et al.* 2005).

Associated cremonophytes: Observations at Toorwaterspoort (west of Willowmore, Eastern Cape) include the following species: *Adromischus subdistichus*, *Bulbine* sp., *Carruanthus peersii*, *Cotyledon woodii*, *Crassula capitella* subsp. *thyrsiflora*, *C. cotyledonis*, *C. muscosa* var. *muscosa*, *C. pellucida* subsp. *marginalis*, *C. perfoliata* var. *minor*, *C. pubescens* var. *radicans*, *C. rupestris*, *C. velutina*, *Drimia uniflora*, *Haemanthus albiflos*, *H. decipiens* var. *decipiens*, *H. viscosa*, *Lampranthus affinis*, *Ornithogalum tortuosum* and *Senecio talinoides*.

Geology: Witteberg quartzite (Cape Supergroup).

DISTRIBUTION

Cyrtanthus inaequalis is restricted to the Groot Swartberg, from Buffelspoort near Ladismith (Western Cape) to Toorwaterspoort in the east (Eastern Cape).

RELATED SPECIES

Related to the non-cremnophytes *Cyrtanthus guthrieae* (Bredasdorp, Western Cape) and coastal *C. elatus* (George to Humansdorp, Eastern Cape) but differing from them by the glaucous, leathery leaves and zygomorphic flowers as well as its very prolific nature of forming basal bulbils. At once distinguished from *C. labiatus*, another obligate cremnophyte from the Kouga and Baviaanskloof, by its narrower, longer leaves, distinctly longer scape and larger flowers.

ADAPTATIONS TO THE CLIFF ENVIRONMENT

Habit: Plants with clusters of epigeous bulbs and spreading leaves, the latter retained in cultivation. A slow-growing, long-lived perennial.

Size and weight: Bulbs small, of medium weight. The small size suggests an adaptation to the limited growing conditions.

Roots: The slightly fleshy roots grow firmly wedged in crevices and soil pockets.

Bulb: The globose bulb is covered with dark, golden, papery tunics turning white with age and forming a protective cover over the fleshy bulbs and bulbils, thus reducing transpiration and penetration of light. Bulb photosynthetically active.

Leaves

Orientation: Ascending-spreading, apically grouped (2 or 3 per bulb).

Succulence: The fleshy leaves are an adaptation to its dry habitat.

Colour: Glaucous, purplish at the base, suggesting adaptations to the exposed, hot habitat.

Age and persistence: Becoming deciduous from the base.

Armament: The exposed bulbs and softer texture of the tunics suggest a reduction in armament in response to the undisturbed cliff habitat in contrast to the surrounding thorny but heavily grazed thicket vegetation.

Sexual reproduction

Inflorescence and flowers: Flowers conspicuous, orange-red and with curved perianth tube, maximising pollination by sunbirds. Flowering time January–February.

Fruit/Seed

Size: Seed 15×5 mm including wing, actual seed 6×5 mm, relatively large size ensuring greater establishment on ledges and in crevices.

Dispersal: Seeds dispersed by wind, propeller action maximising its flying ability and ensuring a well-dispersed distance, settling in crevices.

Time: Seeds ripening in autumn and winter, coinciding with winter rainfall, an ideal time for seedling establishment and survival. Germination after 14–21 days.

Vegetative reproduction: *Cyrtanthus inaequalis* is prolific from the basal tunics, producing bulbils of about 12×11 mm. They will not easily roll off a ledge as they are oval-globose to angular and pointed to one side, ideal for establishment in crevices. The bulbils are covered with dark purplish tunics and their angular (not globose) shape provides maximum resistance and anchorage. This successful dispersal strategy ensures that ledges and crevices are continuously being populated with clones, important for long-term survival on the cliffs.

CONSERVATION STATUS

A local endemic, not threatened (Hilton-Taylor 1996).

ADDITIONAL NOTES

Horticulture: *Cyrtanthus inaequalis* is a slow grower and thrives in dappled shade in cultivation. It is ideal for thicket gardens and plants are best grown in containers and on rockeries and window sills. It is also suitable for establishment in terraforce and gabions. Easily grown from bulbils, division or seed or grown as a specimen pot plant, not shy to flower. Outside its habitat it should preferably be grown under controlled conditions in a greenhouse.

VOUCHER

Van Jaarsveld 17415 (NBG).

ILLUSTRATIONS AND MAP

Figures 6a–6d, Map 6.

7. *Cyrtanthus junodii* P.Beauv. in Bulletin de l'Herbier Boissier, Ser. 2, 7: 437 (1907).

Cremonophyte growth form: Cluster-forming, epigeous, bulbous (of medium weight, cliff hugger).

Growth form formula: A:B:D:C:La (e) (vb)

Etymology: After Henri-Alexandre Junod (1863–1934), missionary and naturalist.

DESCRIPTION AND HABITAT

Deciduous, semi-epigeous to epigeous, cluster-forming geophytes, 200–450 mm in diameter. Bulbs ovoid, 30–70 × 30–60 mm, sprouting from base, tapering to a neck; tunics dense, reddish brown, membranous, becoming papery and greyish brown. Leaves 1–6, lorate, up to 250–380 × 20–28 mm, leathery, purplish at base, green distally, gently recurved, sometimes somewhat twisted sideways near apex; surface smooth, obscurely striate; apex acute. Scape 220–500 mm long, green; spathe valves 2, erect, ovate-lanceolate, 30–50 × 15–19 mm long, yellowish brown; pedicels variable in length, 15–40 mm long (shorter than spathe valves), ascending, reddish brown. Flowers 6–9, umbellate, horizontally presented, secund, subpendulous; perianth tubular, curved, dilating towards throat, 35–55 mm long; tube 4 mm wide at base, red, yellow at apex of lobes, 10–12 mm wide at base; lobes 8–12 × 4–6 mm long. Stamens biseriate, arising from throat, not exerted. Style yellowish, exerted; stigma trifid, lobes about 2 mm long. Capsule and seed not seen.

Phenology: Flowering time in summer (December).

Pollinators: Sunbirds.

Habitat and aspect: Vertical south-facing sandstone cliffs. Plants firmly rooted in crevices. The average daily maximum temperature is about 20°C and the average daily minimum about 10°C. Winters are colder with frost and with occasional snow. Rainfall mainly in summer, 1500–1750 mm per annum.

Altitude: 1500–200 m.

Associated vegetation: Strydpoort Summit Sourveld of the Grassland Biome (Mucina *et al.* 2005).

Associated cremnophytes: At the Wolkberg in the Limpopo Province, *Cyrtanthus junodii* grows together with *Aloe thompsoniae*, *Crassula pellucida* subsp. *alsinoides*, *C. sarcocaulis*, *C. setulosa*, *Merwillia plumbea* and *Senecio oxyriifolius*.

Geology: Basalt.

DISTRIBUTION

Confined to the upper Wolkberg peaks in the Limpopo Province.

RELATED SPECIES

Cyrtanthus junodii is not closely related to other *Cyrtanthus* species. It is superficially similar to *C. flanaganii*, another cremnophyte from the Drakensberg midlands, with yellow flowers.

ADAPTATIONS TO THE CLIFF ENVIRONMENT

Habit: Plants forming semi-epigeous to epigenous clusters up to 200–450 mm in diameter. The bulbs firmly wedged in crevices. A slow-growing, long-lived perennial.

Size and weight: Heads of medium weight.

Bulb: Semi-epigeous to epigeous, ovoid. The leathery, semisucculent leaves suggest an adaptation to the xeric habitat.

Leaves

Orientation: Ascending, appearing in spring and adjustable (phenotypic) according to the availability of light.

Succulence: Fleshy and adapted to its dry habitat.

Colour: Green.

Age and persistence: Deciduous, leaves withering in the autumn, maximising survival on the dry rock face.

Armament and camouflage: Lack of a camouflage defence strategy and the conspicuous clustered habit suggest an adaptation to the safe cliff habitat in the absence of disturbances.

Sexual reproduction

Inflorescence and flowers: Conspicuous, compact umbels of red flowers, pollinated by sunbirds.

Fruit/Seed

Size: Not seen.

Dispersal: Capsule dehiscent, seeds presumably flat and wind-dispersed.

Time: Summer.

Vegetative reproduction: Plants sprout from the base, forming clusters and ensuring long-term survival.

CONSERVATION STATUS

Cyrtanthus junodii is classified as vulnerable (Raimondo *et al.* 2009). Although it is known only from the Wolkberg in Limpopo Province, it is not threatened owing to the inaccessible cliff habitat.

ADDITIONAL NOTES

Horticulture: *Cyrtanthus junodii* is suited to temperate highveld gardens. It is best grown in a sandy mixture. Feed during spring and summer and apply a winter rest period. It can be propagated by division and does well in cultivation. Its very easy growing nature maximises its survival rate on the cliff face. It thrives in containers.

VOUCHER

Van Jaarsveld 16231 (NBG).

ILLUSTRATIONS AND MAP

Plate 7, Figures 7a–7e, Map 7.

8. *Cyrtanthus labiatus* R.A.Dyer in *Bothalia* 13: 135 (1980).

Cremonophyte growth form: Solitary to cluster-forming, bulbous (of medium weight, cliff hugger).

Growth form formula: A:B:Lper:C:La (e) (vb)

Etymology: Latin *labiatus*, lipped, referring to the two-lipped flowers, an adaptation to sunbird pollination.

DESCRIPTION AND HABITAT

Bulb epigeous, globose, 40–75 × 60–75 mm, purplish green, solitary or forming groups, bulbiferous from base; tunics withering papery brown. Leaves synanthous, evergreen, 2–4, glaucous, lorate-elliptic to strap-shaped, 180–300 × 14–20 mm; apex obtuse. Scape 120–300 × 23 mm, glaucous, up to 8-flowered; bracts 50 × 5 mm, triangular-lanceolate, soon withering; pedicels 20–25 mm long. Perianth red, zygomorphic, labiate, 50–60 mm long, tubular, curved; tube 10 mm long, infundibuliform; upper lobes 4, linear-oblongate, forming a hood, lower lobes 2. Stamens fused to tepals, free for 10 mm; anthers yellow, 3 mm long, oblong. Style 40 mm long, 3-lobed; ovary oblong-triangular, 6 × 4 mm. Capsule 20–25 mm long. Seed black, 15 × 5 mm.

Phenology: Flowering from midsummer to autumn (December–January). Seeds wind-dispersed.

Habitat and aspect: Mainly ledges of vertical south- and east-facing quartzitic sandstone cliffs. Plants grow on narrow to larger inaccessible rocky ledges. The average daily maximum temperature is about 25°C and the average daily minimum about 10°C. Winters are cooler but frost is a rarity or absent. Rainfall in summer and winter, 400–500 mm per annum (cyclonic winter rainfall and thunder showers in summer).

Altitude: 300–900 m.

Associated vegetation: Mainly Gamtoos Thicket of the Albany Thicket Biome (Mucina *et al.* 2005).

Associated cremonophytes: Other cremonophytes observed at the Kouga Dam include: *Adromischus cristatus* var. *zeyheri*, *Cotyledon tomentosa* subsp. *tomentosa*, *Crassula rupestris* subsp. *rupestris* ‘Kouga form’, *Gasteria glomerata*, *Haworthia gracilis* var. *picturata*, *H. viscosa*, *Othonna triplinervia* and *Plectranthus verticillatus*.

Geology: Quartzitic sandstone (light-coloured and smooth-textured), Peninsula Formation (Cape Supergroup). Substrate with many ledges, crevices and fissures, sufficient for establishment.

DISTRIBUTION

Cyrtanthus labiatus is restricted to the Baviaanskloof Mountains and Kouga Dam region west of Hankey, limited to river valleys of the Cape Fold Belt mountains.

RELATED SPECIES

Related to the non-cremnophytes *Cyrtanthus guthrieae* (Bredasdorp, Western Cape) and coastal *C. elatus* (George to Humansdorp, Eastern Cape) but differing from them by its glaucous, leathery leaves and zygomorphic flowers as well as its very prolific nature of basal bulbils. Differs from *C. inaequalis* by its smaller, broader leaves as well as the longer perianth.

ADAPTATIONS TO THE CLIFF ENVIRONMENT

Habit: Plants with clusters of epigeous bulbs and spreading leaves, the latter retained in cultivation. A slow-growing, long-lived perennial.

Size and weight: Bulbs small, of medium weight. Small size suggests an adaptation to the limited growing conditions.

Roots: The slightly fleshy roots grow firmly wedged in crevices and soil pockets.

Bulb: The globose bulb is covered with dark, golden, papery tunics turning white with age and forming a protective cover over the fleshy bulbs and bulbils, thus reducing transpiration and penetration of light. Bulb photosynthetically active.

Leaves

Orientation: Ascending-spreading, apically grouped (2 per bulb).

Succulence: The fleshy leaves are an adaptation to its dry habitat.

Colour: Glaucous, purplish at the base, suggesting adaptation to the exposed, hot habitat.

Age and persistence: Becoming deciduous from the base.

Armament: The exposed bulbs and softer texture of the tunics suggest a reduction in armament in response to the undisturbed cliff habitat in contrast to the surrounding thorny but heavily grazed thicket vegetation.

Sexual reproduction

Inflorescence and flowers: Flowers red and conspicuous, with curved perianth tube, maximising pollination by sunbirds. Flowering time January–February.

Fruit/Seed

Size: Seed 15×5 mm including wing, actual seed 6×5 mm, relatively large size ensuring greater establishment on ledges and in crevices.

Dispersal: Seeds dispersed by wind, propeller action maximising its flying ability and ensuring a well-dispersed distance, settling in crevices.

Time: Seeds ripening in autumn and winter, coinciding with winter rainfall, an ideal time for seedling establishment and survival. Germination after 14–21 days.

Vegetative reproduction: *Cyrtanthus labiatus* are prolific from the basal tunics, producing bulbils of about 12 × 11 mm. They will not easily roll off a ledge as they are oval-globose to angular and pointed to one side, ideal for establishment in crevices. The bulbils are covered with dark purplish tunics and their angular (not globose) shape provides maximum resistance and anchorage. This successful dispersal strategy ensures that ledges and crevices are continuously being populated with clones, important for long-term survival on the cliffs.

CONSERVATION STATUS

A local endemic, not threatened (Hilton-Taylor 1996).

ADDITIONAL NOTES

Horticulture: *Cyrtanthus labiatus* is a slow grower and thrives in dappled shade in cultivation. It is ideal for thicket gardens and plants are best grown in containers and on rockeries and window sills. It is also suitable for establishment in terraforce and gabions. Plants easily grown from bulbils, division or seed or as specimen pot plants, not shy to flower. Outside its habitat it should preferably be grown under controlled conditions in a greenhouse.

VOUCHER

Van Jaarsveld 11070 (NBG).

ILLUSTRATIONS AND MAP

Plate 8, Figures 8a–8c, Map 8.

9. *Cyrtanthus montanus* R.A.Dyer in *The Flowering Plants of Africa* 44: t. 1756 (1977).

Cremnophyte growth form: Solitary to cluster-forming, bulbous (of medium weight, cliff hugger).

Growth form formula: A:B:Lper:C:La (e) (vb)

Etymology: Latin *montanus*, mountain, referring to the mountainous habitat.

DESCRIPTION AND HABITAT

Bulb epigeous, globose, 65 × 70 mm, purplish greenish, solitary or forming groups, bulbiferous from base; papery tunics withering grey-brown. Leaves synanthous, evergreen, and 2–4 lorate-elliptic to 300 × 20 mm ascending, glaucous. Scape up to 100 mm long; bracts 2, linear-lanceolate, up to 50 mm long, with smaller bracteoles with flowers; umbels up to 10-flowered; pedicels up to 30 mm long. Perianth red, erect, up to 50 mm long; tube

infundibuliform, up to 15 mm long; outer tepals 3, linear-lanceolate, up to 9 mm wide, inner tepals up to 11 mm wide. Stamens 2-seriate; filaments 9–11 mm long. Ovary oblong, up to 6 mm long; stigma filiform, tricuspidate, Capsule oblong. Seeds compressed, black.

Phenology: Flowering in late summer and autumn (March). Seeds wind-dispersed.

Pollinators: Butterflies.

Habitat and aspect: Vertical south-facing quartzitic sandstone cliffs. Plants grow on narrow to larger inaccessible rocky ledges. The average daily maximum temperature is about 25°C and the average daily minimum about 10°C. Winters are cooler but frost is a rarity or absent. Rainfall occurs in winter and summer, 400–500 mm per annum (cyclonic winter rainfall and thunder showers in summer).

Altitude: 250–500 m.

Associated vegetation: Mainly Gamtoos Thicket of the Albany Thicket Biome (Mucina *et al.* 2005).

Associated cremnophytes: Observations at the Kouga Dam include: *Adromischus cristatus* var. *zeyheri*, *Cotyledon tomentosa* subsp. *tomentosa*, *Crassula rupestris* subsp. *rupestris* ‘Kouga form’, *Gasteria glomerata*, *Haworthia gracilis* var. *picturata*, *H. viscosa*, *Othonna triplinervia* and *Plectranthus verticillatus*.

Geology: Quartzitic sandstone (light-coloured and smooth-textured), Peninsula Formation (Cape Supergroup). Substrate with many ledges, crevices and fissures sufficient for establishment.

DISTRIBUTION

Cyrtanthus montanus is distributed from Ladismith (Western Cape) to Hankey in the Eastern Cape and is restricted to river valleys of the Cape Fold Belt mountains.

RELATED SPECIES

Related to the non-cremnophytes *Cyrtanthus guthrieae* (Bredasdorp, Western Cape) and coastal *C. elatus* (George to Humansdorp, Eastern Cape) but differing from them by its glaucous, leathery leaves and somewhat different flowers as well as its very prolific nature of basal bulbils.

ADAPTATIONS TO THE CLIFF ENVIRONMENT

Habit: Plants with clusters of epigeous bulbs and spreading leaves, the latter retained in cultivation. A slow-growing, long-lived perennial.

Size and weight: Bulbs of medium weight.

Roots: The slightly fleshy roots grow firmly wedged in crevices and soil pockets.

Bulb: The globose bulb is covered with dark, golden, papery tunics turning white with age and forming a protective cover over the fleshy bulbs and bulblets, thus reducing transpiration and penetration of light. Bulb photosynthetically active.

Leaves

Orientation: Ascending-spreading, apically grouped (2 per bulb).

Succulence: The fleshy leaves are an adaptation to its dry habitat.

Colour: Glaucous, purplish at the base, suggesting adaptation to the exposed hot habitat.

Age and persistence: Becoming deciduous from the base.

Armament: The exposed bulbs and softer texture of the tunics suggest a reduction in armament in response to the undisturbed cliff habitat in contrast to the surrounding thorny but heavily grazed thicket vegetation.

Sexual reproduction

Inflorescence and flowers: Flowers red and conspicuous, maximising visibility for pollination in the vertical cliff environment. Its open nature attracts butterflies, the main pollinating agents.

Fruit/Seed

Dispersal: Seed with solitary wing, wind-dispersed, propeller action maximising its flying ability and ensuring a well-dispersed distance, settling in crevices.

Time: Seeds ripening in autumn and winter, coinciding with winter rainfall, an ideal time for establishment of seedlings and for survival. Germination after 14–21 days.

Vegetative reproduction: *Cyrtanthus montanus* is very prolific from the basal tunics, producing bulbils of about 10 × 8 mm. They will not easily roll off a ledge as they are oval-angular and pointed to one side, ideal for establishment in crevices. The bulbils are covered with dark purplish tunics, their angular (not globose) shape providing maximum resistance and anchorage. This successful dispersal strategy ensures that ledges and crevices are continuously being populated with clones, important for long-term survival on the cliffs. (Birds breeding on cliff faces often also have eggs that are not round.)

CONSERVATION STATUS

A local endemic, not threatened (Hilton-Taylor 1996).

ADDITIONAL NOTES

Horticulture: *Cyrtanthus montanus* is a slow grower but does well in cultivation, best in dappled shade in thicket gardens (Van Jaarsveld 2000). It is ideal for containers, rockeries and window sills. It is also suitable for establishment in terraforce and gabions. Plants easily

grown from bulbils, division or seed or grown as specimen pot plants. Outside the habitat it should preferably be grown under controlled conditions in a greenhouse.

VOUCHER

Van Jaarsveld 12144 (NBG).

ILLUSTRATIONS AND MAP

Figures 9a–9d, Map 9.

HAEMANTHUS L.

10. *Haemanthus albiflos* Jacq., *Plantarum rariorum Horti Caesarei Schoenbrunnensis descriptiones et icones* 1: 31, t. 59 (1797). (Kouga Dam cliff-face forms.)

Cremonphyte growth form: Cluster-forming, epigeous, bulbous (of medium weight, cliff hugger).

Growth form formula: A:B:Lper:C:La (e) (vb)

Etymology: Latin *albiflos* (*albus*, white, *flos*, flower), referring to the white flowers.

DESCRIPTION AND HABITAT

Evergreen bulbous geophytes. Bulbs ovoid to medianally compressed, up to 80 mm broad, sprouting from base, cluster-forming (up to 12 heads, rarely more), epigeous to half-hypogeous; tunics truncate at top, green when exposed to light. Leaves strap-shaped to elliptic, adpressed to ground or spreading, flat or canaliculate, smooth or rarely pubescent; margin ciliate; apex obtuse to acute. Inflorescence 50–350 mm high; scape compressed to 14 mm wide; umbel compact, compressed to 70 mm wide, with 4–8 spathe valves. Flowers up to 12, exceptionally up to 50, white; pedicels up to 10 mm long; perianth funnel-shaped, up to 23 mm long; tube up to 7 mm long, with spreading oblong segments 10–18 × 1.0–2.5 mm. Ovary spherical, up to 3 mm in diameter. Berry ovoid, up to 10 mm in diameter, white to red.

Phenology: Flowering mainly from January–October, but with a peak between April and August. Seeds dispersed by birds from autumn onwards.

Pollinators: Insects.

Habitat and aspect: Vertical cliffs of dry river valleys or coastal cliffs (all aspects but more so on sheltered southern faces). The average daily maximum temperature varies from 22–24°C and average daily minimum from 12–14°C; extremes of up to 40°C have been recorded. Winters are cooler but frost is absent. Rainfall throughout the year, but with a peak in spring and summer, ranging from 300–1000 mm (thunder showers or cyclonic winter rain). Plants firmly rooted in crevices, size often depending on the growing space allowed by the crevice.

Altitude: 15–1500 m

Associated vegetation: Mainly Eastern Valley Bushveld of the Sub-Escarpment Savanna Bioregion (Savanna Biome), also Thicket, Grassland and Indian Ocean Coastal Belt, rarely Nama-Karoo Biome (Mucina *et al.* 2005).

Associated cremnophytes: On the Suurberg (cliffs in the Witrivier) it is associated with *Bulbine latifolia*, *B. suurbergensis*, *Crassula intermedia*, *C. perfoliata* var. *minor*, *Haworthia angustifolia* var. *baylissii*, *Lampranthus affinis*, *Ornithogalum juncifolium* and *O. longibracteatum*.

Geology: Quartzitic sandstone, Witteberg and Table Mountain Groups (Cape Supergroup) and mudstone and shale rocks of the Beaufort Group (Cape Supergroup). Substrate with sufficient ledges, crevices and fissures for establishment of plants.

DISTRIBUTION

From Still Bay (Western Cape) in the west to Zululand in KwaZulu-Natal and inland to Graaff-Reinet and Queenstown. Mainly in regions below the escarpment and especially on coastal cliffs. Although *Haemanthus albiflos* is widespread, some forms appear to be obligate cremnophytes, such as those found at the Kouga Dam.

RELATED SPECIES

Haemanthus albiflos is closely related to *H. pauculifolius*, another cremnophyte (see further on) from Mpumalanga. They differ from the flat-ground species *H. deformis* (southern KwaZulu-Natal) by their smaller, round, epigeous, cluster-forming, photosynthetically active bulbs and softer leaves.

ADAPTATIONS TO THE CLIFF ENVIRONMENT

Habit: Plants forming globose clusters, exploiting the vertical cliff-face habitat and absence of disturbance by larger herbivores. A fairly slow-growing, long-lived perennial.

Size and weight: Heads of medium weight.

Bulb: Epigeous, ovoid to medianally compressed, fleshy and tolerant of warm, dry, vertical conditions. It is epigeous and photosynthetically active, maximising light absorption. The succulent nature suggests an adaptation to the xeric habitat.

Leaves

Orientation: Distichous, spreading, ascending to recurved, maximising absorption of light. Leaf orientation varies according to the aspect and availability of light. The leaves are phenotypically adjustable to the vertical habitat and aspect. The tunics are fleshy and conserve water.

Succulence: Fleshy, often hairy, suggesting morphological adaptations to its dry habitat.

Colour and texture: Light green, without markings, with soft texture.

Age and persistence: Evergreen, reflecting the climatic pattern of year-round rainfall. Each bulb with up to 6 leaves (Snijman 1984), maximising absorption of light. Leaves persisting for up to three years. Bulblets often forming at base of damaged leaves, ideal for establishment in crevices or on ledges (see Vegetative reproduction below).

Armament and camouflage: The soft leaf texture suggests a reduction in armament in response to the undisturbed cliff habitat in contrast to the thorny but heavily grazed thicket and subtropical coastal vegetation. Lack of a camouflage defence strategy and the conspicuous clustered habit also reflect adaptation to the safe cliff habitat in the absence of disturbances.

Sexual reproduction

Inflorescence and flowers: Ascending, compact umbels of conspicuous whitish to white-pink flowers.

Fruit/Seed

Size: Berry, red to white, fleshy when ripe, 10 mm in diameter.

Dispersal: Fruits released when soft and white to reddish, dispersed by frugatory birds sitting rock ledges.

Time: Fruits ripening in summer and autumn, coinciding with the rainy season. Germination of seed up to about 21 days.

Vegetative reproduction: *Haemanthus albiflos* suckers from the base, forming dense clusters. The fleshy bulb scales will root when detached, forming bulblets. The bulblets or other fragments will root, establishing new colonies. The continual sprouting from the base and rooting of leaf fragments fallen into crevices represent a sufficient vegetative backup dispersal strategy for the harsh cliff-face environment.

CONSERVATION STATUS

A local endemic, not threatened.

ADDITIONAL NOTES

Horticulture: Plants easily grown by division or from seed, thriving in cultivation. It is best suited to thicket and bushveld gardens and grows well on shady rockeries, embankments and gabions. It also does well as a pot plant. Water sparingly throughout the year and feed during spring and summer. Its very easy growing nature maximises survival rate on the cliff face. Its polymorphic nature (genetic variability and phenotypic plasticity) ensures adaptation to local conditions and it is dispersed over long distances by birds. It is well established in horticulture.

VOUCHER

Van Jaarsveld 16920 (NBG).

ILLUSTRATIONS AND MAP

Figures 10a–10c, Map 10.

11. *Haemanthus humilis* Jacq. subsp. *humilis*, Jacquin, Plantarum rariorum Horti Caesarei Schoenbrunnensis descriptiones et icones 4: 6, t. 411 (1804).

Cremonophyte growth form: Cluster-forming, epigeous, bulbous (of medium weight, cliff hugger).

Growth form formula: A:B:D:C:La (e) (vb)

Etymology: Latin *humilis*, humble, pertaining to the low growing habit.

DESCRIPTION AND HABITAT

(Based on obligate cliff-face forms at Tandjiesberg and the Valley of Desolation near Graaff-Reinet.) Deciduous, epigeous geophytes. Bulbs ovoid to medianally compressed, up to 80 mm broad, cluster-forming (up to 10 heads, rarely more), epigeous to half-hypogeous; tunics truncate at top, green when exposed to light. Leaves 2, strap-shaped to elliptic, ascending to recurved, becoming deciduous towards summer, glabrous, glaucous green; margin ciliate; apex obtuse to acute. Inflorescence 50–200 mm high; scape compressed to 14 mm wide; umbel compact, compressed to 70 mm wide, with 4–8 spathe valves. Flowers 15–50, dark rose-pink; pedicels up to 11 mm long; perianth funnel-shaped, up to 23 mm long; tube up to 5 mm long, with spreading oblong segments 10–18 × 1–2 mm. Ovary spherical, up to 2 mm in diameter. Berry ovoid, up to 10 mm in diameter, white.

Phenology: Flowering mainly in midsummer (November–February) when plant is deciduous.

Pollinators: Insects.

Habitat and aspect: Vertical cliffs of mainly inland mountains, growing on all aspects but more so on south- and east-facing cliffs. The average daily maximum temperature is about 25°C and average daily minimum 10°C; extremes of up to 35°C have been recorded. Winters are cooler but frost is absent. Rainfall mainly in summer, 400–1000 mm per annum (thunder showers or rarely cyclonic winter rain). Plants firmly rooted in crevices, size often depending on the growing space allowed by the crevice.

Altitude: 460–1400 m.

Associated vegetation: Mainly Camdeboo Escarpment Thicket of the Albany Thicket Biome (Mucina *et al.* 2005).

Associated cremonophytes: On the Tandjiesberg (near Graaff-Reinet), it is associated with *Adromischus fallax*, *Ceterach cordatum*, *Cotyledon orbiculata* var. *orbiculata*, *Crassula exilis* subsp. *cooperi*, *C. perforata*, *C. sarcocaulis*, *Litanthus pusillus*, *Ornithogalum* sp. and *Othonna capensis*.

Geology: Mudstone (Emakwezini Formation), Beaufort Group (Karoo Supergroup). Substrate with efficient ledges, crevices and fissures for establishment of plants.

DISTRIBUTION

Eastern Cape, cliffs on the southern escarpment mountains near Graaff-Reinet.

RELATED SPECIES

Haemanthus humilis subsp. *humilis* is closely related to *H. montanus*, a geophyte with subterranean bulbs and white flowers.

ADAPTATIONS TO THE CLIFF ENVIRONMENT

Habit: Plants forming globose clusters, exploiting the vertical cliff-face habitat and absence of disturbance by larger herbivores. A fairly slow-growing, long-lived perennial.

Size and weight: Heads of medium weight.

Bulb: Epigeous, ovoid to medianally compressed, fleshy and tolerant of warm, dry, vertical conditions. It is epigeous and photosynthetically active, maximising light absorption. The succulent nature suggests an adaptation to the xeric habitat.

Leaves

Orientation: Leaves appearing soon after the flowers in February, distichous, spreading, ascending to recurved, maximising absorption of light. Orientation varying according to aspect and availability of light. The leaves are phenotypically adjustable to the vertical habitat and aspect.

Succulence: Fleshy with a hairy margin, suggesting morphological adaptations to the dry habitat.

Colour: Light grey-green, reflecting excessive light.

Age and persistence: Deciduous, leaves withering in spring and new ones appearing only in February, maximising survival on the arid rock face.

Armament and camouflage: The soft leaf texture suggests a reduction in armament in response to the undisturbed cliff habitat in contrast to the thorny but heavily grazed thicket and subtropical coastal vegetation. Lack of a camouflage defence strategy and the conspicuous clustered habit also reflect adaptation to the safe cliff habitat in the absence of disturbances.

Sexual reproduction

Inflorescence and flowers: Ascending, compact umbels of conspicuous dark rose-pink flowers.

Fruit/Seed

Size: Berry fleshy, orange to white, 5–10 mm in diameter, seed white, 5 mm in diameter.

Dispersal: Berries released when soft, dispersed by frugatory birds sitting on rock ledges.

Time: Berries ripening in summer and autumn, coinciding with the rainy season. Germination of seed up to about 21 days.

Vegetative reproduction: *Haemanthus humilis* suckers from the base, forming dense clusters. The fleshy bulb scales will root if they become detached, forming bulblets. The bulblets or other fragments will root and establish new colonies. The continual sprouting from the base and rooting of leaf fragments that have fallen into crevices are an efficient vegetative backup dispersal strategy for this harsh cliff-face environment.

CONSERVATION STATUS

A local endemic, not threatened.

ADDITIONAL NOTES

Horticulture: Easily grown by division or from seed, thriving in cultivation. Best for dry thicket gardens, grown on rockeries and in containers. Its very easy growing nature maximises survival rate on the cliff face. Its polymorphic nature (genetic variability and phenotypic plasticity) ensures adaptation to local conditions; birds ensure long-distance dispersal.

VOUCHER

Van Jaarsveld 16702 (NBG).

ILLUSTRATIONS AND MAP

Figures 11a–11c, Map 11.

12. *Haemanthus pauculifolius* Snijman & A.E.van Wyk in *South African Journal of Botany* 59,2: 247–250 (1993).

Cremonophyte growth form: Cluster-forming, epigeous, bulbous (of medium weight, cliff hugger).

Growth form formula: A:B:Lper:C:La (e) (vb)

Etymology: Latin *pauculifolius* (*paucus*, few, *folium* leaf), referring to the usually single leaf produced per season.

DESCRIPTION AND HABITAT

Evergreen bulbous geophytes. Bulbs ovoid, 40–50 mm in diameter, sprouting from base, cluster-forming, epigeous to half-hypogeous, green, smooth. Leaves few, usually 1 (rarely 2), fleshy, strap-shaped to linear-lanceolate, canaliculate, tomentose, 70–120(–325) × 20–45 mm; apex acute. Inflorescence 50–190 mm high; scape compressed to 7 mm wide; umbel compact, compressed to 30 mm wide, with 4 spathe valves. Flowers up to 19, white; pedicels up to 3 mm long; perianth funnel-shaped, up to 35 mm long; tube up to 13 mm long, with spreading lanceolate segments 17–20 × 3–4 mm. Berry spherical, up to 15 mm in diameter, orange. Seed ovoid, 10 mm long.

Phenology: Flowering mainly from late autumn to winter. Seeds dispersed by birds in late winter and spring, in time for the spring rains.

Pollinators: Insects.

Habitat and aspect: Vertical cliffs and steep rocky slopes of the escarpment and mountains, ranging from dry river valleys to mountain slopes, on all aspects but more so on south- and east-facing cliffs. Plants firmly rooted in crevices, size often depending on the growing space allowed by the crevice. The average daily maximum temperature varies from 26–28°C and average daily minimum from about 12–14°C; extremes of up to 45°C have been recorded. Winters are cooler but frost is absent. Rainfall occurs mainly in summer, 600–800 mm per annum (mainly thunder showers).

Altitude: 600–900 m.

Associated vegetation: Mainly Barberton Serpentine Sourveld of the Savanna Biome (Mucina *et al.* 2005).

Associated cremnophytes: At Joes Luck Mine (Eureka City, Barberton), the plants grow with *Aloe spicata*, *Cotyledon orbiculata*, *Crassula sarcocaulis*, *Kalanchoe rotundifolia*, *Plectranthus neochilus* and *Sarcostemma viminalis*.

Geology: Mainly shale and lava (Barberton Supergroup), quartzitic sandstone of the Black Reef Formation (Transvaal Supergroup). Substrate with sufficient ledges, crevices and fissures for establishment of plants.

DISTRIBUTION

Mpumalanga, from Barberton in the south to Blyderivierspoort north of Graskop, below the escarpment and a locality in Swaziland to the south.

RELATED SPECIES

Haemanthus pauculifolius is closely related to *H. albiflos* and differences are discussed under that species.

ADAPTATIONS TO THE CLIFF ENVIRONMENT

Habit: Plants forming globose clusters, exploiting the vertical cliff-face habitat and absence of disturbance by larger herbivores. A fairly slow-growing, long-lived perennial.

Size and weight: Heads of medium weight.

Bulb: Epigeous, ovoid to medianally compressed, fleshy and tolerant of warm, dry, vertical conditions. It is epigeous and photosynthetically active, maximising light absorption. The succulent nature can be seen as a response to its xeric habitat.

Leaves

Orientation: Distichous and spreading, sometimes recurved, maximising absorption of light. Orientation varying according to aspect and availability of light. The leaves are phenotypically adjustable to the vertical habitat and aspect.

Succulence: Fleshy and hairy, suggesting morphological adaptation to the dry habitat.

Colour: Light green, without markings.

Age and persistence: Evergreen, the solitary (occasionally with a smaller one) leaf is annually replaced, the reduction in leaves interpreted as a response to conditions on the very dry, hot cliffs and as a shift to bulb succulence. The epigeous bulbs are green and photosynthetically active. *Haemanthus albiflos* is closely related, widespread and a facultative cremnophyte (except the Kouga cliff form).

Armament and camouflage: The soft leaf texture suggests a reduction in armament in response to the undisturbed cliff habitat in contrast to the thorny but heavily grazed thicket and bushveld. Lack of a camouflage defence strategy and the conspicuous clustered habit also reflect adaptation to the safe cliff habitat in the absence of disturbances.

Sexual reproduction

Inflorescence and flowers: Ascending, compact umbels of conspicuous white flowers.

Fruit/Seed

Size: Conspicuous red, fleshy berry up to 10 mm in diameter.

Dispersal: Berries released when fully ripe (becoming orange), dispersed by frugatory birds perching on the rocky ledges.

Time: Berries ripening in winter, dispersed in time for spring rain. Germination of seed within about 21 days.

Vegetative reproduction: Suckers from the base, forming dense clusters. The fleshy bulb scales will root when detached, forming bulblets. Bulblets or other fragments will root, forming new colonies. Continual sprouting from the base and rooting of fragments fallen into crevices represent a sufficient vegetative backup dispersal strategy for the harsh cliff-face environment.

CONSERVATION STATUS

Classified as rare (Raimondo *et al.* 2009). A local endemic, not threatened.

ADDITIONAL NOTES

Horticulture: Best for bushveld gardens and grown in partial shade. A slow grower that does well in cultivation (containers or rockeries) and plants are easily grown by division, from bulb scales or from seed. Outside its bushveld habitat is best grown under controlled conditions in a greenhouse. Its ease of growth maximises its survival rate on the cliff face.

VOUCHERS

Van Jaarsveld 19365, 19373 (NBG).

ILLUSTRATIONS AND MAP

Plate 12, Figures 12a & 12b, Map 12.

ASPHODELACEAE

Aloe L.

13. *A. arborescens* Mill. subsp. *mzimnyi* Van Jaarsv. & A.E.van Wyk
14. *A. catengiana* Reynolds
15. *A. challisii* Van Jaarsv. & A.E.van Wyk
16. *A. corallina* I.Verd.
17. *A. dabenorisana* Van Jaarsv.
18. *A. dewinteri* Giess
19. *A. haemanthifolia* A.Berger & Marloth
20. *A. hardyi* Glen
21. *A. kouebokkeveldensis* Van Jaarsv. & A.B.Low
22. *A. meyeri* Van Jaarsv.
23. *A. mutabilis* Pillans
24. *A. nubigena* Groenew.
25. *A. omavandae* Van Jaarsv.
26. *A. pavelkae* Van Jaarsv., Swanepoel, A.E.van Wyk & Lavranos
27. *A. pictifolia* D.S.Hardy
28. *A. reynoldsii* Letty
29. *A. soutpansbergensis* I. Verd.
30. *A. thompsoniae* Groenew.

Bulbine Wolf

31. *B. cremnophila* Van Jaarsv.
32. *B. latifolia* (L.f.) Schult. & Schult.f. var. *curvata* Van Jaarsv.
33. *B. meiringii* Van Jaarsv.
34. *B. natalensis* Baker
35. *B. pendens* G.Will. & Baijnath
36. *B. ramosa* Van Jaarsv.
37. *B. retinens* Van Jaarsv. & S.A.Hammer
38. *B. rupicola* G.Will.
39. *B. suurbergensis* Van Jaarsv. & A.E.van Wyk
40. *B. thomasiae* Van Jaarsv.

Gasteria Duval

41. *G. batesiana* G.D.Rowley var. *batesiana*
42. *G. batesiana* G.D.Rowley var. *dolomitica* Van Jaarsv. & A.E.van Wyk
43. *G. croucheri* (Hook.f.) Baker subsp. *pendulifolia* (Van Jaarsv.) Zonn.
44. *G. doreeniae* Van Jaarsv. & A.E.van Wyk
45. *G. glauca* Van Jaarsv.
46. *G. glomerata* Van Jaarsv.
47. *G. pillansii* Kensit var. *ernesti-ruschii* (Dinter & Poelln.) Van Jaarsv.
48. *G. rawlinsonii* Oberm.
49. *G. tukhelensis* Van Jaarsv.

Haworthia Duval

50. *H. angustifolia* Haw. var. *baylissii* (C.L.Scott) M.B.Bayer
51. *H. attenuata* Haw. (Haw.) var. *attenuata* (Enon form)
52. *H. cymbiformis* Haw. (Duval) var. *ramosa* (G.G.Sm.) M.B.Bayer

- 53. *H. cymbiformis* Haw. (Duval) var. *setulifera* (Poelln.) M.B.Bayer
- 54. *H. glabrata* (Salm-Dyck) Baker
- 55. *H. gracilis* Poelln. var. *picturata* M.B.Bayer
- 56. *H. marumiana* Uitewaal var. *batesiana* (Uitewaal) M.B.Bayer
- 57. *H. marumiana* Uitewaal var. *marumiana*
- 58. *H. mirabilis* Haw. (Haw.) var. *consanguinea* M.B.Bayer
- 59. *H. scabra* Haw. var. *starkiana* (Poelln.) M.B.Bayer
- 60. *H. turgida* Haw. var. *turgida*
- 61. *H. zantneriana* Poelln.

***Trachyandra* Kunth**

- 62. *T. tabularis* (Baker) Oberm.

ALOE L.

13. *Aloe arborescens* Mill. subsp. *mzimnyati* Van Jaarsv. & A.E. van Wyk in Aloe 42,3: 40–42 (2005a).

Cremonophyte growth form: Cluster-forming, subpendulous, branched (of medium weight to heavy, cliff squatter).

Growth form formula: E:F:P:R:C:Ar (vb)

Etymology: After the Buffalo River (Zulu, *Mzimnyati*) in KwaZulu-Natal where the plants were collected.

DESCRIPTION AND HABITAT

Arborescent, much-branched, rounded shrubs up to 0.76 m high, about the same in diameter. Roots fleshy, 3 mm in diameter, pale, root tips yellow. Branches 5–7 mm in diameter, with leaves crowded in apical rosettes of about 200 mm in diameter. Leaves linear-lanceolate, 130–210 × 8–10 mm at base, spreading, green but turning reddish green in dry winter, apices recurved; margin armed with yellowish teeth 1–2 mm long. Inflorescence 240–330 mm long, bearing conical racemes 80–100 mm long. Perianth subclavate, 22–25 mm long, orange-red to yellow. Capsule 10–17 × 4–5 mm. Seeds 1.5–2.0 × 1 mm.

Phenology: Flowering mainly in midwinter (July–August). Seeds dispersed by wind in early spring (end of September), just before the spring rains.

Pollinators: Sunbirds.

Habitat and aspect: Known only from vertical quartzitic sandstone cliffs (east- and south-facing) along the lower Mzimnyati River (Buffalo River) near confluence with the Thukela River. Plants occur scattered in rock crevices and are difficult to reach where they are firmly rooted in spaces large enough to support the roots and stem clusters. Vegetation of the region is mainly savanna and grassland. Average summer temperature is about 26°C and for winter 14°C. Rainfall experienced mainly in summer, with averages of 800–1000 mm per annum.

Altitude: 700–1000 m.

Associated vegetation: Thukela Valley Bushveld of the Sub-Escarpment Savanna Bioregion of the Savanna Biome (Mucina *et al.* 2005).

Associated cremnophytes: *Aloe arborescens* subsp. *mzimnyati* grows in association with *Bulbine natalensis*, *Cotyledon orbiculata*, *Crassula orbicularis*, *Cyanotis speciosa*, *Plectranthus madagascariensis* and *Schizobasis angolensis*.

Geology: Quartzitic sandstone of the Natal Group (Cape Supergroup). Texture rough, with many fissures, ledges and crevices ideal for establishment of plants.

DISTRIBUTION

Aloe arborescens subsp. *mzimnyati* is known only from the Buffalo (Mzimnyati) River close to its confluence with the Thukela River, the largest river in KwaZulu-Natal.

RELATED SPECIES

Aloe arborescens subsp. *mzimnyati* differs from *Aloe arborescens* subsp. *arborescens* by its smaller stature and flowers which are 22–25 mm long, ranging from red to yellow.

ADAPTATIONS TO THE CLIFF ENVIRONMENT

Habit: Plants with ascending to drooping stems and leaves. Long-lived perennial.

Size and weight: Heads medium-sized to large, of medium weight to heavy.

Stem: Branches grey, fibrous and firm.

Leaves

Orientation: Leaves ascending to becoming drooping.

Colour: Green, no powdery bloom, perhaps an adaptation to the shady, south-facing cliffs.

Age and persistence: Perennial, deciduous from the base, resulting in apical rosettes.

Armament: The soft teeth on the leaf margins of *Aloe arborescens*, and especially subsp. *mzimnyati*, compared to other non-cremnophilous aloes, suggest a reduction in armament due to a reduction in herbivory.

Sexual reproduction

Inflorescence and flowers: Young inflorescence ascending or drooping but curving up as it matures, presenting the raceme(s) in the typical erect position.

Fruit/Seed

Size: Seed 1.5–2.0 × 1 mm, an ideal size for establishment in crevices.

Dispersal: Light, angular seeds shaken from the capsules and dispersed by wind.

Time: Seeds dispersed in spring, coinciding with the start of the rainy season.
Germination within 14–21 days.

Vegetative reproduction: Plants sprout from the base and branches will root when finding a suitable crevice. Detached branches will also root. The succulent nature ensures long-term survival on the cliffs.

CONSERVATION STATUS

Although it is not well represented in herbaria, it is locally common and not threatened.

ADDITIONAL NOTES

Horticulture: *Aloe arborescens* subsp. *mzimnyati* is a worthwhile introduction to horticulture. Just as the typical *Aloe arborescens* subsp. *arborescens*, it is easily grown from cuttings or seed. Plants grown at Kirstenbosch will be released and introduced through the annual plant sale of the Botanical Society of South Africa. It is widely adaptable and can be grown in bushveld or subtropical coastal gardens.

VOUCHER

Van Jaarsveld 18211 (NBG).

ILLUSTRATIONS AND MAP

Plate 13, Figures 13a–13d, Map 13.

14. *Aloe catengiana* Reynolds in *Kirkia* 1: 160 (1961). (Omavanda form.)

Cremnophyte growth form: Cluster-forming, pendulous, branched (of medium weight to heavy, cliff hanger).

Growth form formula: E:F:P:R:C:Rls (vb)

Etymology: After Catenga in Angola where the plants were first recorded.

DESCRIPTION AND HABITAT

Arborescent, much-branched, spreading, pendent shrubs up to 0.7 m wide. Roots fleshy. Branches 8–12 mm in diameter, with leaves tending to be crowded in apical rosettes of about 300 mm in diameter. Leaves linear-lanceolate, 130–160 × 25–30, spreading, green but turning reddish in dry season; upper surface flat to convex, lower surface convex, spotted in proximal half, striate towards base and stem; margin armed with yellowish teeth 2–4 mm long; apices recurved, acute. Inflorescence up to 400 mm long, branched in lower half, at first pendent and apices bending up, with conical cylindrical-acuminate racemes up to 160 mm long and 40 mm in diameter; pedicels 10 mm long; bracts ovate-acuminate scarious, up to 5 × 3 mm. Perianth

scarlet, cylindrical, slightly decurved, up to 28×7 mm; outer segments free for 10 mm, inner segments broader, apices obtuse. Anthers becoming shortly exerted. Stigma exerted to 2 mm. Seed not seen.

Phenology: Flowering mainly in autumn (April–May). Seeds dispersed by wind in winter, just before the spring rains.

Pollinators: Sunbirds.

Habitat and aspect: East-facing sandstone cliffs on the Omavanda escarpment margin. *Aloe catengiana* grows firmly wedged in crevices and the rosette becomes pendent from a young age. The plants are rare and restricted to inaccessible places. The vegetation in the region below is arid mopane savanna, with several species of *Commiphora* prominent. Omavanda is within the tropics, with hot summers and dry, warm winters without frost. Rainfall mainly in summer, 300–500 mm per annum.

Altitude: 1800–2000 m.

Associated vegetation: Dry savanna with main species: *Combretum apiculatum*, *Combretum zeyheri*, *Cyphostemma currorii*, *Entandrophragma spicatum*, *Kirkia acuminata* and *Mundulea sericea*.

Associated cremnoophytes: *Cotyledon orbiculata*, *Cyphostemma currorii*, *Euphorbia subsalsa*, *E. monteiroi*, *Kalanchoe lanceolata* and *Sarcostemma viminale*. Other non-succulent species include: *Ficus glumosa*, *F. ilicina* and *Petalidium coccineum*. On wider ledges, species such as *Cussonia angolensis*, *Nicotiana africana* and *Nuxia congesta* are encountered.

Geology: Sandstone of the Damara Sequence. Substrate with many ledges, crevices and fissures, ideal for establishment of plants.

DISTRIBUTION

In Namibia *Aloe catengiana* is known only from the upper vertical, quartzitic sandstone cliffs (east- and south-facing) along the northeastern Baynes Mountains. It also occurs east of Catengue Railway Station in Angolan below the inland escarpment.

RELATED SPECIES

Aloe catengiana (Omavanda, Namibia) differs from typical *Aloe catengiana* (Catengue, Angola), in its smaller heads, pendent spreading growth as well as its inflorescence, which is only 2- or 3-branched.

ADAPTATIONS TO THE CLIFF ENVIRONMENT

Habit: With spreading to drooping stems. A long-lived perennial with a medium growth rate.

Size and weight: Heads of medium weight, but plants becoming large and heavy.

Stem: Branches grey, fibrous and firm.

Leaves

Orientation: Ascending, recurved and occasionally becoming drooping.

Colour: Greyish green, turning reddish to yellowish in the dry season.

Age and persistence: Persisting, ultimately becoming deciduous from the base, resulting in apical rosettes.

Armament: The soft teeth on the leaf margins of *Aloe catengiana* suggest a reduction in armament due to a reduction in herbivory.

Sexual reproduction

Inflorescence and flowers: Young inflorescence drooping but the tips curved upwards.

Fruit/Seed

Size: Not seen.

Dispersal: Light, angular seeds shaken from the capsules and dispersed by wind.

Time: Seeds dispersed in spring, coinciding with the start of the rainy season.

Vegetative reproduction: *Aloe catengiana* proliferates from the base, forming dense, drooping clusters. Stems root when finding a new crevice and fallen branches will also root when wedged in a suitable crevice. The continual basal sprouting of new shoots and rooting of stems in new crevices by extended stem growth represent a sufficient vegetative backup dispersal strategy for the harsh cliff-face environment.

CONSERVATION STATUS

Rare, but not threatened.

ADDITIONAL NOTES

Horticulture: A worthwhile introduction to horticulture, best grown in dry savanna gardens (Van Jaarsveld 2010). It propagates readily from cuttings planted in a well-drained, sandy mixture and grows fairly fast. Plants thrive on steep embankments, in large hanging baskets or on window sills. Outside its habitat, it is best grown under controlled conditions in containers in a greenhouse. Plants grown at Kirstenbosch are being increased by vegetative means and will be released and introduced through the annual plant sale and from the nursery at Kirstenbosch.

VOUCHER

Van Jaarsveld 18805 (NBG).

ILLUSTRATIONS AND MAP

Figures 14a–14c, Map 14.

15. *Aloe challisii* Van Jaarsv. & A.E.van Wyk in Aloe 43,2 & 3; 36–39 (2006a).

Cremonophyte growth form: Cluster-forming, pendulous rosettes (light to medium weight, cliff hanger).

Growth form formula: F:P:R:C:Ar (vb) (eg)

Etymology: This aloe was first collected by Mr Chris Challis, aloe and succulent plant enthusiast, while exploring a hiking trail at Verlorenkloof, Mpumalanga.

DESCRIPTION AND HABITAT

Perennial succulent suckering from base and forming small, dense groups up to 200 mm in diameter. Roots fleshy. Branches pendent. Leaves soft, flaccid, rosulate, 4–7 per branch, linear-triangular, 100–200(–250) × 8–10(–20) mm, curved and pendent from rock faces, very fleshy especially in rainy season and becoming almost subterete and channelled in dry season, smooth, slightly glaucous, bluish green, white-spotted at base; abaxial side convex, adaxial side flat or slightly channelled in rainy season, becoming channelled in dry season, striate, purplish green towards base; margin serrate, semitranslucent, white, cartilaginous, up to 1.5 mm broad at base, 0.2 mm broad elsewhere; teeth 1 × 0.4 mm, 1–3 mm apart; apex acute to subacute, armed with 5 or 6 teeth. Inflorescence simple, decumbent, 140–160 mm tall; peduncle 100 mm long, 5–6 mm broad at base, biconvex and slightly flattened at base, terete upwards, with 4 sterile bracts 8–9 mm long and clasping up to 9 mm at base; raceme short, subcapitata, 40–45 mm long, up to 15-flowered; floral bracts scarious, deltoid, acuminate, 8–9 × 4 mm; pedicels 10–15 mm long, ascending, orange. Perianth subclavate, pendent, 25 mm long, bright orange-red; apices obtuse to subacute, yellow, green-tipped; tube cylindrical-triangular; segments with a median green stripe, free to base, outer three concave, 25 × 3 mm, widening to 6 mm, linear-oblong, canaliculate, inner three not as deeply canaliculate, widening to 6 mm; base 5 mm in diameter, widening to 7 mm up to halfway and then narrowing towards apex. Stamens yellowish, 20–22 mm long. Ovary oblong, 5–6 × 2 mm, grooved, brownish green; style 18 mm long. Capsule 16 × 5 mm. Seeds oblong, angular, 3–4 × 1.5 mm, grey-black.

Phenology: Flowering mainly in spring (October–November).

Pollinators: Sunbirds.

Habitat and aspect: *Aloe challisii* is known only from the upper vertical, quartzitic, sandstone cliffs (south- and southeast-facing) along the southern part of the Steenkampsberg, which is frequently covered in cloud. Plants occur scattered among moss in rock crevices and are difficult to reach, firmly rooted in crevices and on ledges large enough to support the roots and stem clusters. The average daily maximum temperature is about 20°C and the average daily minimum about 8°C. Rainfall is high, 1500–1750 mm per annum, and is experienced mainly in summer.

Altitude: 1800–2000 m.

Associated vegetation: Lydenburg Montane Grassland of the Grassland Biome (Mucina *et al.* 2005).

Associated cremnophytes: The species is found in association with other temperate, high-altitude plants such as *Crassula pellucida* subsp. *brachypetala*, *C. sarcocaulis*, *C. setulosa* var. *rubra*, *C. setulosa* var. *setulosa*, *Elaphoglossum* sp., *Ledebouria saundersiae*, *Mohria caffrorum*, *Morella pilulifera*, *Rhodohypoxis baurii*, *Senecio orbicularis* and a species of *Streptocarpus*.

Geology: Quartzitic sandstone (Black Reef Formation, Transvaal Supergroup). Light-textured (grey), rough- to smooth-textured, with many fissures, ledges and crevices for establishment of plants.

DISTRIBUTION

Aloe challisii is as yet known only from the upper sandstone cliffs of the Steenkampsberg southwest of Lydenburg in Mpumalanga.

RELATED SPECIES

There are some 125 species of *Aloe* indigenous to South Africa and Namibia (Glen & Hardy 2000). *Aloe challisii* is the 17th species of *Aloe* (21%) and the fourth member of section *Leptoaloe* recorded as confined to sheer cliff faces in South Africa and Namibia. This section also includes *A. nubigena*, *A. thompsoniae* and *A. soutpansbergensis*, all of them with soft, flaccid leaves with small or no (*A. nubigena*) teeth on the leaf margins. *Aloe nubigena* and *A. soutpansbergensis* also have a pendent habit. *Aloe challisii* is at once distinguished from other cremnophilous species in section *Leptoaloe* by its downward curving leaves (epinastic growth), short, subcapitate inflorescence (140–160 mm long), subclavate perianth (25 mm long), pedicels (10–15 mm long) and small floral bracts (8–9 × 4 mm). It is further distinguished by its bluish green, subterete leaves. It is closest to *A. soutpansbergensis*, which has an inflorescence 180–200 mm long and horizontally orientated racemes with forward projected flowers 27 mm long (pedicels 25 mm long, floral bracts 17 × 5 mm and leaves green, dorsiventrally flattened). *Aloe challisii* is also distinguished by its spring flowering season while the others in section *Leptoaloe* flower in summer or autumn.

ADAPTATIONS TO THE CLIFF ENVIRONMENT

Habit: Plants forming clusters among moss and other cremnophytes occupying smaller crevices and ledges.

Size and weight: Of light to medium weight.

Stem: Caulescent, grey, spreading, subpendulous to pendulous.

Leaves

Orientation: Rosulate, subterete, curving downwards owing to epinastic growth and pendent (positively geotropic).

Succulence: Very fleshy, becoming very succulent in summer, an adaptation to the dry winters when the cliffs become very dry.

Colour: Bluish green.

Age and persistence: Fairly fast-growing, long-lived, perennial, deciduous from the base.

Armament: Leaf margin serrate, semitranslucent, white, cartilaginous, up to 1.5 mm broad at base, 0.2 mm broad elsewhere; teeth 1×0.4 mm, 1–3 mm apart. The teeth are soft, providing little armament in response to the safe cliff-face habitat (inaccessible to larger herbivores).

Sexual reproduction

Inflorescence and flowers: Young inflorescence curving upwards as it matures, presenting the racemes in the typical erect position.

Fruit/Seed

Size: Seed $3\text{--}4 \times 1.5$ mm, an ideal size for establishment in crevices.

Dispersal: Light, greyish black, angular seeds shaken from the capsules and dispersed by wind.

Time: Seeds dispersed in winter and autumn, ready for the early spring and summer rains. Germination in about 14–21 days.

Vegetative reproduction: Plants prolific from the base, forming dense clusters in rock crevices among tufts of grass or other cremnophytes. This continuous vegetative renewal ensures a long-term foothold.

CONSERVATION STATUS

Although this small aloe is confined to the Steenkampsberg, it is locally abundant and protected by the inaccessible habitat and therefore not threatened. Its status has been determined as VU D2 (Raimondo *et al.* 2009).

ADDITIONAL NOTES

Horticulture: Best grown in afroalpine or summer-rainfall grassland gardens in a slightly acid peat and sand mixture (Van Jaarsveld 2006b, 2010). Feed regularly in spring and summer. An easily and fast-growing species. Away from its habitat it is best kept in a greenhouse and kept moist and cool in summer. *Aloe challisii* is prolific from the base, soon becoming cluster-forming. The drooping nature of the soft, flaccid leaves is retained in cultivation.

VOUCHER

Van Jaarsveld & Challis 19801 (NBG).

ILLUSTRATIONS AND MAP

Plate 15, Figures 15a–15c, Map 15.

16. *Aloe corallina* I. Verd. in The Flowering Plants of Africa 45: t. 1788 (1979).

Cremnophyte growth form: Cluster-forming, pendulous rosettes (of medium weight to heavy, cliff hanger).

Growth form formula: E:F:P:R:C:Ar (vb) (eg)

Etymology: The epithet *corallina* refers to the coral-red flowers.

DESCRIPTION AND HABITAT

Plants slow-growing, pendulous, with leaves in apical rosettes, dividing and forming small pendent clusters (up to 6 heads) up to 600 mm in diameter and on stems up to 700 mm long. Roots up to 3 mm in diameter. Stems up to 700 mm long, up to 80 mm in diameter. Leaves firm, densely rosulate (rosettes up to 600 mm in diameter in solitary specimens), drawn together in a mitre-shaped head (dry season), lanceolate-acuminate, up to 500 × 110 mm; surface firm, leathery, grey-green; margin entire to slightly denticulate; apex acute. Inflorescence 600–700 mm long, branched in distal half, with up to 13 racemes forming a loose panicle, rarely solitary; scape curving upwards from pendulous rosettes, exposing ascending racemes; racemes elongate; pedicels up to 12 mm long. Perianth subpendulous, coral-red, 32 × 7 mm. Fruiting capsule oblong, 10–14 × 5–7 mm. Seeds angular, 3 × 1.5 mm, dark brown, angular.

Phenology: Flowering mainly in winter (May–June).

Pollinators: Sunbirds.

Habitat and aspect: Dolomite cliffs, on all aspects, but usually on the shady south-facing slopes. Temperatures in the Cunene Valley are high throughout the year, especially in summer. Plants are firmly rooted in crevices and on ledges large enough to support the roots and stem clusters. Rainfall occurs mainly in summer, ranging from 75–150 mm per annum.

Altitude: 400–1200 m.

Associated vegetation: Arid savanna.

Associated cremnophytes: *Ceraria longipedunculata*, *Ficus cordata*, *F. glumosa*, *F. ilicina*, *Kalanchoe laciniata*, *K. lanceolata*, *Plectranthus hereroensis* and *Sterculia rogersii*.

Geology: Dark Proterozoic Namibian dolomite (Otavi Group, Damara Sequence). The dolomite substrate is dark and rough in texture, with many fissures and crevices.

DISTRIBUTION

A dolomite endemic, confined to sheer cliff faces of the Baynes Mountains in the Cunene River Valley of northern Namibia as well as southern Angola. Plants are often locally abundant.

RELATED SPECIES

Aloe corallina comes closest to *A. dewinteri*, a solitary, larger, also cremnophilous species from the dolomite cliffs near Sesfontein and the adjacent Khowarib Poort. The latter has

larger open rosettes, inflorescences that are branched low down and bicoloured flowers (yellow and red) and the leaves have slightly larger teeth. It is also related to *A. kaokoensis*, a larger robust species with open, spreading rosettes and large panicles. The small size of *A. corallina* can be viewed as an adaptation to its cliff environment.

ADAPTATIONS TO THE CLIFF ENVIRONMENT

Habit: Plants with medium-sized caulescent clusters, occupying larger crevices and ledges. *Aloe corallina* is a slow grower and long-lived perennial. Where within reach, stems and leaves heavily grazed.

Size and weight: Heads medium-sized, of medium weight to heavy.

Stem: Caulescent, grey, pendulous stems and thus less investment in woody tissue.

Leaves

Orientation: Distinctly incurved, pendulous (positively geotropic).

Colour: Grey-green, without a powdery bloom, margins reddish. The grey colouring deflecting the rays of the sun.

Age and persistence: Long-lived, deciduous from the base.

Armament: Juvenile leaves are armed with brownish teeth of 1×1 mm (5–7 mm apart) but as the plant matures the teeth become smaller and sometimes disappear completely, suggesting a reduction in energy expenditure (production of teeth) but possibly also revealing the evolutionary history of plants evolving away from the cliff face.

Sexual reproduction

Inflorescence and flowers: Young inflorescence curving upwards as it matures, presenting the racemes in the typical erect position.

Fruit/Seed

Size: Seed 3×1.5 mm, an ideal size for establishment in crevices.

Dispersal: Light, angular seeds shaken from the capsules and dispersed by wind.

Time: Seeds dispersed in winter and autumn, ready for the early spring and summer rains. Germination in about 14–21 days.

Vegetative reproduction: *Aloe corallina* is prolific from the base, forming drooping clusters. The stems root when finding a new crevice and fallen branches will also root when wedged in a suitable crevice. The continual renewal of shoots and rooting of stems in new crevices by extended stems represent a sufficient vegetative backup dispersal strategy for the harsh cliff-face environment.

CONSERVATION STATUS

Classified as rare (Loots 2005). Although confined to dolomite cliffs along the lower Cunene River, plants grow in abundance and are therefore not threatened.

ADDITIONAL NOTES

Horticulture: Best for dry, sunny, subtropical savanna and desert gardens. An easily grown species but outside its habitat it is best grown in a greenhouse where environmental conditions can be controlled. Although it is a dolomite endemic, it adapts well to acidic soils. Plants react well to summer feeding with an organic fertiliser (Van Jaarsveld 2006b, 2010).

VOUCHER

Van Jaarsveld 16482 (NBG).

ILLUSTRATIONS AND MAP

Plate 16, Figures 16a–16c, Map 16.

17. *Aloe dabenorisana* Van Jaarsv. in *Journal of South African Botany* 48,3: 419–424 (1982b).

Crempnophyte growth form: Pendent, capitate, cluster-forming, recurved, leafy, branched (of medium weight to heavy, cliff hanger).

Growth form formula: E:F:P:R:C:Ar (vb) (eg)

Etymology: After the Dabenoris Mountain (Bushmanland, Northern Cape) where the plants were discovered by Mr A.R. Mitchell, a British citizen.

DESCRIPTION AND HABITAT

Plants slow-growing, long-lived, perennial (from seed 5–7 years), forming pendulous clusters (rarely solitary), branched from base, with short elongated stems up to 300 mm long. Roots slightly fleshy. Leaves in apical rosette up to 450 mm in diameter, narrowly lanceolate-acuminate, up to 240 mm long, 50 mm in diameter, recurved, sometimes deflexed; surface green tinged red; margin green to reddish, armed with small deltoid teeth. Inflorescence 2–4-branched, pendulous, recurved, up to 300 mm long; racemes capitate to pointed. Flowers subpendent. Perianth orange-red, green-tipped, 25 mm long. Fruiting capsule ascending-spreading. Seed not seen.

Phenology: Flowering mainly in midsummer (December–January).

Pollinators: Sunbirds.

Habitat and aspect: South-facing quartzitic sandstone cliffs. Plants are firmly rooted in crevices large enough to support the roots and stem clusters. The average daily maximum temperature is about 27°C and about 12°C in winter (in summer it can reach about 35–40°C).

The southern slopes are cooler and shady in the winter months and frost is absent. Rainfall occurs mainly from autumn (thunder showers) to spring and ranges from about 75–150 mm per annum.

Altitude: 700–1000 m.

Associated vegetation: Eastern Gariep Rocky Desert of the Desert Biome (Mucina *et al.* 2005).

Associated cremnophytes: *Adromischus diabolicus*, *Conophytum fulleri*, *Crassula exilis* subsp. *sedifolia*, *C. garibina* and *Tylecodon sulphureus* var. *armianus*.

Geology: Light-coloured quartz of the Hom Formation (Bushmanland Group), with many ledges, fissures and crevices, ideal for establishment of plants

DISTRIBUTION

Aloe dabenorisana is confined to the sheer south-facing cliffs of the Dabenoris and Pellaberg Mountains.

RELATED SPECIES

Aloe dabenorisana is related to *A. pearsonii*, which is a much larger, erect species (smaller heads) of the Northern Cape. *Aloe dabenorisana* differs in its larger apical rosettes, pendulous nature, green leaf surface and lack of short, biconvex, reddish grey-green, persistent leaves along the erect stems. *Aloe dabenorisana* differs from *A. pavelkae* in its much shorter stems and leaves that are distinctly recurved.

ADAPTATIONS TO THE CLIFF ENVIRONMENT

Habit: Plants with drooping stems and recurved leaves. A slow grower, long-lived perennial with a sturdy leaves.

Size and weight: Its larger size ensures its survival under very high summer temperatures and maximises moisture retention by the leaves.

Stem: Branches pendulous and fibrous, thus less investment in woody tissue.

Leaves

Orientation: Open rosettes of recurved leaves maximise exposure to the open shade.

Colour: Green, turning reddish when under moisture stress.

Age and persistence: Persistent and often remaining functional for many years, thus acting as a water resource and staying photosynthetically functional.

Armament: The smaller teeth on the leaf margins suggest a reduction in armament as a direct result of the reduction in herbivory.

Sexual reproduction

Inflorescence and flowers: Young inflorescence drooping but curving up as it matures, presenting the raceme(s) in the typical erect position.

Fruit/Seed

Size: Seed not seen.

Dispersal: Light seeds shaken from the capsules and dispersed by wind.

Time: Seeds dispersed in autumn, coinciding with autumn rains and start of the winter rainy season.

Vegetative reproduction: *Aloe dabenorisana* is prolific from the base, forming drooping clusters. The stems root when finding a new crevice and fallen branches will also root when wedged in a suitable crevice. The continual renewal of shoots and rooting of stems in new crevices by extended stem growth represent a sufficient vegetative backup dispersal strategy for the harsh cliff-face environment.

CONSERVATION STATUS

Although rare, *Aloe dabenorisana* is not threatened (Hilton-Taylor 1996; Raimondo *et al.* 2009).

ADDITIONAL NOTES

Horticulture: Best for dry, subtropical desert gardens, grown on shady embankments, on the shady side of buildings or drooping from window sills (Van Jaarsveld 2006b, 2010). Outside its habitat, plants are difficult to grow and prone to fungal diseases such as crown rot and root rot (the latter due to a *Fusarium* sp.). Grow in a warm but shady position in a slightly acid soil. Water should be provided sparingly throughout the year. Propagation from stem cuttings, rooted in sandy soil in summer. Keep in light shade.

VOUCHERS

Van Jaarsveld & Kritzinger 6426, Van Jaarsveld & Patterson 6638 (NBG).

ILLUSTRATIONS AND MAP

Plate 17, Figures 17a–17d, Map 17.

18. *Aloe dewinteri* Giess in *Bothalia* 11: 120 (1973).

Cremonophyte growth form: Solitary, open, acaulescent or very shortly stemmed rosette (heavy, cliff squatter).

Growth form formula: A:S:Lper:R:So:La

Etymology: After Dr Bernard de Winter (1924–), Director of the former Botanical Research Institute in Pretoria.

DESCRIPTION AND HABITAT

Plants slow-growing, acaulescent or short-stemmed with leaves in horizontal exposed rosettes up to 800 mm in diameter. Stem up to 60 mm in diameter. Roots up to 3 mm in diameter. Leaves firm, densely rosulate, erect becoming spreading and recurved, lanceolate-acuminate, up to 560 × 100 mm; surface firm, leathery, grey-green; margin denticulate, bearing small yellowish brown teeth 2 mm long; apex acute. Inflorescence up to 900 mm long, branched in basal half, with up to 3 racemes, occasionally solitary; scape curving upwards from horizontal rosettes; racemes elongate; pedicels 5 mm long. Perianth subpendulous, 30 × 7 mm long, pink becoming cream-white as it matures. Fruiting capsule oblong, 15 × 8 mm. Seeds 3 × 1.5–2 mm, dark brown, angular.

Phenology: Flowering mainly in summer (December–January).

Pollinators: Sunbirds.

Habitat and aspect: Dolomite cliffs and has been recorded from most aspects, but more so from the shady south-facing slopes. Plants are firmly rooted in crevices and on ledges large enough to support the roots and stem clusters. Temperatures are high, especially in summer, with cooler but warm, dry winters. Rainfall occurs mainly in summer, ranging from 75–150 mm per annum.

Altitude: 600–1200 m.

Associated vegetation: Arid savanna and subtropical desert.

Associated cremnohytes: *Ceraria* sp., *Ficus cordata*, *F. ilicina*, *Kalanchoe laciniata*, *Plectranthus hereroensis*, *Sterculia rogersii* and *Urginea* sp.

Geology: Dark Proterozoic Namibian dolomite (Otavi Group, Damara Sequence), rough in texture and with many fissures.

DISTRIBUTION

Aloe dewinteri is a dolomite endemic, confined to the sheer cliff faces of the escarpment mountains east of Sesfontein (Kaokoland, Namibia) and plants are more often found on shady southern slopes where they are often locally abundant.

RELATED SPECIES

Aloe dewinteri comes closest to *A. corallina*; the differences are discussed under that species. It is also related to *A. kaokoensis*, the latter with much larger rosettes and a paniculate inflorescence. Its small size can be seen as an adaptation to its cliff-face environment.

ADAPTATIONS TO THE CLIFF ENVIRONMENT

Habit: Plants with medium-sized to large acaulescent rosettes, occupying larger crevices and ledges. Growth is slow, but a long-lived perennial. Where within reach, stems and leaves heavily grazed.

Size and weight: Heads medium-sized, heavy.

Stem: Short, caulescent, grey, spreading to pendulous, thus less investment in woody tissue.

Leaves

Orientation: In an open rosette and recurved (negatively geotropic). Leaves with a firm but smooth texture, at first ascending-spreading and ultimately recurved, with maximum exposure to the open shade.

Colour and texture: Grey-green without a powdery bloom, margins reddish. The firm texture and colour in response to the very hot, dry desert environment.

Age and persistence: Long-lived, deciduous from the base.

Armament: Juvenile and mature leaves armed with brownish teeth 1 × 1 mm (5–7 mm apart).

Sexual reproduction

Inflorescence and flowers: Young inflorescence curving upwards as it matures, presenting the racemes in the typical erect position.

Fruit/Seed

Size: Seed 3 × 1.5–2 mm, an ideal size for establishment in crevices.

Dispersal: Light, angular seeds shaken from the capsules and dispersed by wind.

Time: Seeds dispersed in winter and autumn, ready for the early spring and summer rains. Germination in about 14–21 days.

Vegetative reproduction: Plants solitary but damaged heads will sprout as a vegetative backup.

CONSERVATION STATUS

Classified as rare (Loots 2005). Limited in distribution but often locally abundant and therefore not threatened.

ADDITIONAL NOTES

Horticulture: Best for dry, sunny, subtropical savanna and desert gardens (Van Jaarsveld 2006b, 2010). An easily grown species but outside its habitat it is best grown in a greenhouse

where environmental conditions can be controlled. Although it is a dolomite endemic, it adapts well to acidic soils. Plants react well to summer feeding with an organic fertiliser.

VOUCHER

Van Jaarsveld 16837 (NBG).

ILLUSTRATIONS AND MAP

Figures 18a–18c, Map 18.

19. *Aloe haemanthifolia* A.Berger & Marloth in *Botanische Jahrbücher* 38: 85 (1905).

Cremnophyte growth form: Cluster-forming (heavy, cliff hugger).

Growth form formula: A:S:Lper:R:C:La (vb)

Etymology: After its habit and likeness to the genus *Haemanthus* (Amaryllidaceae).

DESCRIPTION AND HABITAT

Plants slow-growing, acaulescent, dividing forming large rounded clusters up to 1.5 m in diameter, 0.7 m high. Leaves distichous, ascending, broadly lorate, fibrous, green, up to 210 × 100 mm, lineate; margin reddish, minutely serrulata; apex rounded. Inflorescence simple, curving upwards, up to 650 mm tall; racemes capitate; pedicels up to 35 mm long. Perianth subpendulous, orange-red, up to 38 long; style and anthers included. Fruiting capsule conical, 30 × 17 mm. Seeds angular, 7 × 4 mm, dark grey.

Phenology: Flowering mainly in spring (October). Seeds dispersed by wind in summer and autumn, just before the spring rains.

Pollinators: Sunbirds.

Habitat and aspect: Sandstone cliffs on exposed north-, east-, west- and south-facing aspects. Plants firmly rooted in crevices and on ledges large enough to support the roots and stem clusters. Summers are cool, winters cooler with occasional snow. The average daily maximum temperature is about 18°C and the average daily minimum about 8°C. Rainfall occurs mainly in winter and ranges from 800–1000 mm per annum (cyclonic winter rainfall).

Altitude: 500–1675 m.

Associated vegetation: Western Altimontane Sandstone Fynbos of the Fynbos Biome (Mucina *et al.* 2005).

Associated cremnophytes: *Adromischus maculata*, *Crassula atropurpurea* var. *watermeyeri*, *C. obtusa*, *Ruschia drepanophylla* and restios (Restionaceae).

Geology: Quartzitic sandstone (Nardouw Subgroup, Table Mountain Group, Cape Supergroup). Light in colour and rough- to smooth-textured, with many ledges, fissures and crevices, ideal for establishment of plants.

DISTRIBUTION

Aloe haemanthifolia is a quartzitic sandstone endemic, confined to sheer cliff faces of the Hex River-Cold Bokkeveld and southern Cedarberg Mountains. Plants are often locally abundant.

RELATED SPECIES

Aloe haemanthifolia comes closest to *A. plicatilis*, an arborescent species from the Hex River Mountains with similar distichous leaves (margin denticulate, fibres lacking), corky bark and elongated racemes; it is also well adapted to fire. Apart from its small size, the heads of *A. haemanthifolia* are much larger and not glaucous green as in *A. plicatilis*. The seed pods are rounded in *A. plicatilis* but conical in *A. haemanthifolia*.

ADAPTATIONS TO THE CLIFF ENVIRONMENT

Habit: Plants with large acaulescent clusters, occupying larger crevices and ledges. *Aloe haemanthifolia* is a slow grower and long-lived perennial with distinctly fibrous leaves. Where within reach, plants heavily grazed (leaves lacking bitter substance), exposing the conspicuous fibrous leaves (Figure 19d).

Size and weight: Heads medium-sized, clusters heavy.

Stem: Acaulescent, thus less investment in woody tissue.

Leaves

Orientation: Ascending-spreading, distichous, becoming drawn together under dry conditions, the distichous orientation preventing full exposure to sunlight in dry, hot weather.

Colour: Green without a powdery bloom, becoming reddish in summer.

Age and persistence: Long-lived, deciduous from the base.

Armament: The smaller, softer, minutely serrulate leaf margins and lack of a bitter substance suggest a reduction in armament (mechanical and chemical) as a direct result of the reduction in herbivory.

Sexual reproduction

Inflorescence and flowers: Young inflorescence curving upwards as it matures, presenting the raceme(s) in the typical erect position.

Fruit/Seed

Size: Seed 7×4 mm, an ideal size for establishment in crevices.

Dispersal: Light, angular seeds shaken from the capsules and dispersed by wind.

Time: Seeds dispersed in summer and autumn, ready for the early autumn rains. Germination in about 14–21 days.

Vegetative reproduction: *Aloe haemanthifolia* is prolific from the base, forming dense clusters. The continual renewal of shoots (suckering from the base) is a sufficient vegetative backup dispersal strategy for the harsh cliff-face environment.

CONSERVATION STATUS

Aloe haemanthifolia has a fairly limited distribution but is often locally abundant and therefore not threatened (Hilton-Taylor 1996).

ADDITIONAL NOTES

Horticulture: Best grown in warm temperate to cool fynbos gardens. Although seeds germinate easily, plants do not do well in a warm climate or in rich alkaline soil. They prefer mineral-poor, acid soil, a well-drained environment and cool conditions. Grown from seed, they take several years before flowering.

VOUCHER

Van Jaarsveld 16291 (NBG).

ILLUSTRATIONS AND MAP

Figures 19a–19d, Map 19.

20. *Aloe hardyi* Glen in *The Flowering Plants of Africa* 49: t. 1942 (1987).

Cremonophyte growth form: Cluster-forming, pendulous, branched, capitate, leafy (heavy, cliff hanger).

Growth form formula: E:F:P:R:C:Ar (vb) (eg)

Etymology: After Mr David Hardy (1931–1998), horticulturist at the former Botanical Research Institute in Pretoria.

DESCRIPTION AND HABITAT

Plants fast-growing, forming loose pendulous clusters, branched from base, with elongated stems up to 1 m long, occasionally solitary. Roots terete, up to 6 mm in diameter, dividing to form a network. Leaves in apical rosettes, deciduous towards base, up to 400–700 × 50–80 mm, flaccid and pendulous or curving down, becoming slightly spreading in rainy season, inwardly curved and becoming drawn together at apex; epidermis glaucous, with powdery bloom, reddish in dry season or during prolonged droughts. Juvenile leaves remaining distichous for up to 3 years. Inflorescence conspicuous, simple, pendulous, recurved, 450–700 mm long; racemes up to 200 mm long, conical. Perianth subpendulous, orange-red, green-tipped, 25–40 × 7 mm. Fruiting capsule ascending-spreading, 25 × 7 mm. Seeds angular, 3 × 2 mm, grey, about 55–70 per capsule.

Phenology: Flowering mainly in midwinter (July). Seeds dispersed by wind in early spring (end of September), just before the spring rains.

Pollinators: Sunbirds.

Habitat and aspect: Vertical cliffs on exposed northern and northwestern aspects, but also on southern and eastern slopes. Plants firmly rooted in crevices large enough to support the roots and stem clusters. Temperature is extremely high, especially on north-facing aspects in summer (35–45°C). Winters are mild and frost is absent. The average daily maximum temperature is about 28°C and the average daily minimum about 14°C. Rainfall occurs mainly in summer, 300–400 mm (thunder showers, October–May).

Altitude: 850–1350 m.

Associated vegetation: Origstad Mountain Bushveld of the Savanna Biome (Mucina *et al.* 2005).

Associated cremnophytes: Opportunistic species such as *Aloe sessiliflora*, *Commiphora marlothii*, *Euphorbia lydenburgensis*, *E. tirucalli*, *Ficus abutilifolia*, *Sarcostemma viminale*, *Sterculia rogersiae* and *Vellozia* sp.

Geology: Dolomite (dark-coloured and rough-textured), Chuniespoort Formation, Malmani Subgroup (Transvaal Supergroup). The rock is dark in colour and rough, with many ledges, fissures and crevices, ideal for establishment of plants.

DISTRIBUTION

Aloe hardyi is a dolomite endemic, confined to the Olifants River Valley between the Strydom Tunnel and Penge Asbestos Mine in the Limpopo Province and adjacent territory of the same geological formation.

RELATED SPECIES

Aloe hardyi belongs to series *Arborescens* and its closest relative is *A. arborescens*, a much-branched, rounded, shrubby species up to 1.5 m tall, from the nearby Drakensberg escarpment mountains. *Aloe hardyi* is also related to *A. mutabilis*, the latter another shrubby, branched cremnophyte with larger open heads. Apart from a slightly smaller size and the few pendulous branches of *A. hardyi*, the leaves in the apical rosette are drawn together, with a much more conspicuous powdery bloom and more glaucous appearance. The leaves of young plants of *A. hardyi* remain distichous for up to three years, but rapidly become rosulate in *A. arborescens*. The adult leaves of *A. hardyi* are furthermore flaccid and become pendent but remain sturdy in *A. arborescens* and *A. mutabilis*. Some forms of *A. arborescens* are glaucous, but not to the same extent as *A. hardyi*. Although some clones of *A. hardyi* are prolific from the base, others remain solitary.

ADAPTATIONS TO THE CLIFF ENVIRONMENT

Habit: Plants with drooping stems and soft, flaccid leaves; even when grown in cultivation this habit is retained. *Aloe hardyi* is a rapid summer grower and long-lived perennial.

Size and weight: Heads medium-sized to large, heavy.

Stem: Branches grey, pendulous, fibrous and strong, thus less investment in woody tissue.

Leaves

Orientation: Apart from curving down (positively geotropic), the leaves are drawn together in the apical rosette, becoming slightly spreading only in the rainy season, an adaptation to the extreme heat generated by the dark dolomitic rocks.

Colour: Glaucous (reflecting the light), with powdery bloom, becoming drawn together in the dry season and with a protective reddish coloration typical of most succulent plants under sunny conditions and water stress.

Age and persistence: Becoming deciduous from the base, resulting in apical rosettes. The large heads and stature can cope better with heat exposure in general and with the very warm conditions in lowveld savanna in summer.

Armament: The teeth on the leaf margins are soft, suggesting a reduction in armament as a direct result of the reduction in herbivory.

Sexual reproduction

Inflorescence and flowers: Young inflorescence drooping but curving up as it matures, presenting the raceme(s) in the typical erect position.

Fruit/Seed

Size: Seed 3×2 mm, an ideal size for establishment in crevices.

Dispersal: Light, angular seeds shaken from the capsules and dispersed by wind.

Time: Seeds dispersed in spring, coinciding with the start of the rainy season. Germination within 14–21 days.

Vegetative reproduction: Stems of *Aloe hardyi* root when finding a new crevice and fallen branches will also root when wedged in a suitable crevice. The continual renewal of shoots of some prolific clones and the rooting of stems in new crevices by extended growth represent a sufficient vegetative backup dispersal strategy for the harsh cliff-face environment.

CONSERVATION STATUS

Although classified as rare (Raimondo *et al.* 2009), it is not threatened owing to the sheer cliff-face habitat.

ADDITIONAL NOTES

Horticulture: Plants easily grown from seed and as specimen pot collections (Van Jaarsveld 2006b, 2010). *Aloe hardyi* is best for dry savanna gardens. Plants thrive with regular feeding

in spring and summer. Although the soil in its native habitat is alkaline, it adapts well to neutral and acidic soils. Some clones are prolific from the base, forming clusters, while others remain solitary. This genetic variability suggests adaptive plasticity. *Aloe hardyi* is prone to fungal crown rot (not in *A. arborescens*). Excellent for balconies, sheer embankments or large hanging baskets. Keep dry in summer.

VOUCHER

Van Jaarsveld 16242 (NBG).

ILLUSTRATIONS AND MAP

Plate 20, Figures 20a–20c, Map 20.

21. *Aloe kouebokkeveldensis* Van Jaarsv. & A.B.Low, in Van Jaarsveld *et al.* in *Aloe* 41,2 & 3: 36–37 (2004a).

Cremonophyte growth form: Solitary rosettes (heavy, cliff squatter).

Growth form formula: A:S:Lper:R:So:La

Etymology: After its habitat, the Cold Bokkeveld (Koue Bokkeveld).

DESCRIPTION AND HABITAT

Plants decumbent to erect, acaulescent; rosettes usually solitary but occasionally dividing to form small groups of up to 3, approximately 0.5–1.0 m in diameter. Mature leaves 12–15, arcuate-ascending to ascending, lanceolate to somewhat acuminate, tapering to an acute, mucronate apex, 400–480 × 100–150 mm, flat above and slightly channelled toward apex, flat to convex below, fleshy and fairly soft in texture, easily bruised; leaf sap colourless, not bitter, becoming sulphur-yellow when dried; margin cartilaginous, with small pinkish white teeth 1 mm long; surface grey-white, often tinged bluish, becoming slightly reddish with drought stress, obscurely striate and irregularly spotted with pale, elongated H-shaped, confluent spots up to 5 mm long. Younger leaves with distinct bluish tinge, densely spotted. Inflorescence a branched corymbose panicle, 1.0–1.4 m tall, branching above the middle; peduncle basally biconvex, becoming subterete, 37 mm wide at base; racemes capitate, 80–100 mm long; bracts thin, scarious, deltoid-acuminate, lower bracts 4 mm wide at base, 8 mm long, distal bracts 2–3 mm wide at base, 5 mm long; pedicels 12–15 mm long. Perianth orange-red, 22–23 mm long, subpendulous, in bud horizontally spreading and slightly curved, base globose, 4–5 mm wide, abruptly narrowing to 3 mm and expanding to 5 mm near apex; outer segments orange, free for 7 mm, 3 mm wide, acute to subacute, apices very pale orange, inner segments free for 8 mm, white with median orange-red stripe, 4 mm wide, spreading, with obtuse apices. Stamens orange, just exerted at mouth. Ovary yellowish green, 6.5 × 3 mm. Style filiform, finally exerted for 3 mm; stigma capitate, minute. Capsules subglobose, 18–20 × 15–18 mm, green, becoming purplish green. Seeds grey-black, winged, 4 × 3 mm.

Phenology: Flowering mainly in spring (November–December). Seeds dispersed by wind in summer in the rainy season.

Pollinators: Sunbirds.

Habitat and aspect: *Aloe kouebokkeveldensis* grows in fully exposed or partially shaded cliff-face habitats, on rocky ledges and in crevices, in shallow soil. It occurs sympatric with *Aloe perfoliata*, which is common in the area. The sandy soil is derived from sandstone and is slightly acid. Summers are dry and hot. The average daily maximum temperature is about 23°C and the average daily minimum about 12°C. Rainfall occurs mainly in winter and ranges from 700–800 mm per annum.

Altitude: 400–600 m.

Associated vegetation: Cederberg Sandstone Fynbos of the Fynbos Biome (Mucina *et al.* 2005).

Associated cremnophytes: *Aloe kouebokkeveldensis* shares its habitat with species such as *Diospyros glabra*, *Dodonaea angustifolia*, *Hymenolepis parviflora*, *Searsia undulata*, *Secamone alpini* and various members of the Restionaceae. Associated succulent species include *Adromischus hemisphaericus*, *Crassula dejecta*, *C. muscosa* var. *muscosa*, *C. rupestris*, *Oscularia lunata* and *Pelargonium alternans*.

Geology: Quartzitic Sandstone of the Table Mountain Group (Cape Supergroup). The rock substrate has many ledges, crevices and fissures and is ideal for establishment of plants.

DISTRIBUTION

Aloe kouebokkeveldensis is confined to the lower southern slopes of the Cold Bokkeveld Mountains southwest of Citrusdal (altitude 600–800 m above sea level) and is known only from a few small populations on north-facing quartzitic sandstone cliffs and steep slopes (Western Cape).

RELATED SPECIES

Aloe kouebokkeveldensis is the sixth member of *Aloe* series *Paniculatae* and the first recorded from fynbos vegetation. Members of the series are characterised by their entire or minutely dentate leaves and subcorymbose panicles, the flowers with a subglobose basal swelling and enlarging towards the throat. *Aloe kouebokkeveldensis* is at once distinguished from other members of this series by a combination of characters, the most conspicuous of these being its large, solitary rosettes of up to 1 m in diameter (occasionally dividing to form small groups) of grey-white, often bluish tinged leaves with elongated, confluent white spots and denticulate margins. Juvenile leaves are densely spotted, soft-textured, with margins that are often wrinkled. The inflorescences grow up to 1.4 m high, making them the largest in the *Paniculatae*. The small orange-red flowers are 22–23 mm long, and are followed by rounded fruiting capsules. A further diagnostic character is the leaf sap, which is not bitter. Plants growing in shade have leaves that are similar in colour to those of *A. reynoldsii*, the easternmost member of this group. *Aloe reynoldsii* occurs in riverine subtropical thicket vegetation and flowers in September and October. *Aloe striata* flowers in August and September and occurs mainly in Nama-Karoo vegetation. It is the most widespread member of the series. *Aloe karasbergensis*, the northernmost species in the group, is confined to Nama-Karoo and Succulent Karoo, but seems to favour winter-rainfall conditions and flowers in January and February. *Aloe buhrii* and *A. komaggasensis* grow in Succulent Karoo along

the western escarpment, their respective flowering periods being October–December and January. The distribution of *A. kouebokkeveldensis* falls between that of *A. buhrii* (Bokkeveld escarpment) in the north and *A. striata* in the east.

ADAPTATIONS TO THE CLIFF ENVIRONMENT

Habit: Large solitary rosettes. A fast winter grower and long-lived perennial with soft leaves.

Size and weight: Heads large and unusual for a general cremnophilous plant, heavy.

Stem: Plants acaulescent or with very short stem.

Leaves

Orientation: Ascending-spreading.

Colour: Grey-whitish green, often bluish tinged, becoming slightly reddish under drought stress, obscurely striate and irregularly spotted with pale, elongated, confluent, H-shaped spots.

Age and persistence: Long-lived, perennial.

Armament: The soft leaves with small teeth suggest a reduction in armament as a direct result of the reduction in herbivory. (*Aloe striata* has grey-white leaves with a smooth, but firm margin.)

Sexual reproduction

Inflorescence and flowers: Orange-red flowers conspicuous on the cliff face, attracting sunbirds.

Fruit/Seed

Size: Seed 4 × 3 mm, an ideal size for establishment in crevices.

Dispersal: Light, grey-black, winged, angular seeds shaken from the capsules and dispersed by wind.

Time: Seeds dispersed from late spring to summer, coinciding with the start of the rainy season. Germination can occur after 14–21 days.

Vegetative reproduction: Heads solitary and without an additional vegetative dispersal strategy. Damaged heads will divide and re-sprout.

CONSERVATION STATUS

Although classified as rare (Raimondo *et al.* 2009), it is not threatened owing to the inaccessible habitat.

ADDITIONAL NOTES

Horticulture: Plants easily grown and best for fynbos and other summer-dry Mediterranean-type gardens (Van Jaarsveld 2006b, 2010). It is best planted on rockeries in full sun. Keep dry in summer and feed annually with compost. It is susceptible to aloe cancer mite, but easily treated with Karba paste painted onto the infected parts. Sow seed in autumn. Plants grow fairly fast and should flower after four years in cultivation.

VOUCHER

Van Jaarsveld & Ems 17744 (NBG).

ILLUSTRATIONS AND MAP

Figures 21a–21c, Map 21.

22. *Aloe meyeri* Van Jaarsv. in *Journal of South African Botany* 47,3: 567–571 (1981a).

Cremonophyte growth form: Cluster-forming, pendulous, leafy, branched (of medium weight to heavy, cliff hanger).

Growth form formula: E:F:P:R:C:Rls (vb) (eg)

Etymology: After Mr Reverend G. Meyer (fl. 1929) who first collected this species in the Richtersveld (Northern Cape).

DESCRIPTION AND HABITAT

Plants slow-growing, long-lived, perennial (from seed 5–7 years), forming loose pendulous clusters, branched from base, with elongated stems up to 1 m long. Roots slightly fleshy. Branches leafy, becoming deciduous only from below or during severe drought. Leaves in an apical rosette up to 260 mm in diameter, spreading in rainy season, inwardly curved, becoming drawn together with a reddish colour in dry season or during prolonged drought, narrowly lanceolate-acuminate, up to 200 mm long, 35 mm in diameter. Inflorescence simple or branched, pendulous, recurved, up to 250 mm long; racemes capitate, not pointed. Flowers subpendent. Perianth orange-red, green-tipped, 20 mm long. Fruiting capsule 9–12 × 4 mm, ascending-spreading. Seeds grey, 3 × 2 mm.

Phenology: Flowering mainly in midsummer and autumn (December–April), but sporadically at other times as well.

Pollinators: Sunbirds.

Habitat and aspect: Vertical quartzitic sandstone cliffs. *Aloe meyeri* grows mainly on exposed northern and northwestern aspects, but also on southern and eastern slopes, the plants firmly rooted in crevices large enough to support the roots and stem clusters. The average daily maximum temperature is about 26°C and the average daily minimum about 14°C. The southern slopes are cooler with shady conditions. Winters are cool and subject to occasional

coastal fog from the west coast; frost is absent. Rainfall occurs mainly from autumn (thunder showers) to spring (cyclonic winter rain), ranging from 75–150 mm per annum.

Altitude: 300–1200 m.

Associated vegetation: Rosyntjieberg Succulent Shrubland of the Succulent Karoo Biome (Mucina *et al.* 2005).

Associated cremnophytes: *Conophytum taylorianum* subsp. *rosynense*, *Othonna cremnophila*, *Trachyandra aridimontana* and *Tylecodon ellaphieae*.

Geology: Quartzitic sandstone of the Rosyntjieberg Formation (Orange River Group). This rock formation has many fissures, ledges and crevices and is ideal for establishment of plants.

DISTRIBUTION

Aloe meyeri is confined to the upper slopes of the Rosyntjieberg and adjacent area of the same geological formation.

RELATED SPECIES

Its closest relative is *Aloe perfoliata* (formerly *A. mitriformis*, *A. comptonii*, *A. distans*), a much larger species from the Western Cape. It differs in a smaller general size of the plants and in armament (teeth small, white), and a lack of the white tubercles on the lower leaf surfaces found on *A. perfoliata*. The flowers are furthermore smaller and green-tipped, in fact the smallest of the subsection *Prolongatae* series *Mitriformis* (to which five species belong, mainly restricted to the winter-rainfall region). *Aloe perfoliata* is also an opportunistic cremnophyte but is usually associated with any quartzitic sandstone or shale outcrop (occasionally on the flats away from rocks), usually confined to exposed sunny positions. Differences with *A. pavelkae* and *A. dabenorisana* are discussed under the first named.

ADAPTATIONS TO THE CLIFF ENVIRONMENT

Habit: Pendent leafy stems and leaves, even when grown in cultivation. *Aloe meyeri* is a slow grower and long-lived perennial with a sturdy leaves.

Size and weight: Compared to related plants in subsection *Prolongatae* (Reynolds 1950), there is a general reduction in size (smallest in the subsection). Its smaller size also allows for more effective anchorage of the rootstock (coping with gravity). Plants of smaller size can cope better with heat absorption under cool growing conditions, a general trend among winter-active succulent plants.

Stem: Branches pendulous, fibrous.

Leaves

Orientation: In apical rosette.

Colour: Glaucous (reflecting light), with powdery bloom, becoming drawn together in the dry season and with a protective reddish coloration typical of most succulent plants under sunny conditions and water stress.

Age and persistence: Persistent and often remaining functional for many years, thus acting as a water resource. Leaves perennial and long-lived (photosynthetically functional), an adaptation to the extremely arid environment, maximising water storage. Replacement of leaves in a poor soil is costly, thus long-term leaves maximising water storage and remaining functional for a long period.

Armament: The smaller teeth on the leaf margins suggest a reduction in armament as a direct result of the reduction in herbivory.

Sexual reproduction

Inflorescence and flowers: Young inflorescence drooping but curving up as it matures, presenting the raceme(s) in the typical erect position.

Fruit/Seed

Size: Seed 3×2 mm, an ideal size for establishment in crevices.

Dispersal: Light, angular seeds shaken from the capsules and dispersed by wind.

Time: Seeds dispersed in autumn, coinciding with the start of the rainy season and period of greatest occurrence of rainfall.

Vegetative reproduction: *Aloe meyeri* is prolific from the base, forming drooping clusters. The stems root when finding a new crevice and fallen branches will also root when wedged in a suitable crevice. The continual renewal of shoots and rooting of stems in new crevices by extended stems represent a sufficient vegetative backup dispersal strategy for the harsh cliff-face environment.

CONSERVATION STATUS

Classified as rare (Hilton-Taylor 1996; Raimondo *et al.* 2009), but it is not threatened owing to its inaccessible cliff-face habitat.

ADDITIONAL NOTES

Horticulture: *Aloe meyeri* is best grown in succulent karoo gardens. It does best on sheer embankments or on a balcony (Van Jaarsveld 2006b). Plants are easily grown from seed or cuttings. It is best grown as a specimen pot collection outside its native habitat (Van Jaarsveld 1981a,b, 2006b, 2010). In moist environments, plants may become prone to fungal crown rot. It does well in a sandy, well-drained soil. Keep dry in summer.

VOUCHER

Van Jaarsveld 6137 (NBG).

ILLUSTRATIONS AND MAP

Plate 22, Figures 22a–22d, Map 22.

23. *Aloe mutabilis* Pillans in South African Gardening and Country Life, July: 168 (1933).

Cremonophyte growth form: Cluster-forming, subpendulous, branched, capitate, leafy (heavy, cliff hanger).

Growth form formula: E:F:P:R:C:Ar (vb)

Etymology: The epithet *mutabilis*, changeable, pertains to the nature of the species.

DESCRIPTION AND HABITAT

Plants fast-growing, caulescent, forming pendulous clusters, branches decumbent, branched from base, with elongated stems up to 1 m long and up to 150 mm in diameter, occasionally solitary. Roots terete, up to 6 mm in diameter, dividing to form a network. Leaves in apical rosettes, deciduous at base of plant, up to 700 × 90 mm, pendulous or curving down, becoming slightly spreading in rainy season, inwardly curved and becoming drawn together at apex; epidermis glaucous, with powdery bloom, reddish in dry season or during prolonged drought. Inflorescence conspicuous, simple, pendulous, recurved, to 1 m long; racemes densely flowered, conical. Perianth subpendulous, buds orange becoming greenish yellow when flower opens, 35 × 7 mm. Fruiting capsule ascending-spreading, 17–25 × 7 mm. Seeds angular, 3 × 2 mm, grey-black.

Phenology: Flowering mainly in midwinter (July). Seeds dispersed by wind in early spring (end of September), just before the spring rains.

Pollinators: Sunbirds.

Habitat and aspect: Mainly north- and northwest-facing cliffs, but also on southern and eastern slopes. Plants are firmly rooted in crevices large enough to support the roots and stem clusters. The average daily maximum temperature is about 24–25°C and the average daily minimum about 8–10°C. Winters are cool, with occasional light frost. Rainfall occurs mainly in summer and ranges from 700–800 mm (thunder showers, October–May).

Altitude: 800–1800 m.

Associated vegetation: Gold Reef Mountain Bushveld and Waterberg Mountain Bushveld of the Central Bushveld Bioregion, Savanna Biome (Mucina *et al.* 2005).

Associated cremonophytes: Opportunistic species such as *Aloe sessiliflora*, *Cotyledon orbiculata*, *Crassula setulosa* var. *jenkinsii*, *C. swaziensis*, *Delosperma vogtsiae*, *Plectranthus ramosior* and *Sterculia rogersiae*.

Geology: Quartzite (Magaliesberg Group, Pretoria Formation of the Transvaal Supergroup), sandstone and conglomerate (Wilge River Formation, Waterberg Group). Substrate has many ledges, crevices and fissures, ideal for establishment of plants.

DISTRIBUTION

Aloe mutabilis is quartzitic sandstone endemic, confined to cliffs in river valleys of Gauteng and Limpopo Province. Plants are commonly found at Chuniespoort near Polokwane.

RELATED SPECIES

Aloe mutabilis is closest to *A. hardyi*, the latter with unicoloured flowers and plants of the latter with positive geotropic growth. *Aloe mutabilis* retains a decumbent habit and has bicoloured flowers.

ADAPTATIONS TO THE CLIFF ENVIRONMENT

Habit: Plants with semidrooping stems and leaves, but mainly due to phenotypic plasticity as this character is not retained in cultivation. It is a rapid summer grower and long-lived perennial.

Size and weight: Heads large, heavy.

Stem: Branches grey, decumbent to subpendulous, fibrous and strong.

Leaves

Orientation: Ascending-spreading.

Colour: Glaucous (reflecting light), with powdery bloom.

Age and persistence: Becoming deciduous from the base, resulting in apical rosettes. The large heads and stature can cope better with heat exposure in general and with the very warm conditions in lowveld savanna in summer.

Armament: The leaves are soft but firm, with small teeth on the margins, suggesting a reduction in armament as a direct result of the reduction in herbivory. (*Aloe arborescens*, a close relative among slopes and boulders, has larger, closely spaced teeth.)

Sexual reproduction

Inflorescence and flowers: Young inflorescence drooping but curving up as it matures, presenting the raceme(s) in the typical erect position.

Fruit/Seed

Size: Seed 3×2 mm, an ideal size for establishment in crevices.

Dispersal: Light, angular seeds shaken from the capsules and dispersed by wind.

Time: Seeds dispersed in spring, coinciding with the start of the rainy season. Germination after 14–21 days.

Vegetative reproduction: *Aloe mutabilis* proliferates from the base, forming semidrooping shrubs. The stems root when finding a new crevice and fallen branches will also root when wedged in a suitable crevice. The continual renewal of vegetative basal shoots and rooting of stems in new crevices by extended stems represent a sufficient vegetative backup dispersal strategy for the harsh cliff-face environment.

CONSERVATION STATUS

Rare, but not threatened (Hilton-Taylor 1996).

ADDITIONAL NOTES

Horticulture: Best suited to bushveld (savanna) gardens (Van Jaarsveld 2010). Plants are easily grown and adaptable. Propagate from cuttings or seed in a sandy mixture. Fairly fast-growing and forming attractive shrubs, flowering in midwinter. It is ideal for steep embankments and larger window sills. An annual dressing of compost will benefit performance.

VOUCHER

Van Jaarsveld & Roux 17204 (NBG).

ILLUSTRATIONS AND MAP

Figures 23a & 23b, Map 23.

24. *Aloe nubigena* Groenew. in *Tydskrif vir Wetenskap en Kuns* 14: 3 (1936).

Cremonophyte growth form: Cluster-forming, pendulous rosettes (light to medium weight, cliff hanger).

Growth form formula: E:F:P:R:C:Ar (vb) (eg)

Etymology: The epithet *nubigena* alludes to its cloud-borne habitat.

DESCRIPTION AND HABITAT

Plants with moderate growth rate to rapid-growing, caulescent, proliferating from base forming small clusters with soft functional leaves produced in apical rosette. Stem horizontal to horizontally pendulous to pendulous, up to 100 mm long, covered with old dried leaf remains. Leaves distichous, linear, pendulous, up to 600 × 20 mm; margin entire to denticulate in some populations, green; surface smooth. Inflorescence a simple spreading to spreading pendulous capitate raceme, up to 210 mm long; pedicels up to 30 mm long. Perianth subpendulous, orange-red, green-tipped, 27 × 7 mm. Fruiting capsule oblong-conical, 20 × 10 mm. Seeds 3 × 1.5 mm, dark brown, angular.

Phenology: Flowering mainly in summer (November–April) and sporadically at other times.

Pollinators: Sunbirds.

Habitat and aspect: Vertical quartzitic sandstone cliffs of the upper eastern escarpment margin. Plants grow firmly rooted in crevices and on ledges large enough to support the roots and stem clusters. The average daily maximum temperature is about 20°C and the average daily minimum about 5°C. It is cool throughout the year, with frequent fog in the summer rainy season. Rainfall occurs mainly in summer, ranging from 1500–2000 mm per annum.

Altitude: 1450–2100 m.

Associated vegetation: Northern Escarpment Quartzite Sourveld of the Grassland Biome (Mucina *et al.* 2005).

Associated cremnophytes: *Aloe arborescens*, *Crassula pellucida* subsp. *alsinoides*, *Drimia robusta*, *Scilla natalensis* and various moss species.

Geology: Quartzitic sandstone (Black Reef Formation, Transvaal Supergroup). Light-textured (grey), rough- to smooth-textured and with many ledges, crevices and fissures, ideal for establishment of plants.

DISTRIBUTION

Aloe nubigena is a quartzitic sandstone endemic of the escarpment mountains near Graskop. It is confined to the moist and well-watered, sheer, east-facing cliffs. Plants are often locally abundant.

RELATED SPECIES

Aloe nubigena comes close to *A. thompsoniae* from the Wolkberg near Pietersburg in Limpopo Province. The latter has open, acaulescent rosettes, often recurved leaves and shorter inflorescences; it grows in a more exposed environment.

ADAPTATIONS TO THE CLIFF ENVIRONMENT

Habit: Plants forming clusters among moss and other cremnophytes occupying smaller crevices and ledges. Where within reach, stems and leaves heavily grazed.

Size and weight: Heads dwarf-sized, light to medium weight.

Stem: Caulescent, grey, spreading, subpendulous to pendulous.

Leaves

Orientation: Distichous, pendulous (positively geotropic), with soft texture and smooth epidermis in response to the moist, mild climate.

Colour: Green.

Age and persistence: Long-lived perennial with medium growth rate, leaves deciduous from the base.

Armament: Plants show variability in leaf armament from completely entire to denticulate in a small region.

Sexual reproduction

Inflorescence and flowers: Young inflorescence curving upwards as it matures, presenting the racemes in the typical erect position.

Fruit/Seed

Size: Seed 3×1.5 mm, an ideal size for establishment in crevices.

Dispersal: Light, angular seeds shaken from the capsules and dispersed by wind.

Time: Seeds dispersed in winter and autumn, ready for the early spring and summer rains. Germination in about 14–21 days.

Vegetative reproduction: *Aloe nubigena* is prolific from the base, forming small, drooping clusters. The stems root when finding a new crevice and fallen branches will also root when wedged in a suitable crevice. The continual renewal of shoots and rooting of stems in new crevices by extended stems represent a sufficient vegetative backup dispersal strategy for the harsh cliff-face environment.

CONSERVATION STATUS

Although limited in distribution, it is often locally abundant and therefore not threatened.

ADDITIONAL NOTES

Horticulture: Best grown in afroalpine or summer-rainfall grassland gardens in a slightly acid peat and sand mixture. Feed regularly in spring and summer. Easy to grow, with a moderate growth rate. Away from its habitat it is best kept in a greenhouse and kept moist and cool in the summer months (Van Jaarsveld 2006b). Plants are prolific from the base, soon becoming cluster-forming.

VOUCHER

Van Jaarsveld 16215 (NBG).

ILLUSTRATIONS AND MAP

Plate 24, Figures 24a–24d, Map 24.

25. *Aloe omavandae* Van Jaarsv., in Van Jaarsveld & Van Wyk in *Haseltonia* 10: 41–43 (2004b).

Cremonophyte life form: Solitary pendulous apical rosettes (heavy, cliff hanger).

Growth form formula: E:F:P:R:C:Ar (vb) (eg)

Etymology: After Omavanda, the eastern part of the Baynes Mountains in the Kaokoveld, northern Namibia.

DESCRIPTION AND HABITAT

Plants cremnophilous, usually solitary and pendent, weighing up to 4.5 kg when adult, stems up to 220 mm long, 35–55 mm thick; bark grey. Roots grey-brown, 3–4 mm thick. Leaves numerous (up to 25 functional), in a dense rosette, arcuate-pendent and becoming mitriform in dry season, triangular-lanceolate, 300–470 mm long, 65–85 mm in diameter at base; upper surface flat but becoming channelled in distal half, pale green to grey-green fading to pinkish green, sparsely white-spotted in basal third, lenticular spots irregularly arranged, lower surface flat to slightly convex at first, becoming convex and shortly keeled toward apex, copiously white-spotted, with the lenticular spots arranged in obscure white bands; margin armed with small, deltoid-acuminate, reddish brown teeth 1–1.5 mm long, 10–15 mm apart, projecting towards leaf apex and arising from the white cartilaginous margin; apex acute, mucronate. Inflorescence 1 or 2 per plant, 500–700 mm long, pendent, with 2–4 lateral branches in upper half, simple in young plants; racemes 250–300 mm long; scape biconvex, 300–450 mm long, purplish, 10–15 mm in diameter at base, with powdery bloom, flattened and marginiform at base for 30–70 mm; pedicels 8–10 mm long, lengthening to 12–14 mm in fruit; bracts 12 × 3 mm, ascending, navicular, linear-lanceolate, acuminate, whitish, thin, scarious, channelled. Perianth orange-red, grey-tipped in bud, cylindrical-trigonal, subclavate, 23–25 mm long, 5 mm in diameter. Capsule erect, 10–15 × 6–10 mm. Seeds angular, winged, grey-black, 3 × 2 mm.

Phenology: Flowering mainly in winter (May–June).

Pollinators: Sunbirds.

Habitat and aspect: Sandstone cliffs of the eastern, western and southern margin of the Omavanda plateau. Plants of *Aloe omavandae* grow firmly wedged in crevices and the rosette becomes pendent from a young age. The plants are often locally abundant, but are always restricted to inaccessible places. The vegetation in the region below is arid mopane savanna, with several species of *Commiphora* prominent. Summers are hot, winters mild and without frost. Rainfall mainly in summer, ranging from 300–500 mm per annum.

Altitude: 1600–1900 m.

Associated vegetation: Arid savanna. The vegetation at the top of the Omavanda escarpment adjacent to the cliffs consists of *Albizia antunesiana*, *A. tanganyicensis*, *Combretum apiculatum*, *C. zeyheri*, *Entandrophragma spicatum*, *Kirkia acuminata* and *Mundulea sericea*.

Associated cremnophytes: Associated succulent plants include *Cotyledon orbiculata*, *Sarcostemma viminalis* and *Kalanchoe lanceolata*. Other non-succulent cremnophilous plants on these cliffs include *Ficus bubu*, *F. glumosa*, *F. ilicina* and *Petalidium coccineum*. On wider ledges species such as *Cussonia angolensis*, *Nicotiana africana* and *Nuxia congesta* are encountered.

Geology: Sandstone of the Damara Sequence (Simplified Geological Map of Namibia, Geological Survey of Namibia 1980). Its substrate has many ledges, crevices and fissures and is ideal for establishment of plants.

DISTRIBUTION

Aloe omavandae is endemic to the eastern Baynes Mountains of the Kaokoveld, northern Namibia. It is restricted to sandstone cliffs of the escarpment margin, from just west of Epupa Falls in the north to Omavanda in the south and to Slangpoort in the west.

RELATED SPECIES

Aloe omavandae is at once distinguished by its pendent, solitary rosettes of grey-green, pendent, spreading leaves densely white-spotted on the upper surface and less so on the lower surface. The leaf margin is armed with deltoid-acuminate, small, reddish brown teeth and the pendent, branched inflorescence bears arcuate-ascending racemes of orange-red flowers 23–25 mm long. It is most closely related to *A. esculenta* from northeastern Namibia, grows on flat terrain. The latter has a prolific nature, forming dense groups. *Aloe esculenta* is at once distinguished by its erect growth and much larger teeth and paniculate inflorescences. It is also related to *A. corallina*, also a cremnophilous taxon with pendent leaf rosettes and whitish green leaves that are not spotted. *Aloe corallina* is confined to dolomite cliffs of the Otjihipa Mountains (western parts of the Baynes Mountains below altitudes of 1000 m). *Aloe corallina* proliferates from the base, forming small groups with firm, narrower, glaucous, acuminate, falcate leaves, almost without teeth and without any white spots. Its flowers are similar to those of *Aloe omavandae*, but larger (30–32 mm long). In vegetative characters, the leaves of *A. omavandae* reminds one of the widespread *A. littoralis* but here the resemblance ends, as *A. littoralis* is a much larger, robust, erect plant with different, larger teeth on the leaf margins and different floral features. It can also be related to *A. esculenta*, which has similar spotted leaves and is commonly found in Ovamboland, the latter an ascending species with short stems forming dense clusters (on flat terrain).

ADAPTATIONS TO THE CLIFF ENVIRONMENT

Habit: Plants with medium-sized caulescent heads, occupying larger crevices and ledges. With medium growth rate, plants long-lived perennials.

Size and weight: Heads medium-sized, becoming heavy.

Stem: Caulescent, grey, pendulous and thus less investment in woody tissue.

Leaves

Orientation: Distinctly incurved, pendulous (positively geotropic). Texture firm, but smooth.

Colour: Green to grey-green, fading to pinkish green, sparsely white-spotted in basal third, the lenticular spots irregularly arranged; lower surface flat to slightly convex at first, becoming convex and shortly keeled toward apex. The grey-green colour deflects the rays of the sun, an adaptation to the bright sunlight.

Age and persistence: Long-lived, deciduous from the base.

Armament: Leaf margin armed with small, deltoid-acuminate, reddish brown teeth 1.0–1.5 mm long, 10–15 mm distant, projecting towards the leaf apex and arising from the white, cartilaginous margin; apex acute, mucronate. The teeth are larger in young plants, becoming smaller with age, perhaps an indication that its ancestors were probably not obligate cremnohytes and had larger teeth.

Sexual reproduction

Inflorescence and flowers: Young inflorescence curving upwards as it matures, presenting the racemes in the typical erect position.

Fruit/Seed

Size: Seed 3 × 2 mm.

Dispersal: Light, grey-black, angular, winged seeds shaken from the capsules and dispersed by wind.

Time: Seeds dispersed in winter and autumn, ready for the early spring and summer rains. Germination in about 14–21 days.

Vegetative reproduction: Usually with solitary drooping heads but damaged heads will re-sprout. Plants occasionally sprout from basal stolons. The stems root when finding a new crevice and fallen branches will also root when wedged in a suitable crevice. This acts as a sufficient vegetative backup dispersal strategy for the harsh cliff-face environment.

CONSERVATION STATUS

Aloe omavandae is restricted to the Omavanda Plateau, but it is locally abundant on the cliffs and therefore not threatened.

ADDITIONAL NOTES

Horticulture: *Aloe omavandae* is best for dry, sunny subtropical bushveld (savanna) gardens (Van Jaarsveld 2010). Keep dry during its resting phase in winter. An easily grown species, but outside its habitat it is best grown in a greenhouse where environmental conditions can be controlled. Plants react well to summer feeding with an organic fertiliser. Propagate from seed sown in spring or summer. Ideal for steep embankments (Van Jaarsveld *et al.* 2005a; Van Jaarsveld 2006b).

VOUCHER

Van Jaarsveld 17480 (NBG).

ILLUSTRATIONS AND MAP

Plate 25, Figures 25a & 25b, Map 25.

26. *Aloe pavelkae* Van Jaarsv., Swanepoel, A.E.van Wyk & Lavranos in *Aloe* 44,3: 75 (2007).

Cremonophyte growth form: Cluster-forming, pendulous, leafy, branched (heavy, cliff hanger).

Growth form formula: E:F:P:R:C:Ar (vb) (eg)

Etymology: After Mr Petr Pavelka who discovered this species on the Sonberg in southern Namibia.

DESCRIPTION AND HABITAT

Plants slow-growing, long-lived, perennial, forming loose pendulous clusters with up to 8 heads, branched from base, with elongated stems up to 1.5 m long. Roots slightly fleshy. Branches with persistent dry leaves, leaf bases becoming deciduous towards base of stem. Leaves in apical rosette up to 350–400 mm in diameter, spreading in rainy season, inwardly curved and becoming drawn together and reddish in dry season or during prolonged drought; 18–28 × 25–70 mm, linear-lanceolate, green, faintly striate; adaxial surface flat, channelled towards apex, abaxial surface convex; margin cartilaginous, white, serrate, teeth 1.5 × 1.5 mm, projected towards apex, 4–8 mm apart; apex acute. Inflorescence simple, rarely branched, up to 240–320 mm long, pendulous for 170–200 mm then recurved to erect position; scape biconvex at base, 6–8 mm in diameter, up to 180–220 long; raceme capitate, not pointed, 45–90 mm long; pedicels ascending-spreading, 20–28 mm long. Flowers subpendent, in a dense capitate raceme. Perianth orange-red, green-tipped, 20 mm long. Fruiting capsule 15–18 × 6–7 mm, ascending-spreading. Seeds blackish grey, 3.5 × 2 mm.

Phenology: Flowering mainly in midwinter (July–August).

Pollinators: Sunbirds.

Habitat and aspect: Vertical quartzitic sandstone cliffs. Plants are firmly rooted in crevices large enough to support the roots and stem clusters, mainly on southern and eastern aspects. The southern slopes are cooler, with shady conditions. Temperatures high during the day and the average daily summer temperature is about 26°C. Winters are cooler and are subject to regular coastal fog from the west coast; frost is absent. Rainfall occurs mainly from autumn (thunder showers) to spring (cyclonic winter rain), ranging from about 50–125 mm per annum.

Altitude: 700–800 m.

Associated vegetation: Succulent Karoo.

Associated cremonophytes: *Conophytum ricardianum*, *Crassula macowaniana*, *C. pseudohemisphaerica*, *C. sericea* var. *velutina*, *C. sladenii*, *Tylecodon bruynsii*, *T. buchholzianus* *T. racemosus* and *T. rubrovenosus*.

Geology: Sandstone of the Kuibis and Schwarzrand Subgroups (Nama Group). The cliff substrate is rough, with many ledges crevices and fissures, ideal for establishment of plants.

DISTRIBUTION

Aloe pavelkae is confined to the upper slopes of the southern mountain range adjacent to the Orange River and adjacent territory of the same geological formation. It mainly includes the Sonberg and Kuamsibberg.

RELATED SPECIES

Aloe pavelkae is related to both *A. meyeri*, a Rosyntjieberg endemic, and *A. dabenorisana* from the Dabenoris and Pellaberg along the South African side of the lower Orange River. It differs from *A. meyeri* in its larger rosettes, green leaves that are not biconvex and only the apical rosette with functional leaves. *Aloe meyeri* is smaller, with glaucous leaves that remain functional over a considerable part of the stem (leafy stems), and flowers in January and February. *Aloe dabenorisana* has similar green leaves but they are distinctly recurved.

ADAPTATIONS TO THE CLIFF ENVIRONMENT

Habit: Pendent, leafy stems and leaves, which it retains even when grown in cultivation. It is a slow grower and long-lived perennial.

Size and weight: There is a slight reduction in size compared to *Aloe perfoliata*, allowing for better anchorage of the rootstock (and coping with gravity). The smaller size also enables the plants to cope better with heat absorption under cool growing conditions, a general trend among winter-active succulents.

Stem: Pendulous, covered with old leaf remains, thus insulated from direct sunlight.

Leaves

Orientation: Apically produced in rosettes.

Colour: Green, without a powdery bloom, becoming drawn together in the dry season and with a protective reddish coloration as a result of the production of anthocyanins, typical of most succulent plants under sunny conditions and water stress.

Age and persistence: Fairly long-lived, becoming deciduous from the base.

Armament: The small teeth on the leaf margins suggest a reduction in armament as a direct result of the reduction in herbivory.

Sexual reproduction

Inflorescence and flowers: Young inflorescence drooping but curving up as it matures, presenting the raceme(s) in the typical erect position.

Fruit/Seed

Size: Seed 3.5×2 mm, an ideal size for establishment in crevices.

Dispersal: Light, angular seeds shaken from the capsules and dispersed by wind.

Time: Seeds dispersed in autumn, coinciding with the start of the rainy season and period of greatest occurrence of rainfall.

Vegetative reproduction: *Aloe pavelkae* is prolific from the base, forming drooping clusters. The stems root when finding a new crevice and fallen branches will also root when wedged in a suitable crevice. The continual renewal of shoots and rooting of stems in new crevices by extended stems represent a sufficient vegetative backup dispersal strategy for the harsh cliff-face environment.

CONSERVATION STATUS

Rare, but not threatened.

ADDITIONAL NOTES

Horticulture: Best grown in succulent karoo gardens. It thrives on sheer embankments or balconies. Plants easily grown from seed or cuttings, and as specimen pot collections outside the native habitat. When grown outside its natural habitat it may become prone to fungal crown rot. Does well in a sandy, well-drained soil. Keep dry in summer.

VOUCHER

Van Jaarsveld 19919 (NBG).

ILLUSTRATIONS AND MAP

Plate 26, Figures 26a–26d, Map 26.

27. *Aloe pictifolia* D.S.Hardy in *Bothalia* 12: 62 (1976).

Cremonophyte growth form: Dwarf-sized globose cluster (of medium weight, cliff squatter).

Growth form formula: A:S:Lper:R:C:La (vb)

Etymology: Latin *picti*, painted, and *folium*, leaf.

DESCRIPTION AND HABITAT

Plants dividing to form small clusters of up to 7 heads and up to 200 mm in diameter. Branches short, pendulous to erect. Leaves at first distichous, becoming rosulate, 80–150 × 10–20 mm, linear-lanceolate, incurved when grown erect, becoming recurved when pendulous, greyish green, becoming reddish green with drought stress, densely white-spotted; margin dentate; teeth small, reddish; apex acute, mucronate. Inflorescence an erectly spreading raceme, up to 350 mm long. Perianth 16 mm long, reddish pink, with yellow throat. Capsules 15 × 6 mm long, mostly pendulous to spreading. Seeds angular, grey-black, up to 4 × 2 mm.

Phenology: Flowering in winter and spring (October–November), but sporadically at other times as well. Seed wind-dispersed.

Pollinators: Sunbirds.

Habitat and aspect: Sandstone cliffs (all aspects) overlooking the Kouga River. The average daily maximum temperature is about 25°C and the average daily minimum about 10°C. Winters are cooler, but frost is a rarity or absent. Rainfall occurs in winter and summer, ranging from 400–500 mm per annum.

Altitude: 250–500 m.

Associated vegetation: Gamtoos Thicket of the Albany Thicket Biome (Mucina *et al.* 2005).

Associated cremnophytes: *Adromischus cristatus* var. *zeyheri*, *Cotyledon tomentosa* subsp. *tomentosa*, *Crassula rupestris* subsp. *rupestris* ‘Kouga form’, *Cyrtanthus flammosus*, *C. montanus*, *Gasteria glomerata*, *Haworthia gracilis* var. *picturata*, *H. viscosa*, *Othonna lobata* and *Plectranthus verticillatus*.

Geology: Quartzitic sandstone (light-coloured and smooth-textured), Peninsula Formation (Cape Supergroup). The cliff substrate has many ledges, crevices and fissures, ideal for establishment of plants.

DISTRIBUTION

Aloe pictifolia is restricted to cliff faces of the Kouga Dam and adjacent Baviaanskloof near Hankey in the Eastern Cape.

RELATED SPECIES

Aloe pictifolia is related to *A. humilis*, a non-cremnophilous species. The latter is a dense, cluster-forming species with grey leaves. It also superficially resembles *A. microstigma*, also a non-cremnophilous species, but much larger. The latter has ascending to incurved leaves, occurring in thicket and succulent karoo vegetation.

ADAPTATIONS TO THE CLIFF ENVIRONMENT

Habit: Conspicuous rounded clusters. Its small size allows effective heat absorption and establishment in small crevices, the plants thus also coping better with gravity. In the dry season, the leaves become dorsiventrally flattened and reddish. This improves the ability of the plants to survive. The plants’ investment in vegetative output (dividing of heads) further enhances occupation of crevices and ultimate survival.

Size and weight: Heads small, of medium weight.

Leaves

Orientation: Adjustable compared to all other aloes. Becoming incurved when growing in full sun, but becoming distinctly recurved and often recurved-falcate in shady crevices (southern and sometimes east-facing slopes) and under overhangs, maximising absorption

of light. This character is retained in cultivation and can be viewed as an adaptation to the variable cliff-face environment.

Succulence: When turgid, the leaves are very fleshy and often biconvex, an adaptation to the dry vertical habitat.

Colour: Grey-green to grey-white, densely spotted, becoming reddish during dry periods as the plants aestivate, blocking out excessive light and reducing photosynthesis. The conspicuous white spotting is perhaps derived from a past camouflage character, now possibly an effective light-regulating tool and an adaptation to the cliff environment in the absence of herbivory.

Presentation: Conspicuous clusters.

Age and persistence: Plants long-lived, with leaves withering from the base.

Armament: The leaf margin is armed with small reddish teeth, much smaller than those of its flat-ground relative, this reduction in armament probably in response to the undisturbed cliff habitat in contrast to the often thorny but grazed surrounding thicket and succulent karoo vegetation.

Sexual reproduction

Inflorescence and flowers: Inflorescence ascending; flowers with conspicuous red-pink perianth.

Fruit/Seed

Size: Seed 4×2 mm, an ideal size for establishment in crevices.

Dispersal: Seed wind-dispersed as in other aloes.

Time: Seeds ripening in spring and summer, coinciding with the rainy season. Germination within 14–21 days.

Vegetative reproduction: Plants divide, forming small, dense clusters. Stems root when finding a new crevice and fallen branches also when wedged in a suitable crevice. Continual dichotomous division of heads, the renewal of shoots and rooting of stems in new crevices by extended stems represent a sufficient vegetative backup dispersal strategy for the harsh cliff-face environment.

CONSERVATION STATUS

Aloe pictifolia has been classified as rare (Raimondo *et al.* 2009). In spite of its localised distribution, it is not threatened by collectors, and seed from a cultivated source has been distributed to nurseries and botanical gardens in various parts of the world.

ADDITIONAL NOTES

Horticulture: Best grown in thicket gardens (Van Jaarsveld 2010). It is an easy grower, propagated by division or from seed and thrives in small containers. This ease of cultivation

suggests a maximum survival reproductive output. Outside its native habitat it is best grown as a container subject under controlled environmental conditions in a greenhouse.

VOUCHER

Van Jaarsveld 11046 (NBG).

ILLUSTRATIONS AND MAP

Plate 27, Figures 27a–27d, Map 27.

28. *Aloe reynoldsii* Letty in *The Flowering Plants of South Africa* 14: t. 558 (1934).

Cremnophyte growth form: Cluster-forming (of medium weight to heavy, cliff squatter).

Growth form formula: A:S:Lper:R:C:La (vb)

Etymology: After Dr G.W. Reynolds (1895–1967), author of *The aloes of South Africa*, first published in 1950.

DESCRIPTION AND HABITAT

Plants rosulate, with moderate growth rate, almost acaulescent, dividing to form rounded clusters with up to 12 heads and up to 0.75 m in diameter, occasionally solitary. Roots terete. Stem up to 50 mm in diameter. Leaves ovate-lanceolate, acuminate, deciduous towards base of plant, up to 350 × 110 mm, spreading; epidermis glaucous, mottled; margin crenulate, with pinkish border. Inflorescence conspicuous, branched, a subcorymbose panicle, up to 600 mm high; racemes subcapitate. Perianth subpendulous, yellow, 28 × 7 mm. Fruiting capsule ascending-spreading, 22 × 10 mm. Seeds angular, 3 × 2 mm, grey.

Phenology: Flowering mainly in spring (September–October). Seeds dispersed by wind in summer in the rainy season.

Pollinators: Sunbirds.

Habitat and aspect: Shale and mudstone cliffs, on exposed northern and northwestern aspects, but also on southern and eastern slopes. Plants grow firmly rooted in crevices large enough to support the roots and stem clusters. Temperatures are high in summer, but mild in winter, the southern slopes cooler, with shady conditions. The average daily maximum temperature is about 20°C and the average daily minimum about 12°C. Rainfall occurs mainly in summer and ranges from 800–250 mm per annum (thunder showers from October–May).

Altitude: 150–1000 m.

Associated vegetation: Eastern Valley Bushveld of the Albany Thicket Biome (Mucina *et al.* 2005).

Associated cremnophytes: *Albuca batteniana*, *Aptenia cordifolia*, *Bulbine natalensis*, *Cotyledon orbiculata*, *Crassula cordata*, *C. lactea*, *C. perfoliata* var. *minor*, *C. perforata*,

Delosperma sp., *Drimia anomala*, *Haworthia cymbiformis*, *Ornithogalum longibracteatum* and a species of *Trichodiadema*.

Geology: Sandstone and mudstone of the Emakwezini Formation (Beaufort Group) of the Karoo Supergroup. Substrate has many ledges, crevices and fissures and ideal for establishment of plants.

DISTRIBUTION

Aloe reynoldsii is endemic to the dry Bashee River Valley, from Collywobbles in the north to near the river mouth at the coast.

RELATED SPECIES

Aloe reynoldsii is closest to *A. striata* from the southern Great Karoo regions. It differs from that species in its prolific dividing nature, smaller rosettes and softer, slightly mottled leaves.

ADAPTATIONS TO THE CLIFF ENVIRONMENT

Habit: Plants forming rounded clusters, a medium summer grower and long-lived perennial with soft leaves.

Size and weight: Heads medium-sized, a reduction in size compared to non-cremnophilous members of this group.

Stem: Branches grey, fibrous and strong, thus less investment in woody tissue.

Leaves

Orientation: Spreading to recurved.

Colour: Glaucous (reflecting light) and mottled.

Age and persistence: Becoming deciduous from the base, resulting in apical rosettes. The medium-sized heads and stature can cope better with heat exposure in general and with the very warm conditions in river valley thicket in summer.

Armament: The softer leaves with small teeth suggest a reduction in armament as a direct result of the reduction in herbivory. (*Aloe striata*, its closest relative, has grey-white leaves with a smooth but firm margin.)

Sexual reproduction

Inflorescence and flowers: Yellow flowers conspicuous on the cliff face, attracting sunbirds.

Fruit/Seed

Size: Seed 3×2 mm, an ideal size for establishment in crevices.

Dispersal: Light, angular seeds shaken from the capsules and dispersed by wind.

Time: Seeds dispersed from late spring to summer, coinciding with the start of the rainy season. Germination within 14–21 days.

Vegetative reproduction: *Aloe reynoldsii* divides, forming small, dense clusters. The stems root when finding a new crevice and fallen branches will also root when wedged in a suitable crevice. The continual dichotomous division of the heads, renewal of shoots and rooting of stems in new crevices by extended stems represent a sufficient vegetative backup dispersal strategy for the harsh cliff-face environment.

CONSERVATION STATUS

Rare, but not threatened (Hilton-Taylor 1996; Raimondo *et al.* 2009).

ADDITIONAL NOTES

Horticulture: *Aloe reynoldsii* is the easiest to grow of the five *Aloe* species belonging to series *Paniculatae* and widely adaptable in cultivation. It is best grown in thicket gardens (Van Jaarsveld 2010). It is easily propagated by division or from seed and does well in containers. This ease of cultivation suggests a maximum survival reproductive output. Outside its native habitat, in a colder climate, it is best grown as a container subject under controlled environmental conditions in a greenhouse.

VOUCHER

Van Jaarsveld 16907 (NBG).

ILLUSTRATIONS AND MAP

Plate 28, Figures 28a–28c, Map 28.

29. *Aloe soutpansbergensis* I. Verd. in *The Flowering Plants of Africa* 34: t. 1391 (1962).

Cremonophyte growth form: Cluster-forming, pendulous rosettes (of light weight, cliff hanger).

Growth form formula: S:Lper:R:C:Lp (vb) (eg)

Etymology: After the Soutpansberg, its habitat in the Limpopo Province.

DESCRIPTION AND HABITAT

Plants rapid-growing, shortly caulescent, proliferating from base, forming clusters up to 300 mm in diameter, bearing soft flaccid leaves. Stem horizontal to horizontally pendulous to pendulous, up to 50 mm long, covered with old dried leaf remains. Leaves at first distichous, becoming rosulate (up to 7), linear, pendulous, 120–460 × 7–9 mm, softly succulent; surface smooth, adaxial side flat to grooved, abaxial surface convex, purplish, spotted towards base; margin denticulate, green. Inflorescence simple, ascending-spreading, up to 200–380 mm

long; raceme 70–110 mm long, subcapitate, horizontally presented, flowers subsecundly and also horizontally presented, becoming subpendent; pedicels 15–20 mm long; bracts 25×12 , whitish, acuminate, conspicuous, enclosing pedicels at first (longer than pedicels). Perianth orange-red, pale white-tipped, 27–32 mm long, broadest at base (7–8 mm in diameter), tapering to 4 mm wide close to apex, lobe apices becoming recurved. Fruiting capsule oblong-conical, 20×10 mm. Seeds small, grey-black.

Phenology: Flowering mainly in summer (December–February).

Pollinators: Sunbirds.

Habitat and aspect: Quartzitic sandstone cliffs, mainly on eastern and southern aspects. Plants are firmly rooted in crevices and on ledges large enough to support the roots and stem clusters. The temperature is moderate in summer, often cool with frequent fog, but with dry, cool winters. Rainfall occurs mainly in summer, ranging from 1500–2000 mm per annum.

Altitude: 1525–1750 m.

Associated vegetation: Soutpansberg Summit Sourveld (Mucina *et al.* 2005).

Associated cremnophytes: *Aloe arborescens*, *Cotyledon barbeyi*, *Crassula pellucida* subsp. *alsinoides*, *C. setulosa*, *C. swaziensis* and *Thorncroftia succulenta*.

Geology: Quartzitic sandstone of the Wyllies Poort Formation (Soutpansberg Group). The sandstone rock substrate has many ledges, crevices and fissures and is ideal for establishment of plants.

DISTRIBUTION

Aloe soutpansbergensis is a quartzitic sandstone endemic of the Soutpansberg near Makhado in the Limpopo Province. Plants are often locally abundant.

RELATED SPECIES

The horizontally presented racemes and forward projected flowers are unique among the South African and Namibian cremnophilous aloes. The tapering perianth, 7–8 mm at the base and tapering to 4 mm, is also unique. *Aloe soutpansbergensis* is related to *A. challisii* and *A. nubigena*, the latter with ascending racemes, pendent flowers, and in *A. nubigena* the leaves usually remain distichous (often with an entire margin). *Aloe challisii* has almost terete, bluish green leaves with epinastic growth, resulting in the down-curving leaves. Differs from *A. woolliana* in its flaccid leaves and stems, probably an adaptation to its sheer cliff-face environment.

ADAPTATIONS TO THE CLIFF ENVIRONMENT

Habit: Plants forming clusters among moss and other cremnophytes occupying smaller crevices and ledges. Where within reach, stems and leaves are heavily grazed.

Size and weight: Heads small, of light weight.

Stem: Shortly caulescent, grey, spreading, subpendulous to pendulous.

Leaves

Orientation: Distichous at first, becoming rosulate and pendulous (positively geotropic), channelled.

Colour: Green, purplish at the base.

Age and persistence: Fairly fast grower and long-lived perennial, with leaves deciduous from the base.

Armament: Leaf margin sparsely denticulate.

Sexual reproduction

Inflorescence and flowers: Racemes simple, ascending-spreading (70–110 mm long), subcapitate, with horizontally presented flowers. Flowers subsecundly presented (and projected forward). This is an adaptation to the sheer habitat. The large floral bracts protect the flowers from damage by perching sunbirds. The orange-red perianth is also unique, broadest at the base (7–8 mm in diameter) and tapering to 4 mm (close to the apices).

Fruit/Seed

Size: Not seen.

Dispersal: Light, angular seeds shaken from the capsules and dispersed by wind.

Time: Seeds dispersed in winter and autumn, ready for the early spring and summer rains.

Vegetative reproduction: *Aloe soutpansbergensis* proliferates from the base, forming small, dense clusters. The stems root when finding a new crevice and fallen branches will also root when wedged in a suitable crevice. The continual suckering from the base or renewal of shoots and rooting of stems is a sufficient vegetative backup dispersal strategy for the harsh cliff-face environment.

CONSERVATION STATUS

Although rare and limited in distribution, it is locally abundant and not threatened (Raimondo *et al.* 2009).

ADDITIONAL NOTES

Horticulture: Best grown in afroalpine or summer-rainfall grassland gardens in a slightly acid peat and sand mixture. Feed regularly in spring and summer. Easy to grow, with a medium growth rate. Away from its habitat, it is best kept in a greenhouse. Keep moist and cool during the summer months. Plants proliferate from the base, soon becoming cluster-forming. Keep partially shaded.

VOUCHER

Van Jaarsveld 19766 (NBG).

ILLUSTRATIONS AND MAP

Figures 29a–29d, Map 29.

30. *Aloe thompsoniae* Groenew. in *Tydskrif vir Wetenskap en Kuns* 14: 64 (1936).

Cremonophyte growth form: Cluster-forming, rosettes (of light to medium weight, cliff hugger).

Growth form formula: A:S:Lper:R:C:La (vb)

Etymology: After Audrey Thompson, daughter of Sheila Thompson (fl. 1970), grower of indigenous plants at Magoebaskloof.

DESCRIPTION AND HABITAT

Plants with moderate growth rate to rapid-growing, acaulescent, rosulate, proliferating from base from subterranean stolons, forming small dense clusters up to 200 mm in diameter, with soft recurved leaves. Stem ascending to horizontal and pendulous on shady cliff faces. Leaves linear, softly succulent, ascending, becoming recurved at apex, pendulous, up to 50–200 × 5–15 mm; margin denticulate, green, mottled towards base; surface smooth; adaxial side channelled. Inflorescence simple, ascending to ascending-spreading, 200–300 mm long, bearing up to 5 sterile bracts; bracts scarious, pale pink, clasping stem, up to 18 mm long, acuminate; floral bracts clasping pedicels, gradually becoming smaller; raceme 50 mm long, capitate, with 12–16 flowers; pedicels up to 15–20 mm long. Perianth subpendulous orange-red, green-tipped, 27–30 × 6–7 mm. Fruiting capsule oblong-conical, 20 × 10 mm. Seeds angular, 3 × 1.5 mm, dark brown.

Phenology: Flowering mainly in summer (November–April) and sporadically at other times.

Pollinators: Sunbirds.

Habitat and aspect: Quartzitic sandstone cliffs and steep slopes (mainly on eastern and southern aspects and more so on the shady south-facing slopes). Plants are firmly rooted in crevices and on ledges large enough to support the roots and stem clusters. They are also found on the summit and boulders, and are not restricted to cliffs. Temperature moderate in summer, with frequent fog, but with dry, cool winters. Rainfall is about 1500–2000 mm per annum.

Altitude: 1650–2100.

Associated vegetation: Northern Escarpment Quartzite Sourveld of the Grassland Biome (Mucina *et al.* 2005).

Associated cremnophytes: *Aloe arborescens*, *Bulbine natalensis*, *Crassula pellucida* subsp. *alsinoides*, *C. setulosa*, *Cyrtanthus junodii*, *Drimia robusta*, *Merwillia plumbea* and various moss species.

Geology: Quartzitic sandstone (Black Reef Formation, Transvaal Supergroup). Light-textured (grey) rough- to smooth-textured, with many ledges, crevices and fissures and ideal for establishment of plants.

DISTRIBUTION

Aloe thompsoniae is a quartzitic sandstone endemic to the Wolkberg near Pietersburg. It is confined to the moist and well-watered, sheer, east-facing cliffs and crevices of large boulders. Plants are often locally abundant.

RELATED SPECIES

Aloe thompsoniae comes closest to *A. nubigena* from the east-facing escarpment mountains in Mpumalanga and differences are discussed under the latter.

ADAPTATIONS TO THE CLIFF ENVIRONMENT

Variability: Plants showing great phenotypic plasticity, adapting according to the situation on the cliffs.

Habit: Plants forming clusters among moss and other cremnophytes occupying smaller crevices and ledges. Where within reach, stems and leaves heavily grazed.

Size and weight: Heads dwarf-sized, of light to medium weight.

Stem: Acaulescent to shortly stemmed, ascending and subpendulous to pendulous when growing on shady cliff faces.

Leaves

Orientation: Rosulate, adaptable according to situation (phenotypic plasticity), pendulous and larger on shady cliffs, as opposed to ascending growth and smaller, recurved leaves in exposed situations.

Colour: Green, mottled towards the base.

Age and persistence: Long-lived perennial with medium growth rate, leaves deciduous from the base.

Armament: Leaf margin denticulate.

Sexual reproduction

Inflorescence and flowers: Young inflorescence curving upwards as it matures, presenting the racemes in the typical erect position.

Fruit/Seed

Size: Seed 3×1.5 mm, an ideal size for establishment in crevices.

Dispersal: Light, angular seeds shaken from the capsules and dispersed by wind.

Time: Seeds dispersed in winter and autumn, ready for the early spring and summer rains. Germination within 14–21 days.

Vegetative reproduction: *Aloe thompsoniae* is prolific from the base, forming small, dense clusters. The stems root when finding a new crevice and fallen branches will also root when wedged in a suitable crevice. The continual renewal of shoots and rooting of stems in new crevices by extended stems represent a sufficient vegetative backup dispersal strategy for the harsh cliff-face environment.

CONSERVATION STATUS

Aloe thompsoniae is rare (Raimondo *et al.* 2009). It is confined to the Wolkberg (limited distribution), often locally abundant and not threatened. Well protected by the precipice and steep terrain.

ADDITIONAL NOTES

Horticulture: Best grown in afroalpine or summer-rainfall grassland gardens in a slightly acid peat and sand mixture (Van Jaarsveld 2010). Feed regularly in spring and summer. Easy to grow, with a medium growth rate. Away from its habitat it is best kept under cool, shady conditions in a greenhouse. Keep moist and cool during the summer months. Plants proliferate from the base, soon forming small clusters.

VOUCHER

Van Jaarsveld 16221 (NBG).

ILLUSTRATIONS AND MAP

Figures 30a–30e, Map 30.

BULBINE Wolf

31. *Bulbine cremnophila* Van Jaarsv., in Van Jaarsveld & Van Wyk in *Aloe* 36,4: 72 (1999).

Cremnophyte growth form: Cluster-forming, short pendent leaves (of light weight, cliff hanger).

Growth form formula: A:S:Lper:R:C:Lp (eg)

Etymology: Greek *kremnos*, cliff, and Greek *phileein*, to love, pertaining to its cliff habitat.

DESCRIPTION AND HABITAT

Plants dwarf-sized, rosulate, clustering, up to 120 mm high, 100 mm in diameter, with 3–8 heads. Roots grey, terete. Leaves up to 7, in a rosette, drawn together but curving downwards, linear-lanceolate, 60–100 × 10–15 mm, channelled above, cymbiform below, glaucous and faintly translucent, covered with powdery bloom, apex acute-mucronate, reddish pink. Inflorescence 200–400(–450) mm long, 17–35-flowered in distal half; raceme 150–300 mm long; peduncle 2 mm in diameter at base, terete; bract deltoid-acuminate, 5 × 1 mm, clasping; pedicels 15–18 mm long. Perianth stellate, becoming reflexed, drooping, about 8–10 mm in diameter; tepals orange-yellow; outer tepals elliptic, 7 × 2 mm, inner tepals ovate to ovate-elliptic, 6 × 2.5 mm, obtuse. Stamens up to 5 mm long. Ovary globose, up to 1.5 mm in diameter. Fruit obovate, 3 × 2.5 mm. Seeds 2 mm in diameter, black.

Phenology: Flowering mainly from spring to early summer (peak end October). Seeds dispersed by wind in summer and early autumn.

Pollinators: Insects.

Habitat and aspect: Vertical cliffs of narrow, shady kloofs (mainly eastern and western aspects). Plants are firmly rooted in crevices, size often depending on the growing space allowed by the crevice. Temperatures are high on summer days (35–40°C). The average daily maximum temperature is about 25°C and the average daily minimum about 10°C. Winters are cooler, but frost is a rarity or absent. Rainfall throughout the year, but with a peak in spring and summer, ranging from 400–500 mm per annum (thunder showers or cyclonic winter rain).

Altitude: 400–1000 m.

Associated vegetation: Gamtoos Thicket of the Thicket Biome (Mucina *et al.* 2005).

Associated cremnophytes: *Albuca cremnophila*, *Cotyledon tomentosa* var. *tomentosa*, *Crassula perfoliata* var. *minor*, *C. perforata* and *Gasteria rawlinsonii*.

Geology: Quartzitic sandstone (light-coloured and smooth-textured), Peninsula Formation (Cape Supergroup). The quartzitic sandstone substrate is rich in ledges, crevices and fissures, ideal for establishment of plants.

DISTRIBUTION

Bulbine cremnophila is endemic to quartzitic sandstone, confined to the narrow kloofs (north-south orientation) of the Baviaanskloof Mountains of the Eastern Cape, west of Hankey.

RELATED SPECIES

Bulbine cremnophila is the smallest of the broad-leaved bulbines. It comes closest to *B. retinens*, another cremnophyte with erect, much longer leaves. *Bulbine rupicola* has short, erect leaves. *Bulbine natalensis* and *B. latifolia* are much larger, solitary species (widely distributed from the Eastern Cape to KwaZulu-Natal) often associated with cliff faces. Both have open rosettes of broad leaves and spreading flowers that are not drooping. *Bulbine latifolia* has firm leaves and *B. natalensis* has leaves with a ciliate margin.

ADAPTATIONS TO THE CLIFF ENVIRONMENT

Habit: Plants with drooping leaves which are retained in cultivation. Rapid-growing, fairly long-lived perennials.

Size and weight: Heads small, of light weight.

Stem: The short branches (up to 40 mm) are grey and covered by persistent old leaves. They are fibrous and strong, thus less investment in woody tissue.

Leaves

Orientation: Apart from curving down (positively geotropic), the leaves are drawn together in the apical rosette, becoming slightly spreading only in the rainy season, suggesting an adaptation to the extreme, dry habitat.

Succulence: The very fleshy leaves are soft, becoming turgid after rain, but are deeply channelled during dry periods, an adaptation to the extreme, dry habitat.

Colour: Glaucous (reflecting light), with powdery bloom. The slight translucent nature allows light to penetrate deeply, an adaptation to the shady cliff environment.

Age and persistence: Becoming deciduous from the base, resulting in apical rosettes.

Armament: The entire leaf margin and softer leaf texture suggest a reduction in armament in response to the undisturbed cliff habitat in contrast to the thorny but heavily grazed surrounding thicket vegetation.

Sexual reproduction

Inflorescence and flowers: Inflorescence ascending to spreading; individual flowers subpendulous to pendulous. Initial orientation of the buds erect, but the flowers curving down as they mature. Orientation of the mature perianth (up to 9 flowers open at the same time) renders the flowers more conspicuous in the narrow, shady kloofs when viewed from below, an adaptation maximising visibility for pollination in the vertical cliff environment.

Fruit/Seed

Size: Seed 2 mm in diameter, an ideal size for establishment in crevices.

Dispersal: Light, black, angular seeds shaken from the capsules and dispersed by wind.

Time: Seeds ripening in autumn, coinciding with the start of the rainy season. Germination within 14–21 days.

Vegetative reproduction: *Bulbine cremnophila* divides, forming dense, rounded clusters. The continual division is an efficient vegetative backup dispersal strategy for this harsh cliff-face environment. Individual branches of the clusters will root under suitable conditions and continue to grow, resulting in survival of the clone. Detached clusters or heads will also root if they fall into a crevice.

CONSERVATION STATUS

Classified as rare (Raimondo *et al.* 2009). A local endemic, not threatened (Hilton-Taylor 1996).

ADDITIONAL NOTES

Horticulture: *Bulbine cremnophila* plants are easily grown from seed or division and thrive in cultivation. It is best grown as a pot plant in small containers simulating the small crevices of the cliff environment. The soil should be sandy and slightly acid, with ample feeding throughout the year. It rapidly becomes turgid after watering. Its very easy growing nature maximises its survival rate. Outside its subtropical thicket habitat, it is best grown under controlled conditions in a greenhouse.

VOUCHER

Van Jaarsveld 7238 (NBG).

ILLUSTRATIONS AND MAP

Plate 31, Figures 31a–31d, Map 31.

32. *Bulbine latifolia* (L.f.) Schult. & Schult.f. var. *curvata* Van Jaarsv., in Van Jaarsveld & Van Wyk in *Aloe* 40,1: 4–5 (2003d).

Cremonophyte growth form: Solitary, pendulous rosette (of medium weight, cliff hanger).

Growth form formula: E:F:P:R:So:Lp (eg)

Etymology: The varietal epithet *curvata* refers to the curved leaves.

DESCRIPTION AND HABITAT

Plants solitary, with pendulous rosette 150 mm in diameter and 250 mm long from short branch 70 mm long. Stem 25 mm in diameter, covered with persistent leaf bases, the latter weathering and forming a fibrous network. Roots grey, fleshy, terete. Leaves 12–15 in a rosette, with firm texture, pendent or curving downwards, linear-lanceolate, 150–250 × 8–12 mm, flat above, rounded below, light green; margin entire; apex attenuate, mucronate. Inflorescence up to 420 mm long, densely flowered in distal third; raceme conical, 150 mm long; peduncle up to 7 mm in diameter at base, biconvex, green to reddish green; bracts deltoid, acuminate, 5 × 1 mm, clasping; pedicels 12 mm long. Perianth stellate, about 15 mm in diameter; tepals bright yellow with greenish yellow median stripes, outer tepals narrowly oblanceolate, 10 × 2 mm, inner tepals elliptic to elliptic-oblanceolate, 9 × 3 mm; apices obtuse to emarginate. Stamens 7 mm long, bearded in central part, 2.5–3 mm. Ovary globose, 1.5 mm in diameter; style erect, up to 7 mm long. Fruit obovate, 3 × 2.5 mm. Seeds 3 × 1.5 mm, black.

Phenology: Flowering mainly from late spring to early summer (October–November). Seeds dispersed by wind in summer and early autumn.

Pollinators: Insects.

Habitat and aspect: Vertical cliffs, at an altitude of about 500 m above the Kouga River at the Kouga Dam (mainly eastern and western aspects). Plants are firmly rooted in crevices, size often depending on the growing space allowed by the crevice. Temperature is high in summer (35–40°C). Winters are cooler, but frost is a rarity or absent. The average daily maximum temperature is about 25°C and the average daily minimum about 10°C. Rainfall occurs throughout the year but with a peak in spring and summer, ranging from 400–500 mm per annum (thunder showers or cyclonic winter rain).

Altitude: 250–500 m.

Associated vegetation: Gamtoos Thicket (Mucina *et al.* 2005).

Associated cremnophytes: *Bulbine latifolia* var. *curvata* is a rare species confined to quartzitic sandstone rock crevices, occurring in full sun or partial shade of rock ledges or other cremnophilous vegetation. It occurs solitary or together with *Albuca cremnophila*, *Aloe perfoliata*, *A. pictifolia*, *Cotyledon tomentosa*, *Crassula perfoliata* var. *minor*, *C. perforata*, *C. rupestris* subsp. *rupestris*, *C. socialis*, *Cyrtanthus montanus*, *Gasteria glomerata* and *Haworthia viscosa*.

Geology: Quartzitic sandstone (light-coloured and smooth-textured), Peninsula Formation (Cape Supergroup). The quartzitic sandstone substrate is rich in sufficient ledges, crevices and fissures, ideal for establishment of plants.

DISTRIBUTION

Bulbine latifolia var. *curvata* is confined to the Kouga Dam near Hankey (Eastern Cape).

RELATED SPECIES

Bulbine latifolia var. *curvata* is at once distinguished by its solitary, pendent habit of firm, linear-attenuate leaves (often becoming reddish in the dry season) from a short stem, the persistent leaf bases weathering to a fibrous, mat-like network. It is further distinguished by its dense flowering racemes. The leaves retain their drooping nature in cultivation. The plants occur on exposed, west-facing, quartzitic sandstone cliff faces. *Bulbine latifolia* var. *curvata* can immediately be distinguished from *B. latifolia* var. *latifolia* by its narrow, drooping leaves. *Bulbine latifolia* var. *curvata* superficially resembles *B. cremnophila*, another cremnophilous species from the same region and further westwards in the Baviaanskloof. The latter, however, is a smaller, cluster-forming species with soft, triangular-lanceolate, glaucous leaves with a distinctly ciliate margin, and lax racemes.

ADAPTATIONS TO THE CLIFF ENVIRONMENT

Habit: Plants conspicuous, with drooping stems and leaves, even when grown in cultivation. *Bulbine latifolia* var. *curvata* is a fairly long-lived perennial with a medium to slow growth rate. Its sluggish growth (compared to that of other *Bulbine* species) could perhaps be due to the mineral-deprived cliff habitat.

Size and weight: Heads of medium weight.

Stem: Short branches (up to 40 mm) are grey and covered by persistent old leaves. They are fibrous and strong, thus less investment in woody tissue.

Leaves

Orientation: Apart from curving down (positively geotropic), the leaves are drawn together in the apical rosette, becoming slightly spreading only in the rainy season, suggesting an adaptation to the extreme dry habitat.

Succulence: The very fleshy leaves are firm, becoming turgid after rain.

Colour: Light green, becoming maroon under drought stress, an adaptation helping the plants to cope with the well-drained cliff environment.

Age and persistence: Long-lived, perennial, becoming deciduous from the base, resulting in apical rosettes.

Armament: The entire leaf margin and softer leaf texture suggest a reduction in armament in response to the undisturbed cliff habitat in contrast to the thorny but heavily grazed surrounding thicket vegetation.

Sexual reproduction

Inflorescence and flowers: Inflorescence densely flowered and conspicuous, ascending to spreading; individual flowers spreading.

Fruit/Seed

Size: Seed 3×1.5 mm, a relatively small size ideal for establishment in crevices.

Dispersal: Light, black, angular seeds shaken from the capsules and dispersed by wind.

Time: Seeds ripening in autumn, coinciding with the start of the rainy season. Germination after 14–21 days.

Vegetative reproduction: Absent.

CONSERVATION STATUS

Although rare, it is a local endemic that is not threatened.

ADDITIONAL NOTES

Horticulture: *Bulbine latifolia* var. *curvata* is easily grown from seed and does well in cultivation. It is best grown as a pot plant in containers, in full sun or partial shade. The soil should be sandy and slightly acid, with ample feeding throughout the year. Its very easy growing nature maximises its survival rate. Outside its subtropical thicket habitat, it is best grown under controlled conditions in a greenhouse.

VOUCHER

Van Jaarsveld 13806 (NBG).

ILLUSTRATIONS AND MAP

Plate 32, Figures 32a–32c, Map 32.

33. *Bulbine meiringii* Van Jaarsv., in Van Jaarsveld & Van Wyk in *Aloe* 40,1: 5–6 (2003d).

Cremonphyte growth form: Cluster-forming (of light to medium weight, cliff squatter).

Growth form formula: A:S:Lper:R:C:Ts:Lp (eg) (vb)

Etymology: Named after Meiringspoort in the northeastern Little Karoo, the location where this species was discovered.

DESCRIPTION AND HABITAT

Dwarf-sized, rosulate succulents up to 100 mm high, dividing to form clusters about 200 mm in diameter, with up to 12 heads. Roots fleshy, terete, slightly fusiform, up to 3 mm in diameter, grey. Tuber oblong, terete, 20–35 × up to 10 mm, slightly thickening towards base, covered with persistent fibrous tunics. Leaves 4–7, curving downwards; lamina glaucous, linear-lanceolate, almost subterete when fully turgid, 80–210 × 6–8 mm; adaxial side flat to convex, abaxial side convex, striate; apex acute, margins denticulate. Inflorescence solitary, 210–260 mm tall, ascending to spreading; flowers lax, borne in distal third, about 14 mm in diameter, 4–6 mm apart; peduncle up to 3 mm wide at base, biconvex, terete distally; bracts deltoid-acuminate, 3–4 mm long, about 1 mm wide at base, membranous, clasping; pedicels 10–12 mm long. Perianth stellate, becoming reflexed; tepals pale yellow, outer tepals elliptic, up to 7 × 2 mm, apices obtuse, inner tepals ovate to ovate-elliptic, up to 6 × 2.5–3.0, apices obtuse. Stamens up to 5 mm long; anthers yellow, oblong, dorsifixed. Ovary globose, up to 1.5 mm in diameter; style erect, up to 5 mm long; stigma capitate. Capsule ovoid, up to 3 × 4 mm. Seeds up to 1.5 × 1 mm, grey-black. Flowering in spring.

Phenology: Flowering in spring (September–October).

Pollinators: Insects.

Habitat and aspect: Plants of *Bulbine meiringii* occur on sheer south-facing quartzitic sandstone cliff faces where they form small clusters. The average daily maximum temperature is about 26°C and the average annual minimum about 9°C. Rainfall occurs in winter and summer, ranging from 200–300 mm per annum.

Altitude: 500–800 m.

Associated vegetation: Western Gwarrieveld of the Succulent Karoo Biome (Mucina *et al.* 2005).

Associated cremnophytes: Associated species include *Adromischus triflorus*, *Crassula perforata*, *C. rupestris*, *Haworthia* sp., *Senecio ficoides* and *S. muirii*.

Geology: Sandstone rock ledges of Peninsula Formation, Table Mountain Group (Cape Super-group). Cliff substrate with many fissures, ledges and crevices, ideal for establishment of plants.

DISTRIBUTION

It is known only from Meiringspoort, near De Rust in the Little Karoo, Western Cape.

RELATED SPECIES

Bulbine meiringii is characterised by its oblong tubers with slightly fusiform roots and by the slender, linear-lanceolate, glaucous leaves. In contrast, *B. cremnophila* has shorter, much fleshier leaves and lacks the oblong tuber and fusiform roots. *Bulbine meiringii* is also closely related to *B. rupicola* occurring towards Klipplaat in the northeast. The latter has ovoid tubers and short, ascending, green, somewhat channelled leaves.

ADAPTATIONS TO THE CLIFF ENVIRONMENT

Habit: Plants growing in clusters. This is a rapid-growing, fairly long-lived perennial.

Size and weight: Heads small, of medium weight.

Stem: Branches short.

Leaves

Orientation: Clustered or grouped. Drooping, leaning from the cliff face, and of a softer, fragile texture.

Succulence: Fleshy.

Colour: Greyish green.

Age and persistence: Becoming very turgid after rain, an adaptation to the extreme, dry habitat.

Armament: Leaf margin entire without armament, suggesting a reduction in armament in response to the undisturbed cliff habitat in contrast to the thorny but heavily grazed surrounding thicket vegetation.

Sexual reproduction

Inflorescence and flowers: Inflorescence ascending, maximising visibility to possible insect pollinators.

Fruit/Seed

Size: Seed 1.5×1 mm, an ideal size for establishment in crevices.

Dispersal: Light, grey-black seeds shaken from the capsules and dispersed by wind.

Time: Seeds ripening in summer, coinciding with the rainfall. Germination within 14–21 days.

Vegetative reproduction: *Bulbine meiringii* divides, forming dense clusters. The continual division and filling of crevices represent an efficient vegetative backup dispersal strategy. Individual branches of the clusters will root and continue to grow, maximising survival (vegetative backup). Detached clusters or heads will also root if they fall into a crevice.

CONSERVATION STATUS

A local endemic, not threatened.

ADDITIONAL NOTES

Horticulture: *Bulbine meiringii* is easily grown by division and thrives in cultivation. It is best grown as a pot plant in containers, in partial shade or full sun. The soil should be sandy and slightly acid, with ample watering and feeding throughout the year. Its very easy growing nature maximises its survival rate. Outside its succulent karoo habitat, it is best grown under controlled conditions in a greenhouse.

VOUCHER

Van Jaarsveld, Vlok & Nanni 12762 (NBG).

ILLUSTRATIONS AND MAP

Plate 33, Figures 33a–33c, Map 33.

34. *Bulbine natalensis* Baker in *Flora capensis* 6: 366 (1896). (Soft, translucent, cliff-face form bearing ciliate leaves.)

Cremonophyte growth form: Solitary to cluster-forming (of light to medium weight, cliff squatter).

Growth form formula: A:S:Lper:R:So:La

Etymology: After KwaZulu-Natal in South Africa.

DESCRIPTION AND HABITAT

Plants solitary or forming small clusters, evergreen, rosulate, with short stem. Roots yellow, fleshy, terete. Leaves 10–14, triangular-lanceolate, grey-green, striate, soft, spreading, 85–130 × 35–45 mm, flat to broadly channelled above, flat to rounded below; margin densely ciliate; cilia 2 mm long; apex acuminate. Inflorescence 1–3, densely flowered, up to 550 mm tall; peduncle flattened at base, 6–7 mm in diameter; bracts linear-lanceolate, 10 × 1 mm; pedicels 9–11 mm. Flowers spreading; perianth stellate, up to 15 mm in diameter, yellow; outer tepals

lanceolate, 6×3 mm, inner tepals 6×4 mm; apices obtuse. Stamens 5 mm long. Ovary globose, 1.5 mm in diameter. Style 6 mm long; stigma capitate. Capsule rounded, 3×3 mm. Seeds 1.5 mm in diameter, grey-black, elliptic.

Phenology: Flowering mainly from spring to early summer (peak end October). Seeds dispersed by wind in summer and early autumn.

Pollinators: Insects.

Habitat and aspect: Cliffs of narrow shady kloofs (mainly eastern and southern aspects) where plants are firmly rooted in crevices, size often depending on the growing space allowed by the crevice. Temperature is high in summer (28–34°C). Winters are cooler but frost is a rarity or absent. The average daily maximum temperature is about 25°C and the average daily minimum about 10°C. Rainfall throughout the year, but with a peak in spring and summer, ranging from 400–500 mm per annum (thunder showers or cyclonic winter rain).

Altitude: 35–600 m.

Associated vegetation: Mainly Indian Ocean Coastal Belt, Albany Thicket and dry Fynbos (Mucina *et al.* 2005).

Associated cremnophytes: *Albuca cremnophila*, *Bulbine cremnophila*, *Cotyledon tomentosa*, *Crassula perforata*, *C. perfoliata* var. *minor* (Baviaanskloof) and *Gasteria rawlinsonii*.

Geology: Quartzitic sandstone (light-coloured and smooth-textured), Peninsula Formation (Cape Supergroup).

DISTRIBUTION

Bulbine natalensis has a wide distribution from the Baviaanskloof and Kouga northeastwards to KwaZulu-Natal, confined to kloofs and narrow, shady cliff faces.

RELATED SPECIES

Bulbine natalensis comes closest to *B. latifolia*, a much larger, solitary species (widely distributed from the Eastern Cape to KwaZulu-Natal) from the flats but also sometimes associated with cliff faces. Both have open rosettes of broad leaves and dense, conical racemes of spreading flowers. *Bulbine latifolia* has firm leaves and *B. natalensis* has leaves with a ciliate margin.

ADAPTATIONS TO THE CLIFF ENVIRONMENT

Habit: Plants with small, spreading to drooping rosettes. *Bulbine natalensis* is a rapid-growing, fairly long-lived perennial.

Size and weight: Heads are small to medium-sized, of light to medium weight (fully turgid adult plants).

Stem: Plants with short, grey stems covered by persistent old leaves. They are fibrous and strong, thus less investment in woody tissue.

Leaves

Orientation: Patent to recurved, exposing maximum foliage to open shade, becoming channelled only under dry conditions.

Succulence: Leaves fleshy and soft, becoming turgid after rain but channelled during dry periods, an adaptation to the extreme, dry habitat.

Colour: Glaucous (reflecting the light); epidermis with powdery bloom. The slight translucent nature allows light to penetrate deeply, an adaptation helping the plants to cope with the shady cliff environment.

Age and persistence: Leaves are very soft, withering from the base.

Armament: Compared to the related *Bulbine latifolia*, the leaf texture is markedly softer, with a fragile, ciliate margin. This reduction in armament can possibly be viewed as a response to the undisturbed cliff habitat in contrast to the thorny but heavily grazed surrounding thicket, savanna (*B. latifolia*) or grassland vegetation.

Sexual reproduction

Inflorescence and flowers: Inflorescence conical and densely flowered, thus conspicuous in the narrow, shady kloofs, maximising visibility for pollination on the vertical cliffs.

Fruit/Seed

Size: Seed 2 mm in diameter, an ideal size for establishment in crevices.

Dispersal: Light, black, angular seeds shaken from the capsules and dispersed by wind.

Time: Seeds ripening in autumn, coinciding with the start of the rainy season. Germination after 14–21 days.

Vegetative reproduction: Absent.

CONSERVATION STATUS

A local endemic, not threatened (Hilton-Taylor 1996). Plants are popular in traditional medicine (Nguni people) and are often sold at muti markets.

ADDITIONAL NOTES

Horticulture: Easily grown from seed and thrives in cultivation. It is best grown as a pot plant in containers, in partial shade. The soil should be sandy and slightly acid, with ample feeding throughout the year. Its very easy growing nature maximises its survival rate. Outside its subtropical thicket habitat, it is best grown under controlled conditions in a greenhouse.

VOUCHER

Van Jaarsveld 17566 (NBG).

ILLUSTRATIONS AND MAP

Figures 34a & 34b, Map 34.

35. *Bulbine pendens* G.Will. & Baijnath in South African Journal of Botany 61,6: 316 (1995).

Cremonophyte growth form: Solitary with pendent leaves type (of light weight, cliff hanger).

Growth form formula: A:B:D:C:Lp:(vb) (eg)

Etymology: The epithet *pendens* pertains to the pendent leaves.

DESCRIPTION AND HABITAT

Plants dwarf-sized, solitary, acaulescent, single or twin-headed geophytes, pendent from cliff faces. Tuber oblong, 30 × 15 mm, stellate, lobes tapering to roots. Leaves 1 or 2, pendent, amplexicaul, with basal sheath 10–20 long, linear, terete, striate, 15–18 × 2–5 mm. Inflorescence solitary, erect, 80–180 mm long, up to 4-flowered; peduncle 1 mm wide at base, terete; bracts deltoid-acuminate, 3–4 × 1 mm, clasping; pedicels up to 25 mm long. Perianth stellate, spreading, about 18 mm in diameter; tepals yellow, outer tepals 8 × 3 mm; inner tepals ovate to ovate-elliptic, 8 × 4 mm; apices obtuse to subacute. Stamens 5 mm long; filaments bearded. Ovary globose, 1.5–2.0 mm in diameter; style erect, 5 mm long; stigma capitate. Capsule obovoid, 3 mm in diameter. Seeds cubical, with elongate apex 1.7 × 0.7 mm, tuberculate, blackish brown.

Phenology: Flowering in spring. Seeds dispersed by wind in summer and early autumn.

Pollinators: Insects.

Habitat and aspect: Vertical cliffs of narrow shady kloof (mainly western and southwestern aspects). Plants firmly rooted in crevices. Temperature is high in summer (35–40°C). Winters are cooler but frost is absent. Rainfall in winter, ranging from 75–150 mm per annum (thunder showers or cyclonic winter rain).

Altitude: 300–800 m.

Associated vegetation: Rosyntjieberg Succulent Shrubland of the Succulent Karoo Biome (Mucina *et al.* 2005).

Associated cremonophytes: *Aloe meyeri*, *Bulbinella gracilis*, *Conophytum angelicae*, *C. wettsteinii*, *Cyrtanthus herrei*, *Trachyandra aridimontana* and *Tylecodon ellaphieae* (Rosyntjieberg).

Geology: Quartzitic sandstone (light-coloured and smooth-textured), Rosyntjieberg Formation (Orange River Group). Substrate with many ledges, crevices and fissures, ideal for establishment of plants.

DISTRIBUTION

A quartzitic sandstone endemic, confined to the narrow kloofs and cliff faces of the Rosyntjieberg and Oemsberg of the Richtersveld Transfrontier National Park. It was recently also found on cliffs along the Skaaprivierspoort northwest of Springbok.

RELATED SPECIES

Bulbine pendens is related to other two-leaved *Bulbine* sp. (*B. vitrea*, *B. diphylla*, *B. francescae*) but is immediately separated by its linear, almost terete, pendent leaves. The others are all chasmophytes.

ADAPTATIONS TO THE CLIFF ENVIRONMENT

Habit: Plants solitary, tuber often horizontal owing to cracks, with 1 or 2 drooping leaves up to 150 mm long. Plants become deciduous in summer, like other geophytes in the region coping with the long, dry summers.

Size and weight: Heads small, of light weight.

Stem: Plants acaulescent, with short, oblong tubers for summer dormancy.

Leaves

Orientation: The leaves are pendent (positively geotropic), withering after spring, an adaptation to the extreme, dry summer habitat.

Colour: Dull green and pellucid, maximising light in the shady environment. The translucent nature allows light to penetrate deeply, an adaptation helping the plants to cope with the shady cliff environment.

Age and persistence: Becoming deciduous in late spring.

Armament: The leaves are very soft and fleshy, thus fragile and without armour, suggesting adaptation to the undisturbed cliff habitat.

Sexual reproduction

Inflorescence and flowers: Inflorescence ascending to spreading, but individual flowers semi-reflexed and orientated towards the light source, maximising visibility to pollinators.

Fruit/Seed

Size: Seed 1.7 mm in diameter, the tuberculate surface and angular shape maximising establishment in crevices.

Dispersal: Light, dark, angular seeds shaken from the capsules and dispersed by wind.

Time: Seeds ripening and dispersed in late spring and summer. Germination within 14–21 days.

Vegetative reproduction: Absent.

CONSERVATION STATUS

Although regarded as a critically rare species (Raimondo *et al.* 2009), it has been found by the author at a second location as Skaaprivierspoort northeast of Springbok. The plants are locally abundant in parts of the Rosyntjieberg as well as at Skaaprivierspoort. It is not threatened.

ADDITIONAL NOTES

Horticulture: *Bulbine pendens* is easily grown from seed or division and does well in cultivation. It is best grown in a shady position as a pot plant in small containers simulating the small crevices of the cliff environment. The soil should be sandy and slightly acid, with ample feeding during autumn and winter. The plant should be allowed to dry out completely for its long summer dormancy. It grows fairly easily, maximising its survival rate. Outside its dry, winter-rainfall habitat, it is best grown under controlled conditions in a greenhouse.

VOUCHER

Van Jaarsveld 2118 (NBG).

ILLUSTRATIONS AND MAP

Plate 35, Figures 35a–35d, Map 35.

36. *Bulbine ramosa* Van Jaarsv., in Van Jaarsveld & Van Wyk in *Aloe* 40,1: 6–7 (2003d).

Cremonophyte growth form: Cluster-forming (of medium weight, cliff squatter).

Growth form formula: A:S:Lper:R:C:La (vb)

Etymology: Latin *ramus*, a branch, after its branching nature.

DESCRIPTION AND HABITAT

Plants rosulate, heads continuously dividing to form clusters up to 120 mm in diameter. Roots fleshy, terete, 3–5 mm in diameter. Stem short, 20–50 mm long, 15–25 mm in diameter, with globose, tuberous basal swelling 5–30 mm in diameter, tunicate; tunics golden brown, only slightly fibrous. Leaves rosulate, 6–8; older leaves spreading, firm, persistent; lamina linear to triangular-lanceolate, 80–110(–220) × (7–)10–15(–23) mm, ascending to slightly falcate, adaxial side flat, sometimes convex when fully turgid, or concave or slightly channelled during dry periods, abaxial side convex; surface smooth, bright green, obscurely striate, soft; leaf sap clear, not a lubricant; apex acute, mucronate; margin entire. Inflorescence 1 or 2, 300–470 mm tall, laxly flowered; flowers 20–35, borne in distal third of inflorescence, slightly drooping, 12–20 mm apart; peduncle flattened, 3–4 mm wide at base, terete distally, tapering up to 2 mm; bracts membranous, withering, lower bracts triangular, acuminate, 2–3 × up to 1 mm; pedicels terete, 11–15 mm long. Perianth yellow, stellate, 18 mm in diameter; outer tepals elliptic, up to 9 × 3 mm, apex obtuse, inner tepals up to 9 × 6 mm, apex obtuse.

Stamens up to 6 mm long; anthers oblong, up to 1 mm long, yellow. Ovary globose, up to 1.5 mm in diameter; style erect, terete, up to 6.5 mm long, yellow; stigma capitate. Capsule rounded, up to 4 × 3 mm. Seeds elliptic, oblong, up to 1.5 mm long, grey-black.

Phenology: Flowering in November.

Pollinators: Insects.

Habitat and aspect: *Bulbine ramosa* occurs on sheer south-facing quartzitic sandstone cliff faces. The average daily maximum temperature is about 26°C and the average daily minimum about 9°C. Rainfall in winter and summer, ranging from 200–300 mm per annum.

Altitude: 400–600 m.

Associated vegetation: Western Gwarrieveld of the Succulent Karoo Biome (Mucina *et al.* 2005).

Associated cremnophytes: Associated species include *Adromischus triflorus*, *Crassula badspootense*, *C. perforata*, *C. rupestris*, *Haworthia* sp., *Senecio ficoides*, *Tridentea choanantha* and *Tylecodon leucothrix*.

Geology: Bokkeveld Group (Cape Supergroup). The quartzitic sandstone substrate has many fissures, ledges and crevices, ideal for establishment of plants.

DISTRIBUTION

Bulbine ramosa is known only from Badspoot near Calitzdorp in the Western Cape.

RELATED SPECIES

Bulbine ramosa is at once distinguished by its bright green dividing rosettes forming small clusters. Its globose tubers and thick roots up to 5 mm in diameter are also distinct. Unlike the juice of many other *Bulbine* species, the leaf sap of this species is not a lubricant. *Bulbine frutescens* has aerial branches and roots without a tuberous base or swollen roots, and the leaf sap is a good lubricant.

ADAPTATIONS TO THE CLIFF ENVIRONMENT

Habit: Plants growing in clusters. A rapid-growing, fairly long-lived perennial.

Size and weight: Heads small and of average weight in fully turgid plants.

Stem: Short branches (up to 40 mm) grey and covered by persistent old leaves. They are fibrous and strong, thus less investment in woody tissue.

Leaves

Orientation: Clustered or grouped, ascending.

Succulence: Very fleshy, of a firm texture.

Colour: Bright green.

Age and persistence: Leaves becoming turgid after rain, an adaptation to the extreme, dry habitat.

Armament: Leaf margin entire without armament, suggesting a reduction in armament in response to the undisturbed cliff habitat in contrast to the thorny but heavily grazed surrounding thicket vegetation.

Sexual reproduction

Inflorescence and flowers: Inflorescence ascending, maximising visibility to possible insect pollinators.

Fruit/Seed

Size: Seed 1.5 mm in diameter, an ideal size for establishment in crevices.

Dispersal: Light, grey-black seeds shaken from the capsules and dispersed by wind.

Time: Seeds ripening in summer, coinciding with the rainfall. Germination within 14–21 days.

Vegetative reproduction: *Bulbine ramosa* divides, forming dense clusters. The continual division and filling of crevices represent an efficient vegetative backup dispersal strategy. Individual branches of the clusters will root and continue to grow, maximising survival (vegetative backup). Detached clusters or heads will also root if they fall into a crevice.

CONSERVATION STATUS

A local endemic, not threatened.

ADDITIONAL NOTES

Horticulture: *Bulbine ramosa* is easily grown by division and thrives in cultivation. It is best grown as a pot plant in containers, in partial shade. The soil should be sandy and slightly acid, with ample watering and feeding throughout the year. Its very easy growing nature maximises its survival rate. Outside its succulent karoo habitat, it is best grown under controlled conditions in a greenhouse.

VOUCHER

Van Jaarsveld 16120 (NBG).

ILLUSTRATIONS AND MAP

Plate 36, Figures 36a–36c, Map 36.

37. *Bulbine retinens* Van Jaarsv. & S.A.Hammer, in Van Jaarsveld *et al.* in Aloe 42,1 & 2: 14–15 (2005b).

Cremnophyte growth form: Cluster-forming (of light to medium weight, cliff squatter).

Growth form formula: A:S:Lper:R:C:La (vb)

Etymology: The epithet *retinens* pertains to the capsules retaining and not immediately releasing the seed.

DESCRIPTION AND HABITAT

Plants rosulate, cluster-forming, small, up to 90 mm high (without flowers), 90 mm in diameter, bearing 3–9 rosettes. Tubers ovate, 12–20 × 10–15 mm, covered with dry remains of amplexicaul leaf bases which weather to a fibrous network; flesh yellow. Roots grey, fleshy, terete, stubby, 1.5 mm in diameter. Leaves 5–7, in apical rosette, forming short neck at base up to 7 mm long, erect, soft-textured, linear, subterete, adaxial side becoming flat towards base, 50–80 × 5–7 mm; surface smooth, grey-green to bluish owing to dense powdery bloom, obscurely striate; apex acute, apiculate. Inflorescence up to 350–490 mm long, erect, 17–35-flowered in distal half; raceme 230–310 mm long; peduncle 2–3 mm in diameter at base, terete; bracts deltoid, acuminate, 2 × 1 mm, clasping; pedicels 14–17 mm long. Perianth stellate, becoming reflexed, drooping, about 15–20 mm diameter; tepals pale orange-yellow, outer tepals elliptic, 11 × 3 mm, inner tepals ovate to ovate-elliptic, 12 × 5 mm, obtuse. Stamens 8 mm long. Ovary globose, 1.5 mm in diameter; style erect, up to 6 mm long. Fruit obovate, up to 6 mm long, 2 mm thick, pendulous, orange when ripe, splitting at carpels but retaining seeds for 1–3 days. Seeds 10–30 per fruit, 2.2 × 1.2 × 0.9 mm, indistinctly angular, dull brownish black, finely pitted.

Phenology: In habitat *Bulbine retinens* flowers in spring and summer. Under cultivation its season is extended. Flowers open midmorning, are sweetly scented and deliquesce by dusk. As is normal in the genus, *Bulbine retinens* is not self-fertile. Seed is dispersed by wind.

Pollinators: Insects.

Habitat and aspect: *Bulbine retinens* is known only from the quartzitic sandstone cliffs along the Kouga River between Haarlem and Joubertina in the Hoeree and Skrikrivier tributaries of the Kouga River, where it is locally abundant. Plants grow in clusters, firmly rooted in crevices, and size often depends on the growing space allowed by the crevice. Temperature is high in summer (30–35°C). Winters are cooler but frost is absent. The average daily maximum temperature is about 24°C and the average daily minimum 10°C. Rainfall occurs throughout the year but more so in summer, ranging from 300–400 mm per annum.

Altitude: 500–800 m.

Associated vegetation: Gamtoos Thicket and dry Fynbos at higher altitudes (Mucina *et al.* 2005).

Associated cremnophytes: Locally common, it grows on sheer rock faces in crevices in shade or sun, solitary or together with other succulents such as *Crassula rupestris* subsp.

rupestris, *Cyrtanthus montanus*, *Haemanthus albiflos*, *Haworthia translucens*, *Ornithogalum longibracteatum*, *Othonna capensis*, *Senecio scaposus* and *Veltheimia capensis*.

Geology: Quartzitic sandstone (light-coloured and smooth-textured), Peninsula Formation (Cape Supergroup). The cliff substrate has many fissures, ledges and crevices, ideal for establishment of plants.

DISTRIBUTION

Known only from the Kouga River (Hoeree and Skrikrivier) in the southwestern part of the Eastern Cape.

RELATED SPECIES

Bulbine retinens is at once distinguished from the other dwarf-sized, cluster-forming, cremnophilous *Bulbine* species by its erect, linear leaves arising from a short neck, its ovate tubers covered with fibrous, reticulate remains of leaf bases, and its peculiar mode of seed retention. *Bulbine retinens* comes closest to *B. cremnophila* of the Baviaanskloof to the north of Hoeree, and the widespread *B. rupicola* of the Kouga Mountains to the east (see Van Jaarsveld & Van Wyk 1999). *Bulbine cremnophila* has distinctly curved, linear-lanceolate leaves, similar in colour and texture to those of *B. retinens*, but the plants tend to be more robust and form smaller clusters. *Bulbine rupicola* is a dwarf-sized species with short, erect, lanceolate, green leaves up to 60 mm long and with ciliate margins.

ADAPTATIONS TO THE CLIFF ENVIRONMENT

Habit: Plants with tight clusters. It is a rapid-growing, fairly long-lived perennial.

Size and weight: Heads small, of light to average weight (fully grown and turgid).

Tubers: The short tubers are grey and covered by persistent old leaves. They are fleshy, maximising water storage in the dry habitat.

Leaves

Orientation: Ascending, linear.

Succulence: Fleshy.

Colour: Glaucous (reflecting the light), with powdery bloom. The slight translucent nature allows light to penetrate deeply, an adaptation helping the plants to cope with the shady cliff environment.

Age and persistence: The leaves are soft, becoming turgid after rain, but reddish and somewhat channelled during dry periods, an adaptation to the extreme, dry habitat.

Armament: The entire leaf margin and softer leaf texture suggest a reduction in armament in response to the undisturbed cliff habitat in contrast to the thorny but heavily grazed surrounding thicket vegetation.

Sexual reproduction

Fruit/Seed

Size: Seed $2.2 \times 1.2 \times 0.9$ mm, 10–30 per fruit.

Dispersal: The invariably pendulous fruits start to swell a few days after pollination and ripen within two weeks. The carpel seams begin to split but the indistinctly angular, dull brownish black, finely pitted seeds are retained within the barely intact fruits for one to three days, unless they are strongly shaken (presumably done by wind in the habitat). All other *Bulbine* species shed their seeds immediately. Unlike many species, *Bulbine retinens* has no well-defined dormancy and is never leafless, although it looks drab in winter.

Time: Seeds ripening in autumn, coinciding with the start of the rainy season. Germination within 14–21 days.

Vegetative reproduction: *Bulbine retinens* divides, forming dense clusters. Branches (or broken branches) will root in suitable crevices. The continual division and filling of crevices represent an efficient vegetative backup dispersal strategy. Broken branches or detached heads will also root if they fall into a crevice.

CONSERVATION STATUS

A local endemic, not threatened.

ADDITIONAL NOTES

Horticulture: *Bulbine retinens* is easily grown by division, doing well in cultivation. It is best grown as a pot plant in containers, in partial shade or full sun. The soil should be sandy and slightly acid, with ample watering and feeding throughout the year. Its very easy growing nature maximises its survival rate. Outside its thicket habitat, it is best grown under controlled conditions in a greenhouse.

VOUCHER

Van Jaarsveld 15747 (NBG).

ILLUSTRATIONS AND MAP

Figures 37a–37c, Map 37.

38. *Bulbine rupicola* G.Will. in *Bradleya* 18: 36 (2000).

Cremonophyte growth form: Cluster-forming mats (of light weight, cliff hugger).

Growth form formula: A:S:Lper:R:C:La (vb)

Etymology: The epithet *rupicola* pertains to its rock-dwelling habitat.

DESCRIPTION AND HABITAT

Plants dwarf-sized, rosulate, forming dense clusters up to 80 mm in diameter and with many heads from oblong to oblong-ovoid tubers (yellow flesh), only one to two heads flowering per cluster. Tubers up to 10–12 × 5–8 mm, grey, covered with fibrous remains of leaves. Roots yellowish, terete to 1 mm in diameter. Leaves up to 3–7, in a rosette, ascending, linear to linear-lanceolate, 15–30 × 6–10 mm, triangular-lanceolate to subterete, green, with soft texture, becoming reddish under dry conditions; upper side flat to convex becoming channelled during dry season, cymbiform below, green and slightly glaucous and faintly translucent, striate, covered with powdery bloom; margin entire; apex acute-mucronate. Inflorescence 50–120 mm long, 3–8-flowered in distal quarter; peduncle 1 mm in diameter at base, terete, reddish; bracts deltoid-acuminate, 1.5 × 1 mm, clasping; pedicels 7 mm long. Perianth stellate, becoming reflexed, slightly drooping to drooping, about 8–14 mm in diameter; tepals yellow with darker brownish central stripe in each tepal, outer tepals obovate-elliptic, 7 × 3 mm, channelled, inner tepals ovate to ovate-elliptic, 6 × 4 mm, obtuse. Stamens up to 5 mm long, bearded. Ovary oblong-globose, up to 1.2 × 2 mm. Fruit a rounded capsule, up to 2.5–3 mm in diameter. Seeds angular, black, 2 × 1 mm, minutely wrinkled.

Phenology: Flowering mainly early November–January. Seeds dispersed by wind in summer.

Pollinators: Insects.

Habitat and aspect: Cliffs of narrow shady kloofs (all aspects). Plants are firmly rooted in crevices, their size often depending on the growing space allowed by the crevice. Temperature is high in summer (30–35°C). Winters are cooler but frost is absent. Rainfall occurs throughout the year, but with a peak in spring and summer, 300–400 mm per annum (thunder showers or cyclonic winter rain).

Altitude: 500–800 m.

Associated vegetation: Gamtoos Thicket and dry Fynbos at higher altitudes (Mucina *et al.* 2005).

Associated cremnophytes: *Albuca cremnophila*, *Crassula perfoliata* var. *minor*, *C. perforata* and *Gasteria glauca*.

Geology: Quartzitic sandstone (light-coloured and smooth-textured), Peninsula Formation (Cape Supergroup). Cliff substrate with many ledges, crevices and fissures, ideal for establishment of plants.

DISTRIBUTION

Bulbine rupicola is a quartzitic sandstone endemic, confined to the narrow kloofs (north-south orientation) of the Kouga River Mountains of the Eastern Cape, west of Hankey.

RELATED SPECIES

Bulbine rupicola comes closest to *B. retinens*, which is larger, with long, linear leaves and fruit that retain the seed for some time. It differs further in its flowering time in December. Both have a prolific nature.

ADAPTATIONS TO THE CLIFF ENVIRONMENT

Habit: Plants growing in tight clusters. It is a rapid-growing, fairly long-lived perennial.

Size and weight: Heads dwarf-sized, of light weight.

Tubers: The short, oblong tubers are grey and covered by persistent old leaves. They are fleshy, maximising water storage in the dry habitat.

Leaves

Orientation: Drawn together in the apical rosette, becoming slightly spreading only in the rainy season, an adaptation to the extreme, dry habitat.

Succulence: Very fleshy.

Colour: Green to slightly glaucous (reflecting the light), with powdery bloom. The slight translucent nature allows light to penetrate deeply, an adaptation helping the plants to cope with the shady cliff environment.

Age and persistence: Becoming deciduous from the base, resulting in apical rosettes. Leaves are soft, becoming turgid after rain, but reddish and somewhat channelled during dry periods, an adaptation to the extreme, dry habitat.

Armament: The entire leaf margin and softer leaf texture suggest a reduction in armament in response to the undisturbed cliff habitat in contrast to the thorny but heavily grazed surrounding thicket vegetation.

Sexual reproduction

Inflorescence and flowers: Inflorescence ascending to spreading but with only one or two developing from a cluster, the few individual flowers subpendulous. Initial orientation of the buds is erect but the flowers curve down as they mature. The subpendulous orientation of the perianth renders the flowers more conspicuous in the narrow, shady kloofs when viewed from below, thus an adaptation maximising visibility for pollination in the vertical cliff environment. The prolific nature maximises survival and compensates for reduced sexual output (fewer inflorescences and flowers).

Fruit/Seed

Size: Seed 2×1 mm, a relatively ideal size for establishment in crevices.

Dispersal: Angular, black seeds shaken from the capsules and dispersed by wind.

Time: Seeds ripening in autumn, coinciding with the start of the rainy season. Germination usually after 14–21 days.

Vegetative reproduction: Plants divide, forming dense clusters. Continual division and filling of crevices represent an efficient vegetative backup dispersal strategy in the harsh cliff-face environment. Individual branches of clusters will root and establish many clones,

continuing growth and maximising survival (vegetative backup). Detached clusters or heads will also root if they fall into a crevice.

CONSERVATION STATUS

A local endemic, not threatened.

ADDITIONAL NOTES

Horticulture: *Bulbine rupicola* is easily grown from seed or division, thriving in cultivation. It is best grown as a pot plant in partial shade and kept in small containers simulating the small crevices of the cliff environment. The soil should be sandy and slightly acid, with ample feeding throughout the year. Its very easy growing nature maximises its survival rate. Outside its subtropical thicket habitat, it is best grown under controlled conditions in a greenhouse.

VOUCHER

Van Jaarsveld 17378 (NBG).

ILLUSTRATIONS AND MAP

Figures 38a–38c, Map 38.

39. *Bulbine suurbergensis* Van Jaarsv. & A.E.van Wyk in *Aloe* 42,3: 48–49 (2005b).

Cremonophyte growth form: Pendent rosettes (of medium weight, cliff hanger).

Growth form formula: E:F:P:R:C:Ar (vb)

Etymology: After the Suurberg, its habitat.

DESCRIPTION AND HABITAT

Plants at first solitary, dividing and becoming branched. Rosettes pendent, up to 150 mm in diameter, 250 mm long, characteristically curving upwards at apices. Stems pendent, up to 700 × 15 mm, characteristically orange-brown when cut, covered with persistent leaf bases, weathering to form a fibrous network; basal part often becoming glabrous, grey-brown, smooth, with aerial roots. Roots grey-brown, fleshy, terete, about 1.5–2.0 mm in diameter. Leaves 6–10 per rosette, ascending to ascending-spreading, linear-lanceolate, 70–170 × 12–18 mm; apex acute, mucronate; lamina flat above, convex to rounded below, becoming channelled during drought, soft-textured, pale green, smooth, obscurely striate; margin entire. Inflorescence 110–350 mm long, sparsely flowered (20–30 flowers) in distal third; raceme up to 100–153 mm long; peduncle up to 5 mm in diameter at base, biconvex, green; bracts deltoid, up to 3 × 0.5 mm, acuminate, clasping; pedicels 8–10 mm long. Perianth stellate, about 13 mm in diameter; tepals bright yellow with greenish yellow median stripes, apices obtuse to emarginate, outer tepals narrowly oblanceolate, up to 7–9 × 1.5–2 mm, inner tepals elliptic to elliptic-oblanceolate, up to 7–8 × 2.5–3 mm. Stamens up to 7 mm long, bearded in central part, with hairs 1–2 mm long. Ovary obovoid, up to 1 mm in diameter; style erect, up to 4.5 mm long. Capsule obovate, up to 3 × 2.5 mm, ascending. Seeds 3 × 1.5 mm, black. Flowering from August to November (Figure 39a).

Phenology: Flowering mainly in spring (August–November). Seeds dispersed by wind in summer and early autumn.

Pollinators: Insects.

Habitat and aspect: Cliffs about above the Witterivier (mainly southern, eastern and western aspects). Plants are firmly rooted in crevices, and size often depends on the growing space allowed by the crevice. Temperature is high in summer (35°C). Winters are cooler but frost is absent. Rainfall throughout the year, but with a peak in spring and summer, ranging from 400–500 mm per annum (thunder showers or cyclonic winter rain).

Altitude: 400–600 m.

Associated vegetation: Sundays Noorsveld of the Albany Thicket Biome (Mucina *et al.* 2005).

Associated cremnophytes: *Bulbine frutescens*, *Chlorophytum comosum*, *Crassula lactea*, *Delosperma truteri*, *Haworthia angustifolia* var. *baylissii*, *H. glauca*, *Ledebouria concolor*, *Litanthus pusillus* and *Ornithogalum longibracteatum*.

Geology: Quartzitic sandstone (light-coloured and smooth-textured), Witteberg Group (Cape Supergroup). The quartzitic sandstone substrate has many fissures, ledges and crevices, ideal for establishment of plants.

DISTRIBUTION

Bulbine suurbergensis is confined to the Suurberg, north of Port Elizabeth (Eastern Cape).

RELATED SPECIES

Bulbine suurbergensis differs from other cremnophilous species by its long, pendent, dichotomous, sparsely branched stems up to 700 mm long, characteristically curving upwards and by its soft, linear-lanceolate leaves. It shares these features as well as the persistent leaf bases weathering to a mat-like, fibrous network with *B. latifolia* var. *latifolia* and var. *curvata*. But here the resemblance ends. Both varieties of *B. latifolia* usually grow solitary, var. *curvata* bearing firm, falcate leaves whereas those of var. *latifolia* are soft and fragile. The latter is usually acaulescent.

ADAPTATIONS TO THE CLIFF ENVIRONMENT

Habit: Plants with long, drooping stems and this habit retained in cultivation. A fairly long-lived perennial with a slow to medium growth rate. The slow growth could perhaps be due to the mineral-deprived cliff habitat.

Size and weight: Heads of medium weight.

Stem: The long, leafless branches are grey and covered by a persistent fibrous network of old leaves. They are fibrous and strong, thus less investment in woody tissue.

Leaves

Orientation: Leaves ascending to spreading in apical rosettes.

Succulence: Very fleshy, firm, becoming turgid after rain.

Colour: Light green, coping with the well-drained cliff environment.

Age and persistence: Long-lived, perennial, becoming deciduous from the base, resulting in apical rosettes.

Armament: The entire leaf margin and softer leaf texture suggest a reduction in armament in response to the undisturbed cliff habitat in contrast to the thorny but heavily grazed surrounding thicket vegetation.

Sexual reproduction

Inflorescence and flowers: Inflorescence densely flowered, conspicuous, ascending to spreading; individual flowers spreading.

Fruit/Seed

Size: Seed 3×1.5 mm, a relatively small size ideal for establishment in crevices.

Dispersal: Light, black, angular seeds shaken from the capsules and dispersed by wind.

Time: Seeds ripening in autumn, coinciding with the start of the rainy season. Germination after 14–21 days.

Vegetative reproduction: *Bulbine suurbergensis* divides dichotomously, forming loose clusters. Branches (or broken branches) will root in suitable crevices. The continual division (and lengthening of branches) represent an efficient vegetative backup dispersal strategy. Broken branches or detached heads will also root if they fall into a crevice.

CONSERVATION STATUS

A local endemic well protected by the sheer habitat and not threatened.

ADDITIONAL NOTES

Horticulture: *Bulbine suurbergensis* is easily grown from cuttings or division and thrives in cultivation. It is best grown as a pot plant in containers, in partial shade. The soil should be sandy and slightly acid, with ample watering and feeding throughout the year. Its very easy growing nature maximises its survival rate. Outside its thicket habitat, it is best grown under controlled conditions in a greenhouse.

VOUCHER

Van Jaarsveld 19228 (NBG).

ILLUSTRATIONS AND MAP

Plate 39, Figures 39a–39c, Map 39.

40. *Bulbine thomasiae* Van Jaarsv., in Van Jaarsveld & Van Wyk in Aloe 40,1: 5–6 (2003d).

Cremonophyte growth form: Cluster-forming, short pendent leaves (of medium weight, cliff squatter).

Growth form formula: A:S:Lper:R:C:Lp (eg) (vb)

Etymology: After Vicki Thomas, in recognition of her work as botanical artist.

DESCRIPTION AND HABITAT

Plants short-stemmed, with pendent dividing rosettes forming clusters of up to 8 heads. Rosettes up to 150 mm long and high, 150 mm in diameter. Tuber ovoid, up to 20 × 18 mm, tapering slightly towards neck, sparsely covered with few soft fibres. Roots terete, up to 2 mm in diameter, grey-brown. Leaves very soft, up to 7, drawn together, pendent or curving downwards, linear-lanceolate to triangular-lanceolate, 80–170 × 14–20(–30) mm; base clasping; lamina with few soft fibres, channelled to flattened above, rounded below, glaucous, becoming reddish pink during dry winters, faintly translucent and striate, covered with short pointed papillae; apex acute, mucronate; margins acute, translucent, minutely ciliate. Inflorescence 250–290 mm long; racemes subcapitate, 40–80 mm long, pointed, densely flowered; flowers secundly arranged; peduncle flattened at base, 4–6 mm in diameter, basal half biconvex, minutely ciliate, subterete distally; bracts deltoid-ovate, cymbiform, 4–5 × up to 3 mm, apex acuminate, keel and margins minutely ciliate, clasping; pedicels 15–20 mm. Perianth becoming reflexed, spreading, about 15 mm in diameter when fully expanded, stellate; tepals orange-yellow, slightly channelled and incurved at tips, outer tepals oblong-obovate, up to 8 × 3 mm, inner tepals ovate-lanceolate, up to 7.5 × 2 mm, obtuse. Stamens up to 6 mm long, bearded in distal quarter; anthers versatile, up to 1 × 0.8 mm. Ovary globose, up to 1.5 mm long. Capsule obovoid, up to 5 × 4 mm, pendent. Seeds up to 2 mm in diameter, angular, black.

Phenology: Flowering mainly from midwinter to spring. Seeds dispersed by wind in summer and early autumn.

Pollinators: Insects.

Habitat and aspect: South-facing cliffs, on upper slopes of escarpment. Temperatures are high in summer and mild in winter. The average daily maximum temperature is about 21°C and average daily minimum about 12°C. Rainfall occurs mainly in summer and ranges from 500–600 mm per annum (thunder showers, October–May).

Altitude: 200–800 m.

Associated vegetation: Eastern Valley Bushveld of the Savanna Biome (Mucina *et al.* 2005).

Associated cremnophytes: *Albuca cremnophila*, *Aloe reynoldsii*, *Cotyledon orbiculata*, *Crassula orbicularis*, *Delosperma* sp., *Haemanthus albiflos* *Haworthia cymbiformis* var. *setulifer* and *Ornithogalum juncifolium*.

Geology: Quartzitic sandstone (light-coloured and smooth-textured), Peninsula Formation (Cape Supergroup). The shale substrate has many fissures, ledges and crevices, ideal for the establishment of plants.

DISTRIBUTION

Bulbine thomasiae is known only from the Bashee River in the Transkei, from Collywobbles to near the river mouth (Eastern Cape).

RELATED SPECIES

Bulbine thomasiae belongs to the broad-leaved *Bulbine* species. It is closest to *B. natalensis* and *B. cremnophila*, both of which are also cremnophilous. It is at once distinguished from these species by its subcapitate, acuminate inflorescence. The first named is a much larger, solitary species with broad, spreading leaves (widely distributed from the Eastern Cape to KwaZulu-Natal) and the second a smaller species with glaucous, glabrous leaves. Both related species have elongated racemes.

ADAPTATIONS TO THE CLIFF ENVIRONMENT

Habit: Plants with drooping stems and leaves, even when grown in cultivation. Growth rate of *Bulbine thomasiae* is rapid. It is a fairly long-lived perennial.

Size and weight: Heads small, of average weight (fully turgid adult clusters).

Stem: Short branches (up to 40 mm) are grey and covered by persistent old leaves. They are fibrous and strong, thus less investment in woody tissue.

Leaves

Orientation: Apart from curving down (positively geotropic), the leaves are drawn together in the apical rosette, becoming slightly spreading only in the rainy season, an adaptation to the extreme, dry habitat.

Succulence: Very fleshy, soft and fragile.

Colour: Glaucous (reflecting the light), sparsely but regularly tuberculate. The slight translucent nature allows light to penetrate deeply, an adaptation helping the plants to cope with the shady cliff environment.

Age and persistence: Becoming deciduous from the base, resulting in apical rosettes. Becoming very turgid after rain, but deeply channelled during dry periods, an adaptation to the extreme, dry habitat.

Armament: The entire, minutely ciliate margin and soft, fragile leaf texture suggest a reduction in armament in response to the undisturbed cliff habitat in contrast to the thorny but heavily grazed surrounding thicket vegetation.

Sexual reproduction

Inflorescence and flowers: Inflorescence drooping but the subcapitate racemes turning upwards; flowers spreading and secundly arranged, pointing away from the cliff face and thus maximising visibility to possible insect pollinators.

Fruit/Seed

Size: Seed 2 mm in diameter, an ideal size for establishment in crevices.

Dispersal: Light, black, angular seeds are shaken from the capsules and dispersed by the wind.

Time: Seeds ripening in autumn, coinciding with the start of the rainy season. Germination after 14–21 days.

Vegetative reproduction: *Bulbine thomasiae* divides, forming dense clusters. The continual division and filling of crevices represents an efficient vegetative backup dispersal strategy. Individual branches of the clusters will root and continue to grow, maximising survival (vegetative backup). Detached clusters or heads will also root if they fall into a new crevice.

CONSERVATION STATUS

A local endemic, not threatened.

ADDITIONAL NOTES

Horticulture: *Bulbine thomasiae* is easily grown from seed or division and does well in cultivation. It is best grown as a pot plant in containers, in partial shade. The soil should be sandy and slightly acid, with ample feeding during spring and summer. Its very easy growing nature maximises survival rate. Outside its subtropical thicket habitat, it is best grown under controlled conditions in a greenhouse.

VOUCHER

Van Jaarsveld 16893 (NBG).

ILLUSTRATIONS AND MAP

Plate 40, Figures 40a–40c, Map 40.

GASTERIA Duval

41. *Gasteria batesiana* G.D.Rowley var. *batesiana*, Rowley in National Cactus and Succulent Journal 10: 32 (1955).

Crempnophyte growth form: Dwarf-sized rosulate cluster (of medium weight, cliff hugger).

Growth form formula: A:S:Lper:R:C:La (vb)

Etymology: Named for J.T. Bates, British trolley bus conductor and succulent plant collector.

DESCRIPTION AND HABITAT

Acaulescent, decumbent to erect, 30–100 × 80–300 mm, proliferating from base to form small to large groups, rarely solitary. Roots terete. Leaves distichous at first, becoming rosulate, 50–180 × 15–40 mm, triangular-lanceolate to linear, erectly spreading, becoming recurved; surface dark green with dense white spots arranged in transverse bands, densely rugulose-tuberculate; margin cartilaginous, serrulate, rarely denticulate; apex acute, rarely obtuse, mucronate. Juvenile leaves lorate, densely tuberculate; apex obtuse, mucronate. Inflorescence racemose, 300–450 mm long; bracts 6–12 × 2–5 mm; pedicels 9 mm long. Perianth 35–40 mm long, stipitate for 3–5 mm, gasteriform basally (narrowly elliptic) over half perianth length, gasteriform portion 6–9 mm in diameter (often triangular in cross section), light pink, distal half white with green striations, inflated to the same diameter as proximal portion (with slight constriction in middle); apices erect, becoming erectly spreading, obtuse, white with green median stripes. Ovary 7 × 3 mm, style 15 mm long, stigma included or exerted for up to 5 mm. Capsule 16–20 mm long. Seeds 4–6 × 2–3 mm.

Phenology: Flowering in spring (September–October), but sporadically at other times as well. Seed wind-dispersed.

Pollinators: Sunbirds.

Habitat and aspect: South-facing cliffs of the northeastern parts of South Africa (northern KwaZulu-Natal and Mpumalanga) where the plants grow in crevices and on ledges in inaccessible places. Temperature is high in summer. Winters are cooler but frost is a rarity or absent. The daily average maximum temperature is about 28°C and the average daily minimum about 13°C. Rainfall mainly in spring and summer, 500–600 mm per annum.

Altitude: 300–1000 m.

Associated vegetation: KwaZulu-Natal Coastal Belt and Barberton Serpentine Sourveld of the Savanna Biome (Mucina *et al.* 2005).

Associated crempnophytes: *Aeollanthus parvifolius*, *Crassula orbicularis*, *C. perfoliata* var. *perfoliata*, *Delosperma tradescantioides*, *Peperomia blanda*, *Plectranthus cylindraceus*, *P. spicatus* and *P. verticillatus*.

Geology: It has been recorded as occurring on rock formations of the following formations: Mesozoic rhyolite (Jozini Formation) of the Lebombo Group, Palaeozoic sandstone and shale

(Madzaringwe Formation) of the Karoo Sequence and quartzitic sandstone (Mozaan Formation) of the Pongola Sequence. The quartzitic sandstone substrate has sufficient ledges, crevices and fissures for establishment of plants.

DISTRIBUTION

Gasteria batesiana var. *batesiana* has been recorded from the Buffalo (Mzimnyati) River in the south (KwaZulu-Natal) to Barberton in Mpumalanga in the north. The var. *dolomitica* is known only from south-facing dolomite cliffs of the Olifants River near Penge in the Limpopo Province (see under that variety).

RELATED SPECIES

Gasteria batesiana var. *batesiana* is at once distinguished by its triangular, spreading to recurved, linear leaves. *Gasteria batesiana* var. *dolomitica* has subterete, linear leaves. *Gasteria batesiana* is closely related to *G. tukhelensis* from cliffs along the Thukela Valley. The latter is much larger, with smooth-textured leaves and a divided inflorescence, the flowers with longer pedicels.

ADAPTATIONS TO THE CLIFF ENVIRONMENT

Habit: *Gasteria batesiana* proliferates from the base, forming small clusters. Its small size allows effective heat absorption and establishment in crevices, the plants thus also coping better with gravity. During the dry season the leaves become dorsiventrally flattened and reddish tinged, the production of anthocyanins further enhancing the ability of the plants to survive.

Size and weight: Heads small, of medium weight.

Leaves

Orientation: Spreading to recurved, maximising absorption of light on the south-facing cliffs.

Colour: Dark green and varying from almost unspotted blackish green to mottled green, becoming reddish during dry periods as the plants aestivate, blocking out excessive light and reducing photosynthesis. The reduction of camouflage in some forms (compared to non-cremnophilous species of *Gasteria*) can be seen as an adaptation to the absence of herbivory in the cliff environment.

Presentation: Conspicuous clusters.

Age and persistence: Plants very slow-growing, long-lived, with leaves withering from the base.

Armament: The leaf margin is cartilaginous and serrulate, the leaves mucronate at the apex, but in comparison with other flat-ground species it represents a reduction in armament in response to the undisturbed cliff habitat in contrast to the often thorny but grazed surrounding savanna vegetation.

Sexual reproduction

Inflorescence and flowers: Inflorescence ascending; perianth large, conspicuous, red-pink, green-tipped, suggesting adaptation maximising attraction of pollinators.

Fruit/Seed

Size: Seed 3×2 mm, a relatively small size ideal for establishment in crevices.

Dispersal: Dispersed by wind.

Time: Germination within 14–21 days.

Vegetative reproduction: *Gasteria batesiana* var. *batesiana* suckers from the base, forming small, dense clusters. The leaves are brittle and will root if they become detached and fall into a crevice, establishing new colonies. Continual sprouting from the base and rooting of leaves or fragments that have fallen into crevices represent a sufficient vegetative backup dispersal strategy for this harsh cliff-face environment.

CONSERVATION STATUS

Classified as near threatened (Raimondo *et al.* 2009). Threatened by medicinal plant collectors. In spite of its localised distribution, seed from a cultivated source has been distributed to nurseries and botanical gardens in various parts of the world.

ADDITIONAL NOTES

Horticulture: Ideal for subtropical bushveld (savanna) gardens (Van Jaarsveld 2010). Plants are best grown in rockeries, dry stone walls or containers, in shade, and are easily grown by division, from leaf cuttings or seed. It does best in pot collections. Keep in partial shade and dry during its winter resting phase. The ease of cultivation suggests a maximum survival reproductive output. Outside its native habitat, it is best grown indoors, protected from the sun and from frost in winter. Well established as a house plant (in cultivation, locally and abroad).

VOUCHER

Van Jaarsveld 22362 (NBG).

ILLUSTRATIONS AND MAP

Plate 41, Figures 41a–41e, Map 41.

42. *Gasteria batesiana* G.D.Rowley var. *dolomitica* Van Jaarsv. & A.E.van Wyk in *Aloe* 36,4: 74 (1999).

Crempnophyte growth form: Dwarf-sized globose cluster (of medium weight, cliff hugger).

Growth form formula: A:S:Lper:R:C:La (vb)

Etymology: Named for J.T. Bates, British trolley bus conductor and succulent plant collector.

DESCRIPTION AND HABITAT

Acaulescent, decumbent to erect, 30–100 × 80–300 mm, proliferating from base forming small to large groups. Roots terete. Leaves distichous at first, becoming rosulate, 50–180 × 15–40 mm, linear to linear lanceolate, almost terete when turgid, ascending-spreading, becoming recurved; surface dark green, with dense white spots arranged in transverse bands, densely rugulose tuberculate; margin cartilaginous, serrulate, rarely denticulate; apex acute, rarely obtuse, mucronate. Juvenile leaves lorate, densely tuberculate; apex obtuse, mucronate. Inflorescence racemose, 300–450 mm long; bracts 6–12 × 2–5 mm; pedicels 9 mm long. Perianth 35–40 mm long, stipitate for 3–5 mm, gasteriform basally (narrowly elliptic) over half perianth length, gasteriform portion 6–9 mm in diameter (often triangular in cross section), light pink, distal half white with green striations, inflated to the same diameter as proximal portion (with slight constriction in middle); apices erect, becoming erectly spreading, obtuse, white with green median stripes. Ovary 7 × 3 mm, style 15 mm long, stigma included or exerted for up to 5 mm. Capsule 16–20 mm long. Seeds 4–6 × 2–3 mm.

Phenology: Flowering in spring (September–October), but sporadically at other times as well. Seed wind-dispersed.

Pollinators: Sunbirds.

Habitat and aspect: South-facing cliffs of the northeastern parts of South Africa (Mpumalanga and Limpopo Province). Plants grow in crevices and on ledges in inaccessible places. Winters are cool but frost is a rarity or absent. The average daily maximum temperature is about 28°C and the average daily minimum about 12°C. Rainfall mainly in spring and summer, and varying from 400–600 mm per annum.

Altitude: 450–600 m.

Associated vegetation: Mainly Bushveld and recorded from Pong Dolomite Mountain Bushveld (Mucina *et al.* 2005).

Associated cremnophytes: *Aeollanthus parvifolius*, *Crassula expansa* subsp. *fragilis*, *Delosperma vandermerwei*, *Orbea hardyi*, *Plectranthus dolomiticus*, *P. spicatus* and *P. verticillatus*.

Geology: Dolomite (ancient Vaalian dolomites of the Chuniespoort Group, Malmani Subgroup, Transvaal Supergroup). The dolomite substrate has many ledges, crevices and fissures, ideal for establishment of plants.

DISTRIBUTION

Gasteria batesiana var. *dolomitica* has so far been recorded only from the Olifantsrivier Gorge near Penge (Mpumalanga and Limpopo Provinces).

RELATED SPECIES

At once distinguished by its linear, almost terete leaves (when fully turgid). The var. *batesiana* has triangular leaves. *Gasteria batesiana* is closely related to *G. tukhelensis* from

cliffs along the Thukela Valley. *Gasteria tukhelensis* is much larger, with smooth-textured leaves and a divided inflorescence, the flowers with longer pedicels.

ADAPTATIONS TO THE CLIFF ENVIRONMENT

Habit: It proliferates from the base, forming small clusters. Its small size allows effective heat absorption and establishment in crevices, the plants thus also coping better with gravity. During the dry season the leaves become dorsiventrally flattened and reddish tinged. This production of anthocyanins improves the ability of the plants to survive. The plants' investment in vegetative output (vigorous prolific nature) further enhances occupation of crevices and ultimate survival.

Size and weight: Heads small, of medium weight.

Leaves

Orientation: Spreading to recurved, maximising absorption of light on the south-facing cliffs.

Colour: Dark green, and varying from almost unspotted blackish green to mottled green, becoming reddish during dry periods as the plants aestivate, blocking out excessive light and reducing photosynthesis. The reduction of camouflage in some forms (compared to non-cremophilous species of *Gasteria*) can be seen as an adaptation to the absence of herbivory in cliff environment.

Presentation: Conspicuous clusters.

Age and persistence: Plants very slow-growing, long-lived, with leaves withering from the base. When turgid, the leaves are very fleshy and subterete or biconvex in the var. *dolomitica*, an adaptation to the dry cliff-face habitat.

Armament: The leaf margin is cartilaginous and serrulate, the leaves mucronate at the apex, but in comparison with other flat-ground species it represents a reduction in armament in response to the undisturbed cliff habitat in contrast to the often thorny but grazed surrounding savanna vegetation.

Sexual reproduction

Inflorescence and flowers: Inflorescence ascending; perianth large, conspicuous, red-pink, green-tipped, suggesting adaptation maximising attraction of pollinators.

Fruit/Seed

Size: Seed 3×2 mm, a relatively small size ideal for establishment in crevices.

Dispersal: Wind-dispersed.

Time: Germination within 14–21 days.

Vegetative reproduction: *Gasteria batesiana* var. *dolomitica* suckers from the base, forming small, dense clusters. The leaves are brittle and will root if they become detached and fall into a crevice, establishing new colonies. Another unique feature of *Gasteria batesiana* var. *dolomitica* is the leaves, which bend backwards and spontaneously form vegetative propagules, rooting in crevices or on ledges. Continual sprouting from the base, rooting of leaves or fragments that have fallen into a crevice and leaf propagules represent a sufficient vegetative backup dispersal strategy for this harsh cliff-face environment.

CONSERVATION STATUS

Classified as critically rare (Raimondo *et al.* 2009). In spite of its localised distribution, it is not threatened and seed from a cultivated source has been distributed to nurseries and botanical gardens in various parts of the world.

ADDITIONAL NOTES

Horticulture: Ideal for subtropical bushveld (savanna) garden (Van Jaarsveld 2010). Plants are best grown in rockeries, dry stone walls or containers, in shade, and are easily grown by division, from leaf cuttings or seed, as specimen pot collections. Keep in partial shade and dry during its winter resting phase. This ease of cultivation suggests a maximum survival reproductive output. Outside its native habitat, it is best grown indoors where it can be protected from the sun and from frost in winter. *Gasteria batesiana* var. *dolomitica* is well established in cultivation, locally and abroad.

VOUCHER

Van Jaarsveld & Hankey 15081 (NBG).

ILLUSTRATIONS AND MAP

Plate 42, Figures 42a–42c, Map 42.

43. *Gasteria croucheri* (Hook.f.) Baker subsp. *pendulifolia* (Van Jaarsv.) Zonn. in *Plant Systematics and Evolution* 251: 217–227 (2005).

Cremonophyte growth form: Cluster-forming, pendent leaves (of medium weight to heavy, cliff hanger).

Growth form formula: A:S:Lper:R:C:La (vb) (eg)

Etymology: The epithet *pendulifolia* (*penduli*, pendulous, and *folium*, leaf) pertains to the pendulous leaves.

DESCRIPTION AND HABITAT

Acaulescent, forming small but dense clusters (off-shooting from base), up to 300 mm in diameter, bearing pendulous leaves in rosettes. Roots slightly fleshy. Leaves spreading-pendulous, linear-lanceolate, up to 470 × 45 mm, without armament, with purplish tinge during dry winter or prolonged drought. Inflorescence conspicuous, simple or branched, up to

500 mm long, pendulous-ascending, tips drooping. Perianth pink, distal half white with green striations to 40 mm long. Fruiting capsule 18–25 mm long, ascending when dry. Seeds black, 3–4 × 2–3 mm.

Phenology: Flowering in spring and summer (October–February), but sporadically at other times as well. Seeds dispersed by wind in summer and autumn (in the wet season).

Pollinators: Sunbirds.

Habitat and aspect: Shady quartzitic sandstone cliffs (southern aspects) overlooking the Umgeni River and adjacent river valleys. The southern slopes are cooler, with shady conditions. Plants are firmly rooted in crevices and on rock ledges large enough to support the roots and stem clusters. Winters are cool but frost is a rarity or absent. The average daily maximum temperature is 27°C. Rainfall occurs mainly from spring to autumn, about 1000–1250 mm per annum (thunder showers), but occasionally also in winter.

Altitude: 100–400 m.

Associated vegetation: KwaZulu-Natal Coastal Belt of the Indian Ocean Coastal Belt (Mucina *et al.* 2005).

Associated cremnophytes: *Aloe arborescens*, *Aptenia cordifolia*, *Cotyledon orbiculata* var. *oblonga*, *Crassula flanaganii*, *C. multicava*, *C. perfoliata* var. *perfoliata*, *Delosperma tradescantioides*, *Petopentia natalensis*, *Plectranthus hadiensis* var. *tomentosus*, *P. purpuratus*, *Portulacaria afra*, *Rhipsalis baccifera* and *Sarcostemma viminale*.

Geology: Natal Group (Cape Supergroup). The sandstone substrate is rich in ledges, crevices and fissures and is ideal for establishment of plants.

DISTRIBUTION

Gasteria croucheri subsp. *pendulifolia* is restricted to cliff faces at Shongweni and Mamba Valley, Durban.

RELATED SPECIES

It differs from *Gasteria croucheri* subsp. *croucheri* in its pendent, linear-lanceolate leaves. When growing in full sun, the leaves are glaucous and compact, without the pendent nature. It differs in the reduction in the general size of the plants and the absence of armament (along the leaf margins) as well as in its inflorescence which is reduced to a simple raceme or occasionally divided from the base.

ADAPTATIONS TO THE CLIFF ENVIRONMENT

Habit: Clustering, with pendent leaves, suggesting an adaptation of maximising light absorption in the shady environment. This form proliferates from basal stolons, forming dense clusters. During the dry season, the leaves become deeply channelled, with a purplish tinge. Its prolific nature compensates for a reduction in floral output. The plant thus invests in vegetative output occupying a rock crevice. The plants are smaller than those of the typical subspecies, this reduction in size allowing them to cope better with gravity.

Size and weight: Heads of medium size and weight.

Leaves

Orientation: Flattened, long-linear, becoming drooping and faintly spotted, an adaptation enabling the plants to maximise absorption of light.

Colour: Slightly glaucous, faintly spotted, becoming purplish during dry periods as the plants aestivate, blocking out excessive light and reducing photosynthesis.

Presentation: Conspicuous clusters.

Age and persistence: Plants long-lived, with leaves withering from the base. The fleshy leaves becoming turgid after rain, but channelled during dry periods, an adaptation to the extreme, dry habitat.

Armament: The leaf margin is entirely smooth, suggesting a reduction in armament in response to the undisturbed cliff habitat in contrast to the often thorny but grazed surrounding thicket vegetation.

Sexual reproduction

Inflorescence and flowers: Inflorescence ascending, with pendulous apices; corolla pink, attracting sunbirds.

Fruit/Seed

Size: Seed 3–4 × 2–3 mm, an ideal size for establishment in crevices.

Dispersal: Light, angular seeds shaken from the capsules and dispersed by wind.

Time: Seeds ripening in summer and autumn, coinciding with the rainy season. Germination within 14–21 days.

Vegetative reproduction: *Gasteria croucheri* subsp. *pendulifolia* suckers from the base, forming dense clusters. The leaves are brittle and will root if they become detached and fall into a crevice, establishing new colonies. Continual sprouting from the base and rooting of leaf fragments that have fallen into a crevice represent a sufficient vegetative backup dispersal strategy for this harsh cliff-face environment.

CONSERVATION STATUS

Classified as vulnerable (Raimondo *et al.* 2009). Threatened and over-exploited. This is a popular item in the medicinal plant trade (Scott-Shaw 1999; Crouch *et al.* 2000).

ADDITIONAL NOTES

Horticulture: *Gasteria croucheri* subsp. *pendulifolia* is a worthwhile introduction to horticulture. It is best grown in moist savanna gardens (Van Jaarsveld & Van Wyk 2001b,

Van Jaarsveld 2006b, 2010). It propagates readily from leaf cuttings planted in a well-drained, sandy mixture and is fairly fast-growing. Plants can also be divided or grown from stolons. Sow seed in spring or summer in a warm, shady position in a sandy, slightly acidic soil and keep moist. *Gasteria croucheri* subsp. *pendulifolia* does well on steep embankments. It is also ideal for large hanging baskets and window sills. Outside its habitat, it is best grown in containers under controlled conditions in a greenhouse. Plants grown at Kirstenbosch are being increased by vegetative means and will be released and introduced through its annual plant sale and from the nursery at Kirstenbosch in future.

VOUCHER

Van Jaarsveld, Baijnath & Heigeldorf 9838 (NBG).

ILLUSTRATIONS AND MAP

Plates 43 & 43a, Figures 43a–43c, Map 43.

44. *Gasteria doreniae* Van Jaarsv. & A.E.van Wyk in *Aloe* 41,4: 81–83 (2004a).

Crempnophyte growth form: Dwarf-sized globose cluster (of light to medium weight, cliff hugger).

Growth form formula: A:S:Lper:R:C:La (vb)

Etymology: After Mrs Doreen Court, botanist and author.

DESCRIPTION AND HABITAT

Plants acaulescent, decumbent to erect, 50–80 mm tall, up to 120 mm in diameter, proliferating from base to form dense clusters up to 150 mm in diameter. Roots fleshy, up to 3 mm in diameter. Leaves distichous, lorate, 35–80 mm long, 14–25 mm in diameter at base, erectly spreading, often becoming patent (apices incurved during dry season); surface minutely asperulous, mottled with dark green and white spots, adaxial surface plane to convex, abaxial side convex; margin tuberculate towards obtuse or acute, mucronate apex. Juvenile leaves distichous, lorate, patent to ascending, similar in texture and colouring to adult leaves. Inflorescence a simple raceme, 120–400 mm long. Scape 3–4 mm broad and flattened at base; floral bracts 5–7 × 2–3 mm, piliferous; pedicels 3–4 mm long, pink. Perianth 15–17 mm long, stipitate for 2–3 mm, globose to globose-ovoid for about a third of perianth length, gasteriform basal portion 6–8 mm wide, pink, distal third pale pink to almost white with green striations, 4 mm in diameter; segments free, apices obtuse, erect becoming erectly spreading. Stamens 10–14 mm long; anthers 2.0–2.5 × 1 mm, included. Ovary 6–7 mm long, green; style 6 mm long; stigma included or just exerted, minute, curved upwards. Capsule 18 mm long, obtuse at apex. Seeds 3–4 × 2–3 mm, black.

Phenology: Flowering in spring (October–November), but sporadically at other times as well. Seed wind-dispersed.

Pollinators: Sunbirds.

Habitat and aspect: Cliffs in the Swartwaterspoort, more so on southern faces. The Swartwatersberg Mountains consist of hard quartzites (Witteberg Group, Cape Supergroup) and are situated 40 km northeast of the location of *Gasteria baylissiana* on the Suurberg (Farm Oudekraal, Witrivier). The average annual daily maximum temperature is about 24°C and the average daily minimum about 11°C. They range from about 600–800 m in altitude, with typical thicket vegetation on the lower slopes and in the poort. Rainfall in the habitat occurs mainly in summer and ranges from 400–500 mm per annum.

Altitude: 350–500 m.

Associated vegetation. Kowie Thicket of the Albany Thicket Biome (Mucina *et al.* 2005).

Associated cremnophytes: *Gasteria doreeniae* shares its cliff-face habitat with the following succulent and bulbous species: *Crassula intermedia*, *C. lactea*, *C. orbicularis*, *C. pellucida* subsp. *marginalis*, *C. perforata*, *Delosperma laxipetalum*, *Haemanthus albiflos* and *Ornithogalum longibracteatum*.

Geology: Witteberg quartzite (Cape Supergroup). The quartzitic sandstone substrate has many ledges, crevices and fissures and is ideal for the establishment of plants.

DISTRIBUTION

Gasteria doreeniae is restricted to cliff faces of Swartwaterspoort in the Eastern Cape.

RELATED SPECIES

Gasteria doreeniae is closely related to the variable *G. bicolor* (non-cremnophyte), but is at once distinguished by its compact growth (plants very shortly stemmed) and short, broad leaves. Superficially not unlike *G. baylissiana* of the adjacent Suurberg, another small, rounded, cluster-forming species. The latter has distinctly tuberculate leaves.

ADAPTATIONS TO THE CLIFF ENVIRONMENT

Habit: Conspicuous globose clusters of distichous heads. It proliferates profusely from the base. Its small size allows effective heat absorption and establishment in crevices, the plants thus also coping better with gravity. During the dry season, the leaves become dorsiventrally flattened and reddish tinged. This improves its ability to survive. The plants' investment in vegetative output (vigorous prolific nature) further enhances occupation of crevices and ultimate survival.

Size and weight: Heads of light to medium weight.

Leaves

Orientation: Distichous, spreading to recurved, maximising absorption of light on the south-facing cliffs.

Colour: Mottled, dull green, becoming reddish in dry periods as the plants aestivate, blocking out excessive light and reducing photosynthesis.

Presentation: Conspicuous clusters.

Age and persistence: Plants long-lived, leaves withering from the base. When turgid, the leaves are very fleshy and often biconvex, an adaptation to the dry vertical habitat.

Armament: The leaf margin is smooth (only slightly crenate-tuberculate at the apex), suggesting a reduction in armament in response to the undisturbed cliff habitat in contrast to the often thorny but grazed surrounding thicket vegetation.

Sexual reproduction

Inflorescence and flowers: Inflorescence ascending; perianth pink, conspicuous.

Fruit/Seed

Size: Seed 3–4 × 2–3 mm, a relatively small size ideal for establishment in crevices.

Dispersal: Capsules ascending and seed released only during strong winds, ensuring a sufficient dispersal distance.

Time: Germination after about 14–21 days.

Vegetative reproduction: *Gasteria doreeniae* suckers freely from the base, forming dense clusters. The leaves are brittle and will root if they become detached and fall into a crevice, establishing new colonies. Continual sprouting from the base and rooting of leaf fragments that have fallen into a crevice represent a sufficient vegetative backup dispersal strategy for this harsh cliff-face environment. Leaves that drop from the cliff face at Swartwaterspoort often root under shrublets, forming small scattered groups—explaining its occurrence in only a narrow strip near the base of the cliffs. Swartwaterspoort is about 15 km west of Riebeeck East in the Eastern Cape and forms part of the Swartwatersberg Mountains (*swart water* means black water, pertaining to the dark but clear water, the dark colour due to the high organic content).

CONSERVATION STATUS

Classified as critically rare (Raimondo *et al.* 2009). In spite of its localised distribution, it is not threatened and seed from a cultivated source has been distributed to nurseries and botanical gardens in various parts of the world.

ADDITIONAL NOTES

Variability: The species varies genetically considerably in a small area (size, shape and texture of leaves, shape of perianth), suggesting adaptable plasticity.

Horticulture: Ideal for thicket gardens. Plants are easily grown by division, from leaf cuttings or seed. It does well in small containers as a specimen pot collection. It should be shaded. This ease of cultivation suggests a maximum survival reproductive output.

VOUCHER

Van Jaarsveld 18763 (NBG).

ILLUSTRATIONS AND MAP

Plate 44, Figures 44a–44c, Map 44.

45. *Gasteria glauca* Van Jaarsv. in *Cactus and Succulent Journal (U.S.)* 70,2: 65–66 (1998).

Cremonophyte growth form: Dwarf-sized globose cluster (of medium weight, cliff hugger).

Growth form formula: A:S:Lper:R:C:La (vb) (rd)

Etymology: Latin *glauca*, pertaining to the glaucous leaf colour.

DESCRIPTION AND HABITAT

Plants proliferating from base to form dense globose clusters up to 250 mm in diameter. Roots up to 2 mm in diameter. Leaves at first distichous, becoming rosulate, 50–70 × 15–18 mm, firm, lorate-lanceolate and falcate to straight, the inner erectly spreading, the outer patent; adaxial surface slightly canaliculate, flat in distal half; abaxial surface convex, with a distinct eccentric keel, both surfaces glaucous; epidermis tuberculate-asperulous; margin tuberculate-denticulate; apex acute, mucronate. Inflorescence racemose, up to 250 mm long; pedicels up to 7 mm long. Perianth 30–43 mm long, gasteriform basally for half of its length or shorter, gasteriform portion reddish pink, variable, up to 10 mm in diameter (globose-elliptic), thence constricted into a tube 4 mm wide. Stamens 25–32 mm long, 3 lengthening in advance; anthers 3 × 1.5 mm long, oblong, included. Ovary 6–2.5 mm long; style 22 mm long; stigma minute. Capsule oblong, 20 × 8 mm. Seed 3 × 2 mm.

Phenology: Flowering in summer (December–January), but sporadically at other times as well. Seed wind-dispersed.

Pollinators: Sunbirds.

Habitat and aspect: Quartzitic sandstone cliffs (east-facing) overlooking the Kouga River (in altitude). Plants grow in crevices and soil pockets (inaccessible rocky ledges). Winters are cool but frost is a rarity or absent. The average daily maximum temperature is about 26°C and the average daily minimum about 11°C. Rainfall in winter (cyclonic) and summer (mainly thunder showers), about 500–600 mm per annum.

Altitude: 400–800 m.

Associated vegetation: Gamtoos Thicket of the Albany Thicket Biome (Mucina *et al.* 2005).

Associated cremonophytes: *Crassula lactea*, *Cyrtanthus montanus*, *Haworthia gracilis* var. *picturata*, *H. viscosa*, *Lampranthus affinis*, *Othonna triplinervia* and *Plectranthus verticillatus*.

Geology: Quartzitic sandstone (light-coloured and smooth-textured), Peninsula Formation (Cape Supergroup). The substrate has many ledges, crevices and fissures and is ideal for establishment of plants.

DISTRIBUTION

Gasteria glauca is restricted to cliff faces of the Kouga River region just west of Guerna Kop.

RELATED SPECIES

Gasteria glauca is related to *G. ellaphieae*, a typically well-camouflaged chasmophyte of the Kouga Dam to the east. The latter has a darker mottled epidermis, with slender, less conspicuous flowers and erect fruiting capsules. With its mottled leaves, *G. ellaphieae* is difficult to spot in its natural habitat. However, although *G. glauca* is conspicuous, on the cliffs it is safe from predation by larger herbivores. It is also related to *G. glomerata* but immediately distinguished by the spirally arranged leaves and flowering time from December–January; *G. glomerata* flowers in October.

ADAPTATIONS TO THE CLIFF ENVIRONMENT

Genetic variability: Plants vary in leaf and perianth size and shape, characters retained in cultivation at Kirstenbosch. This variability in a small population suggests genotypic plasticity.

Habit: It profusely proliferates from the base, forming small, dense clusters. Its small size allows effective heat absorption and establishment in crevices, the plants thus also coping better with gravity. During the dry season, the leaves become dorsiventrally flattened and reddish tinged. This improves its ability to survive. The plants' investment in vegetative output (vigorous prolific nature) further enhances occupation of crevices and ultimate survival.

Size and weight: Heads small.

Leaves

Orientation: Spreading to recurved, maximising light absorption on the east-facing cliffs.

Colour: Grey-green, unspotted, becoming reddish during dry periods as the plants aestivate, blocking out excessive light and reducing photosynthesis. The reduction of camouflage in comparison to non-cremophilous species of *Gasteria* can be seen as an adaptation to the absence of herbivory in the cliff environment.

Presentation: Conspicuous clusters.

Age and persistence: Plants long-lived, leaves withering from the base. When turgid, the leaves are very fleshy and often biconvex, an adaptation to the dry vertical habitat.

Armament: The leaf margin is tuberculate-dentate, the leaves mucronate at the apex, but in comparison with flat-ground species it represents a reduction in armament in response to the undisturbed cliff habitat in contrast to the often thorny but grazed surrounding thicket vegetation.

Sexual reproduction

Inflorescence and flowers: Inflorescence ascending; perianth red-pink, large and conspicuous compared to that of the chasmophytic species *Gasteria baylissiana* and *G. ellaphieae*, suggesting an adaptation maximising attraction of pollinators.

Fruit/Seed

Size: Seed about 3×2 mm, a relatively small size ideal for establishment in crevices.

Dispersal: Another unique feature is the capsules that remain pendulous or become spreading (only occasionally erect). The capsules of all other *Gasteria* species (except *G. glomerata*) become distinctly erect. This feature (retained in cultivation) suggests a local dispersal strategy, the seeds dropping when the capsules ripen and not dependent on wind dispersal to the same extent as in other species. This corresponds to the very localised distribution on a few cliff faces. The spreading to erect capsules suggest wind dispersal, but to a lesser degree.

Time: Seeds ripening in summer and autumn, coinciding with the rainy season. Germination within 14–21 days.

Vegetative reproduction: *Gasteria glauca* suckers from the base, forming dense clusters. The leaves are brittle and will root if they become detached and fall into a crevice, establishing new colonies. Continual sprouting from the base and rooting of leaf fragments that have fallen into crevices represent a sufficient vegetative backup dispersal strategy for this harsh cliff-face environment.

CONSERVATION STATUS

Although classified as critically rare (Raimondo *et al.* 2009), it is not threatened and seed from a cultivated source has been distributed to nurseries and botanical gardens in various parts of the world.

ADDITIONAL NOTES

Horticulture: *Gasteria glauca* is a worthwhile introduction to horticulture. It is best grown in thicket gardens (Van Jaarsveld 2010). It propagates readily from leaf cuttings planted in a well-drained, sandy mixture and is fairly fast-growing. Plants can also be divided or grown from stolons. Sow seed in spring or summer in a warm, shady position in a sandy, slightly acidic soil and keep moist. *Gasteria glauca* is excellent for containers and miniature rock gardens. Outside its habitat, it is best grown in containers under controlled conditions in a greenhouse. Plants grown at Kirstenbosch are being continuously increased and made available to the general public. This ease of cultivation suggests a maximum survival reproductive output.

VOUCHER

Van Jaarsveld & Welsh 14760 (NBG).

ILLUSTRATIONS AND MAP

Figures 45a–45d, Map 45.

46. *Gasteria glomerata* Van Jaarsv. in Bradleya 9: 100 (1991a).

Cremnophyte growth form: Dwarf-sized globose cluster (of light to medium weight, cliff hugger).

Growth form formula: A:S:Lper:R:C:La (vb) (rd)

Etymology: Latin *glomerata*, closely together in a head, alluding to the growth habit.

DESCRIPTION AND HABITAT

Plants proliferating from base to form dense globose clusters up to 200 mm in diameter. Roots up to 2 mm in diameter. Leaves distichous, 15–50 × 15–25 mm, lorate to widely ovate, the inner erectly spreading, the outer patent or recurved, biconvex in cross section to almost terete, becoming dorsiventrally flattened during dry season; both surfaces glaucous, immaculate; epidermis minutely tuberculate-asperulous; margin entire, minutely crenulate-tuberculate in distal quarter; apex truncate or obtuse, mucronate. Inflorescence an erectly spreading raceme, 120–200 mm long. Perianth 20–27 mm long, gasteriform basally for slightly more than half of the perianth length, gasteriform portion reddish pink, variable, 6–9(–10) mm in diameter (globose-elliptic to globose), thence constricted into a tube 4 mm wide. Stamens 18–20 mm long, 3 lengthening in advance; anthers 2 mm long, oblong, included. Ovary 4–5 mm long, 2 mm in diameter. Style 10–11 mm long; stigma minute. Capsules 14–16 × 8 mm long, mostly pendulous to spreading. Seeds 3 × 2 mm, black.

Phenology: Flowering in spring (October–November), but sporadically at other times as well. Seed wind-dispersed.

Pollinators: Sunbirds.

Habitat and aspect: Mainly south-facing quartzitic sandstone cliff faces overlooking the Kouga River, the plants growing in crevices and soil pockets of inaccessible rocky ledges. Summers are hot and dry. Winters are cooler but frost is a rarity or absent. The average daily maximum temperature is about 27°C and the average daily minimum about 12°C. Rainfall occurs mainly in summer and winter, about 300–400 mm per annum.

Altitude: 400–700 m

Associated vegetation: Gamtoos Thicket of the Albany Thicket Biome (Mucina *et al.* 2005).

Associated cremnophytes: *Adromischus cristatus* var. *zeyheri*, *Cotyledon tomentosa* subsp. *tomentosa*, *Crassula rupestris* subsp. *rupestris* 'Kouga form', *Cyrtanthus flammosus*, *Gasteria glomerata*, *Haworthia gracilis* var. *picturata*, *H. viscosa*, *Othonna lobata* and *Plectranthus verticillatus*.

Geology: Quartzitic sandstone (light-coloured and smooth-textured), Peninsula Formation (Cape Supergroup). Substrate with many ledges, crevices and fissures ideal for establishment of plants.

DISTRIBUTION

Restricted to cliff faces of the Kouga Dam in the lower reaches of the Kouga River region.

RELATED SPECIES

Gasteria glomerata is related to *G. baylissiana*, a typically well camouflaged chasmophyte of the Witteberg north of Port Elizabeth. The latter has a darker mottled epidermis, with smaller, less conspicuous flowers and erect fruiting capsules. With its mottled leaves, *G. baylissiana* is difficult to spot in its natural habitat.

ADAPTATIONS TO THE CLIFF ENVIRONMENT

Habit: Conspicuous globose clusters of distichous heads. It proliferates profusely from the base. Its small size allows effective heat absorption and establishment in crevices, the plants thus also coping better with gravity. During the dry season, the leaves become dorsiventrally flattened and reddish tinged. This improves its ability to survive. The investment in vegetative output (vigorous prolific nature) further enhances occupation of crevices and ultimate survival.

Size and weight: Heads small, of light to medium weight.

Leaves

Orientation: Distichous, spreading to recurved, maximising absorption of light on the south-facing cliffs.

Colour: Grey-green, unspotted, becoming reddish during dry periods as the plants aestivate, blocking out excessive light and reducing photosynthesis. The reduction of camouflage in comparison to non-cremophilous species of *Gasteria* can be seen as an adaptation to the absence of larger herbivores in the cliff environment.

Presentation: Conspicuous clusters.

Age and persistence: Plants long-lived, leaves withering from the base. When turgid, the leaves are very fleshy and often biconvex, an adaptation to the dry vertical habitat.

Armament: The leaf margin is smooth (only slightly crenate-tuberculate at the apex), suggesting a reduction in armament in response to the undisturbed cliff habitat in contrast to the often thorny but grazed surrounding thicket vegetation.

Sexual reproduction

Inflorescence and flowers: Inflorescence ascending; perianth red-pink, conspicuous, its large size compared to that of chasmophytes such as *Gasteria baylissiana* and *G. ellaphieae* suggesting an adaptation maximising attraction of pollinators.

Fruit/Seed

Size: Seed 3×2 mm, a relatively small size ideal for establishment in crevices.

Dispersal: Another unique feature is the capsules, some remaining pendulous and others becoming spreading or erect. The capsules of all other *Gasteria* species (except *G. glauca*) become distinctly erect. This feature (retained in cultivation) suggests a local

dispersal strategy, the seeds dropping when the capsules ripen and not dependent on wind dispersal to the same extent as in other species. This corresponds to the very localised distribution consisting of six to eight closely spaced cliff faces in the Kouga Dam region. The spreading to erect capsules suggest wind dispersal, but with a reduced role.

Time: Seeds ripening in late spring, coinciding with the rainy season. Germination within 14–21 days.

Vegetative reproduction: *Gasteria glomerata* suckers from the base, forming dense, rounded clusters. The leaves are brittle and will root if they become detached and fall into a crevice, establishing new colonies. Continual sprouting from the base and rooting of leaf fragments that have fallen into a crevice represent a sufficient vegetative backup dispersal strategy for this harsh cliff-face environment.

CONSERVATION STATUS

Although it is classified as critically rare (Raimondo *et al.* 2009), it is not threatened and seed from a cultivated source has been distributed to nurseries and botanical gardens in various parts of the world.

ADDITIONAL NOTES

Variability: The species varies genetically considerably in a small area (size, shape and texture of leaves, shape of perianth), suggesting adaptable plasticity.

Horticulture: A worthwhile introduction to horticulture, especially the house plant trade (Van Jaarsveld 2010). It can also be grown out of doors in partial shade in rock crevices in rockeries. It is, however, best grown in thicket gardens. It propagates readily from leaf cuttings planted in a well-drained, sandy mixture and is fairly fast-growing. Plants can also be divided or grown from stolons. Sow seed in spring or summer in a warm, shady position in a sandy, slightly acidic soil and keep moist. *Gasteria glomerata* grows well in miniature rock gardens. Outside its habitat, it is best grown in containers under controlled conditions in a greenhouse. Plants grown at Kirstenbosch are being continuously increased and made available to the general public. Today it is well established in ornamental horticulture throughout the world. This ease of cultivation suggests a maximum survival reproductive output.

VOUCHER

Van Jaarsveld & Sardien 11054 (NBG).

ILLUSTRATIONS AND MAP

Plate 46, Figures 46a–46c, Map 46.

47. *Gasteria pillansii* Kensit var. *ernesti-ruschii* (Dinter & Poelln.) Van Jaarsv. in Aloe 29,1: 17 (1992a).

Cremonophyte growth form: Dwarf-sized mat-forming cluster (of light to medium weight, cliff hugger).

Growth form formula: A:S:Lper:R:C:La (vb)

Etymology: The specific epithet commemorates Mr N.S. Pillans (1884–1964), a botanist at the Bolus Herbarium who collected plants near Clanwilliam and grew this plant in his garden in Rosebank, Cape Town. The variety is named for Ernst Rusch (1867–1957), a Namibian farmer who collected plants in southern Namibia.

DESCRIPTION AND HABITAT

Plants proliferating from base to form dense mats up to 300 mm in diameter. Roots up to 2 mm in diameter. Leaves distichous, 20–70 × 15–30 mm, lorate to widely ovate, spreading, patent, dorsiventrally compressed, becoming turgid during moist winters; both surfaces mottled dull green; epidermis minutely asperulous; margin entire, minutely crenulate-tuberculate; apex truncate or obtuse, mucronate. Inflorescence an erectly spreading raceme, 60–300– mm long. Perianth 25–30 mm long, reddish pink, gasteriform shortly at base, thence constricted into a tube 5–6 mm wide. Stamens with anthers included or shortly exposed. Ovary 4–5 mm long; 2 mm in diameter; style about 25 mm long; stigma minute. Capsule 14–16 × 8 mm long, becoming erect. Seeds 3 × 2 mm, black.

Phenology: Flowering in summer (December–January). Seed wind-dispersed.

Pollinators: Sunbirds.

Habitat and aspect: An obligate cremnophyte of the lower Orange River Valley of the Lorelei, Sonberg and Kuamsibberg Mountains. Plants are confined to sheer south-facing aspects, growing in crevices and soil pockets of inaccessible rocky ledges that are in permanent shade in the winter months. Summers are hot and dry. Winters are cooler and frost is absent. The average daily maximum temperature is about 27°C and the average daily minimum about 10°C. Rainfall mainly in winter, about 50–100 mm per annum.

Altitude: 400–700 m.

Associated vegetation: Succulent Karoo.

Associated cremnophytes: *Aloe pavelkae*, *Conophytum ricardianum*, *Crassula pseudohemisphaerica*, *C. sericea* var. *sericea*, *Cyrtanthus herrei*, *Tylecodon bruynsii*, *T. buchholzianus* subsp. *buchholzianus* and *T. racemosus*.

Geology: Quartzitic sandstone (light-coloured to reddish and smooth-textured), Nama Group Karoo Supergroup). Substrate with many ledges, crevices and fissures, ideal for establishment of plants.

DISTRIBUTION

Gasteria pillansii var. *ernesti-ruschii* is restricted to cliff faces of southern Namibia and is mainly confined to the Ai-Ais Richtersveld Transfrontier National Park, which is in the lower reaches of the Orange River and just east of Rosh Pinah.

RELATED SPECIES

Gasteria pillansii var. *ernesti-ruschii* is related to the var. *pillansii*, a very variable taxon to the south. The latter is immediately differentiated by its much larger and longer, ascending-spreading, lorate leaves.

ADAPTATIONS TO THE CLIFF ENVIRONMENT

Habit: Conspicuous dense, mat-forming clusters of distichous, patent leaves. It profusely proliferates from the base. Its small size allows effective heat absorption and establishment in crevices, the plants thus also coping better with gravity. During the dry season, the leaves become reddish and flattened. This improves its ability to survive. The plants' investment in vegetative output (vigorous prolific nature) further enhances occupation of crevices and ultimate survival.

Size and weight: Heads small, of light to medium weight.

Leaves

Orientation: Distichous, patent, maximising absorption of light on the shady south-facing cliffs.

Colour: Dull mottled green, spotted, becoming reddish during dry periods as the plants aestivate, blocking out excessive light and reducing photosynthesis.

Presentation: Conspicuous clusters.

Age and persistence: Plants long-lived, leaves withering from the base. When turgid, the leaves are very fleshy.

Armament: The leaf margin is smooth (only slightly crenate-tuberculate at the apex), suggesting a reduction in armament in response to the undisturbed cliff habitat in contrast to the often thorny but grazed surrounding succulent karoo.

Sexual reproduction

Inflorescence and flowers: Compared to solitary *Gasteria* species such as *G. excelsa*, which forms a large paniculate inflorescence, *G. pillansii* var. *ernesti-ruschii* has a smaller, spreading inflorescence (and only a very limited number per clone). This suggests an effective vegetative backup associated with so many cremophilous succulent plants. The inflorescence is ascending-spreading, the perianth red-pink and conspicuous. The large perianth size compared to that of chasmophytes such as *G. baylissiana* and *G. ellaphieae* suggests rich flowering, an adaptation maximising attraction of pollinators on the cliff face.

Fruit/Seed

Size: Seed 3 × 2 mm, a relatively small size ideal for establishment in crevices.

Dispersal: Capsules becoming erect after fertilisation, the erect capsules suggesting wind dispersal. Strong gusts of wind, common to the cliff habitat, will lift the seeds from the capsules and disperse them.

Time: Seeds ripening in late spring, coinciding with the rainy season. Germination within 14–21 days.

Vegetative reproduction: *Gasteria pillansii* var. *ernesti-ruschii* suckers from the base, forming dense, rounded clusters. The leaves are brittle and will root if they become detached and fall into a crevice, establishing new colonies. Continual sprouting from the base and rooting of leaf fragments that have fallen into a crevice represent a sufficient vegetative backup dispersal strategy for this harsh cliff-face environment.

CONSERVATION STATUS

In spite of its localised distribution, it is not threatened and seed from a cultivated source has been distributed to nurseries and botanical gardens in various parts of the world.

ADDITIONAL NOTES

Horticulture: *Gasteria pillansii* var. *ernesti-ruschii* thrives in cultivation. Outside its habitat, it is best grown in small containers under greenhouse conditions where moisture can be controlled. Plants can also be divided or grown from stolons. Sow seed in autumn in a warm, shady position in a sandy, slightly acidic soil and keep moist. Excellent for miniature rock gardens. The ease of cultivation suggests a maximum survival reproductive output.

VOUCHER

Van Jaarsveld 21065 (NBG).

ILLUSTRATIONS AND MAP

Plate 47, Figures 47a & 47b, Map 47.

48. *Gasteria rawlinsonii* Oberm. in *The Flowering Plants of Africa* 43: t. 1701 (1976).

Cremonophyte growth form: Leafy pendent stems, clusters (of medium weight to heavy, cliff hanger).

Growth form formula: E:F:P:R:C:Rls (eg)

Etymology: Named for S.I. Rawlinson, South African collector and grower of succulent plants.

DESCRIPTION AND HABITAT

Plants caulescent, pendulous, prolific from base, with long pendent stems up to 1 m long. Stems foliate, occasionally branched; internodes 10–20 mm apart. Roots succulent, up to 3 mm in diameter. Leaves distichous or spirally arranged, linear, lorate, slightly falcate, 30–80

× 10–25 mm; both surfaces green, not spotted, or with faint white spots, abaxial surface convex, without a keel; epidermis asperulous; margin sparsely denticulate, sometimes unarmed; prickles turning black with age; apex recurved obtuse, mucronate. Inflorescence racemose, 100–500 mm long; bracts 5 mm long, 2 mm broad at base. Perianth reddish pink, variable, 16–25 mm long, stipitate for 1–3 mm, gasteriform basally over more than half the perianth length (globose-elliptic or globose), thence constricted to a tube 4–6 mm in diameter, gasteriform portion pink, 6–9 mm in diameter; tube pink or white, occasionally with green striations. Stamens 17 mm long; anthers 2 mm long. Ovary oblong-ovoid, 5 × 2–3 mm; style 11–12 mm long. Capsule 18 mm long, oblong-ovoid. Seeds 3–4 mm wide.

Phenology: Flowering in spring (October–November), but sporadically at other times as well. Seed wind-dispersed.

Pollinators: Sunbirds.

Habitat and aspect: Quartzitic sandstone cliffs in kloofs of the Baviaanskloof and Kouga Mountains, on all aspects but more so on south-facing ones. These kloofs are often very narrow and shady. It is hot in summer, mild to warm in winter and frost is absent from the habitat. Average daily maximum temperature is about 25°C and the average daily minimum about 9°C. Rainfall mainly in winter and summer, an average of about 200–300 mm per annum.

Altitude: 300–700 m.

Associated vegetation: Gamtoos Thicket of the Albany Thicket Biome (Mucina *et al.* 2005).

Associated cremnophytes: *Adromischus cristatus* var. *zeyheri*, *Albuca cremnophila*, *Cotyledon tomentosa* subsp. *tomentosa*, *Cyrtanthus montanus*, *C. labiatus*, *Delosperma esterhuyseniae*, *Haworthia gracilis* var. *picturata*, *H. viscosa*, *Othonna lobata* and *Plectranthus verticillatus*.

Geology: Quartzitic sandstone, Peninsula Formation (Cape Supergroup). The quartzitic sandstone substrate has many ledges, crevices and fissures, ideal for establishment of plants.

DISTRIBUTION

Gasteria rawlinsonii is restricted to the Baviaanskloof Mountains, occurring in sheer, narrow, often shady north-south-running kloofs.

RELATED SPECIES

Gasteria rawlinsonii with its long, pendent stems is unique in the genus. *Gasteria bicolor* of the thickets to the east is the only other *Gasteria* with leafy stems. That species has very different mottled leaves (well camouflaged in its habitat), smaller and pinkish flowers and a decumbent habit. When detached as a result of disturbance, the leaves proliferate and form new plantlets.

ADAPTATIONS TO THE CLIFF ENVIRONMENT

Habit: Conspicuous clusters of pendent, leafy stems. It profusely proliferates from the base, forming clusters. It occupies larger to smaller ledges. The plants' investment in vegetative output (vigorous prolific nature) further enhances occupation of crevices and ultimate survival.

Size and weight: Heads medium-sized, adult specimens of medium weight to heavy.

Stems: Fibrous and very tough, not brittle, suggesting an adaptation coping with gravity.

Leaves

Orientation: Distichous (more exposed, xeric habitats) or spirally distichous (shady places), spreading and becoming slightly recurved, the spirally distichous type maximising absorption of light. This distichous form grows along the western, drier part of the range.

Colour: Dull brownish green to reddish green, faintly mottled in the spirally distichous types. The reduction of camouflage in comparison to non-cremnophilous species of *Gasteria* can be seen as an adaptation to the cliff environment.

Presentation: Conspicuous clusters.

Age and persistence: Plants long-lived, with long leafy stems (covered with perennial and functional leaves withering from the base). When turgid, the leaves are very fleshy and often biconvex, thus with enough water stored for existence in the dry, cliff-face habitat.

Armament: The leaf margin is almost smooth in the distichous form (only slightly crenate-tuberculate at the apex), suggesting a reduction in armament in response to the undisturbed cliff habitat in contrast to the often thorny but grazed surrounding thicket vegetation. The spirally distichous form occurs in regions to the east where the rainfall is slightly higher and the kloofs narrower and shadier, the unique black prickles perhaps an adaptation that deters the often cremnophilous (and roosting place at night) chacma baboon (*Papio ursinus*). Other plants, such as *Ficus* species with long aerial roots and hanging branches, enable primates (baboons and monkeys) to reach this form.

Sexual reproduction

Inflorescence and flowers: Inflorescence drooping; perianth red-pink, conspicuous. It does not flower from all stems, compensating by its prolific vegetative output. The large perianth size compared to that of other thicket species suggests an adaptation maximising attraction of pollinators.

Fruit/Seed

Size: Seed 4×3 mm, a relatively small size ideal for establishment in crevices.

Dispersal: As in other species of *Gasteria*, the spreading to erect capsules suggest wind dispersal.

Time: Seeds ripening in late spring, coinciding with the rainy season. Germination after 14–21 days.

Vegetative reproduction: *Gasteria rawlinsonii* suckers freely from the base, forming dense hanging clusters. Continual sprouting from the base and rooting of stems that have fallen into a crevice act as a sufficient vegetative backup dispersal strategy for this harsh cliff-face environment. Unlike in other *Gasteria* species, the leaves are not brittle, and do not proliferate

when detached (in rare cases plants might proliferate), suggesting a loss of this ability due to its cliff habitat.

CONSERVATION STATUS

In spite of its localised distribution and rare status (Raimondo *et al.* 2009), it is not threatened and seed from a cultivated source has been distributed to nurseries and botanical gardens in various parts of the world.

ADDITIONAL NOTES

Variability: The species varies genetically considerably within a small area (size, shape and texture of leaves, shape of perianth), suggesting adaptable plasticity. It is a slow-growing cremnophyte with two forms grading into each other, the first with leaves remaining distichous and with a short inflorescence; the second with spirally arranged leaves and longer inflorescences, the gasteriform portion of the perianth globose.

Horticulture: *Gasteria rawlinsonii* is a worthwhile introduction to horticulture. It is best grown in thicket gardens (Van Jaarsveld 2006b, 2010). It is ideal for embankments, large hanging baskets and balconies in shady positions and excellent for growing in containers and miniature rock gardens. Best propagated by division, from stem cuttings or seed, grown as a specimen pot collection. Sow seed in spring or summer in a warm, shady position in a sandy, slightly acidic soil and keep moist. Outside its habitat, it is best grown in containers under controlled conditions in a greenhouse. Plants grown at Kirstenbosch are being continuously increased and made available to the general public. Today it is well established in ornamental horticulture throughout the world. The ease of cultivation suggests a maximum survival reproductive output.

VOUCHER

Van Jaarsveld 7134 (NBG).

ILLUSTRATIONS AND MAP

Plate 48, Figures 48a–48c, Map 48.

49. *Gasteria tukhelensis* Van Jaarsv., in Van Jaarsveld & Van Wyk in *Bothalia* 35,2: 164–166 (2005c).

Crempnophyte growth form: Cluster (of medium weight to heavy, cliff hugger).

Growth form formula: A:S:Lper:R:C:La (vb)

Etymology: From the Thukela River, KwaZulu-Natal.

DESCRIPTION AND HABITAT

Plants acaulescent, decumbent, 250 mm high, up to 700 mm in diameter, proliferating from base, cluster-forming (3–8 heads). Roots succulent, up to 5 mm in diameter. Leaves rosulate, 120–250 mm long, up to 30–50 mm broad at base, triangular-lanceolate, falcate and curving

upwards, sometimes becoming recurved; adaxial surface deeply canaliculate, plane towards apex, faintly white-spotted; abaxial surface somewhat convex with distinct eccentric keel and faintly spotted; spots arranged in obscure transverse bands; both surfaces shiny dark green with smooth epidermis; margin minutely denticulate to almost entire; apex obtuse or acute, often acuminate, mucronate. Juvenile leaves distichous, lorate, patent to ascending; epidermis tuberculate, densely white-spotted, spots arranged in transverse bands; apex obtuse, mucronate.

Inflorescence racemose, up to 560 mm long, with 2 side branches; racemes horizontally spreading, up to 300 mm long; scape 4–5 mm broad at base, flattened; floral bracts 7×2 mm, piliferous; pedicels 17 mm long, pink. Perianth 40–43 mm long (up to 11 flowers open at the same time), stipitate for 3–4 mm, gasteriform basally (narrowly elliptic) over half perianth length, gasteriform portion 6 mm wide (subcylindrical), pink, distal half white with green striations, inflated to the same diameter as basal portion (with slight constriction in middle); apices erect, becoming erectly spreading, obtuse; margins of inner segments free, channelled at base for 10–12 mm, margins diverging gradually towards apex. Stamens 34–37 mm long; anthers 3×1.5 mm, included or shortly exerted. Ovary 8 mm long, 3 mm in diameter, green; style 31 mm long, stigma included or shortly exerted, curved upwards, minute. Capsule 23–32 mm long, clavate, triangular in cross section, obtuse at apex, 6–8 mm in diameter. Seeds $5-7 \times 2-3$ mm, black.

Phenology: Flowering in late spring and summer (November, December) but sporadically at other times as well. Seeds dispersed by wind in summer and autumn (during the wet season).

Pollinators: Sunbirds.

Habitat and aspect: Cliff faces above the Thukela River. It grows in crevices in humus-rich ledges on shale and mudstone rocks in dry savanna (succulent thickets). The rosettes grow in crevices, in the shade of succulent thicket consisting of *Bulbine natalensis*, *Cotyledon orbiculata*, *Crassula nudicaulis*, *C. orbicularis*, *C. perfoliata* var. *perfoliata*, *Delosperma lebomboensis*, *Gerrardanthus macrorrhizus*, *Petopentia natalensis* and *Plectranthus hadiensis* var. *tomentosus*. Although the vegetation of the KwaZulu-Natal region is well known, the flora of the sheer cliff faces in the Thukela region is still poorly known and likely to yield more new species. The Thukela Valley has a dry subtropical climate and is situated in a rain shadow. Summers are very hot, temperatures frequently above 30°C. The average daily maximum temperature is about 27°C and the average daily minimum about 14°C. Winters are mild, frost is absent or very light. Rainfall occurs mainly in summer, ranging from 500–700 mm per annum.

Altitude: 350–400 m.

Associated vegetation: Eastern Valley Bushveld of the Savanna Biome (Mucina *et al.* 2005).

Associated cremnophytes: Taller shrubs are *Aloe arborescens*, *A. rupestris*, *Commiphora harveyi*, *Euphorbia tirucalli*, *E. evansii*, *Ficus ingens* and *Portulacaria afra*. The small species include *Aptenia cordifolia*, *Crassula multicava*, *C. perfoliata* var. *perfoliata*, *Delosperma tradescantioides*, *Petopentia natalensis*, *Rhipsalis baccifera* and *Sarcostemma viminalis*.

Geology: Mudstone of the Vryheid Formation (Ecca Group) of the Karoo Supergroup.

DISTRIBUTION

Gasteria tukhelensis is known only from the lower Thukela Valley near Kranskop, and as yet only from the type collection, but probably occurs elsewhere along the river, in similar habitats.

RELATED SPECIES

Gasteria tukhelensis is at once distinguished from *G. batesiana* by its much larger rosettes of falcate, dark green leaves, often becoming recurved and with a shiny, faintly spotted surface. The leaf margin is minutely denticulate to almost entire. The inflorescence can be a simple raceme (with up to 11 flowers open at the same time), but in adult plants with a pair of side branches. It is prolific from the base, forming clusters on the sheer southwest-facing cliffs above the northern bank of the Thukela River, east of Ngubevu near Kranskop. It is at once distinguished from *G. pendulifolia* by the shiny leaf surface, slightly tuberculate when young. Floristically it can be placed within *Gasteria* series *Longifoliae*. The long, slender perianth comes closest to that of *G. acinacifolia* of the coastal Eastern Cape and eastern extreme of the Western Cape. In *G. tukhelensis* the perianth is 42 mm long and only gently bent, not as markedly as in *G. batesiana*. The perianth in *G. batesiana* is usually shorter, 35–40 mm. The long, slender pedicels are 17 mm long, compared to 6–12 mm in *G. batesiana*. The fruiting capsules also differ from those of *G. batesiana*, being more slender and 23–32 mm long compared to 16–20 mm in *G. batesiana*.

ADAPTATIONS TO THE CLIFF ENVIRONMENT

Habit: Clustering, with ascending rosettes suggesting an adaptation to maximise light absorption in its shady environment. *Gasteria tukhelensis* proliferates from basal stolons, forming dense clusters.

Size and weight: Heads of medium weight to heavy in large clusters.

Leaves

Orientation: Ascending-spreading.

Colour: Mottled green, faintly spotted, becoming purplish during dry periods as the plants aestivate, blocking out excessive light and reducing photosynthesis.

Presentation: Conspicuous clusters.

Age and persistence: Plants long-lived, leaves withering from the base.

Armament: Leaf margin minutely denticulate to almost entire.

Sexual reproduction

Inflorescence and flowers: Inflorescence spreading, with pendulous apices; corolla pink, attracting sunbirds.

Fruit/Seed

Size: Seed 5–7 × 2–3 mm, a size sufficient for establishment in crevices.

Dispersal: Angular seeds shaken from the capsules and dispersed by wind.

Time: Seeds ripening in summer and autumn, coinciding with the rainy season.
Germination within 14–21 days.

Vegetative reproduction: *Gasteria tukhelensis* suckers from the base, forming dense clusters. The leaves are brittle and will root if they become detached and fall into a crevice, establishing new colonies. Continual sprouting from the base and rooting of leaf fragments that have fallen into crevices represent a sufficient vegetative backup dispersal strategy for this harsh cliff-face environment.

CONSERVATION STATUS

Although classified as rare (Raimondo *et al.* 2009), it is not threatened owing to the safe cliff-face habitat.

ADDITIONAL NOTES

Variability: The species varies genetically considerably within a small area (size, shape and texture of leaves, shape of perianth), suggesting adaptable plasticity.

Horticulture: Ideal for bushveld and subtropical coastal gardens (Van Jaarsveld 2010), but should preferably be planted in partial shade. Plants are easily grown by division, from leaf cuttings or seed. It does well in containers as a specimen pot collection. This ease of cultivation suggests a maximum survival reproductive output.

VOUCHER

Van Jaarsveld 17996 (NBG).

ILLUSTRATIONS AND MAP

Plate 49, Figures 49a–49e, Map 49.

HAWORTHIA Duval

50. *Haworthia angustifolia* Haw. var. *baylissii* (C.L.Scott) M.B.Bayer in *Aloe* 36, 4: 72 (1999).

Cremonophyte growth form: Cluster-forming, recurved leaves (of light weight, cliff hugger).

Growth form formula: A:S:Lper:R:C:La (vb)

Etymology: After Roy Bayliss (1909–1994), enthusiastic collector of succulent plants.

DESCRIPTION AND HABITAT

Plants dwarf-sized, rosulate, prolific from base, forming semiglobose clusters up to 60 mm high, up to 120 mm in diameter and consisting of up to 12 heads. Rosettes about 55 mm in diameter. Roots grey, terete. Leaves triangular-lanceolate, up to 20, in a rosette, erect at first,

becoming spreading and recurved; upper side flat to slightly channelled, cymbiform below; surface smooth, green, becoming purplish during dry periods; margin ciliate, apex acute, aristate. Inflorescence racemose, 130–250 mm long, 8–15-flowered in distal half; bracts white, clasping, up to 3 mm long, ovate-acuminate; pedicels 1.5 mm long. Perianth tubular, curved, ascending-spreading, 15–18 mm long, white with green midstripe. Ovary tubular, 2 × 1.5 mm, green; stigma 1 mm long, widening and truncate at apex.

Phenology: Flowering mainly from spring to early summer (October–November). Seeds dispersed by wind in summer and early autumn.

Pollinators: Insects.

Habitat and aspect: Cliffs of narrow shady kloof aspects. Plants firmly rooted in crevices, and size often depending on the growing space allowed by the crevice. Temperature high in summer (35–40°C). Winters are cooler but frost is absent. Rainfall throughout the year but with a peak in spring and summer, ranging from 400–500 mm per annum (thunder showers or cyclonic winter rain).

Altitude: 400–500 m.

Associated vegetation: Mainly Sundays Thicket of the Albany Thicket Biome (Mucina *et al.* 2005).

Associated cremnohytes: *Bulbine latifolia*, *Crassula intermedia*, *C. perfoliata* var. *minor*, *Haworthia glauca*, *Lampranthus affinis*, *Ledebouria concolor* and *Ornithogalum juncifolium*.

Geology: Quartzitic sandstone (light-coloured and smooth-textured), Witteberg Group, Witpoort Formation (Cape Supergroup). Substrate with many ledges, crevices and fissures, ideal for establishment of plants.

DISTRIBUTION

Haworthia angustifolia var. *baylissii* is a quartzitic sandstone endemic, confined to the narrow gorge cut by the Witrivier through the Suurberg Mountains of the Eastern Cape.

RELATED SPECIES

Haworthia angustifolia var. *baylissii* is related to the var. *angustifolia*, a chasmophyte occurring on exposed rocky outcrops in grassy fynbos. The latter has narrow, lanceolate, acuminate leaves and is sufficiently camouflaged.

ADAPTATIONS TO THE CLIFF ENVIRONMENT

Habit: Globose clusters in shady cliffs.

Size and weight: Heads small, of light weight.

Leaves

Orientation: Flattened, becoming recurved, an adaptation maximising absorption of light in the shady environment.

Colour: Green, becoming purplish during dry periods as the plants aestivate, blocking out excessive light and reducing photosynthesis.

Presentation: Conspicuous globose clusters.

Age and persistence: Plants long-lived, soft leaves withering from the base. The very fleshy leaves are soft, becoming turgid after rain but channelled during dry periods, an adaptation to the extreme, dry habitat.

Armament: The soft leaf texture and entire margin (occasionally ciliate) suggest a reduction in armament in response to the undisturbed cliff habitat in contrast to the thorny but heavily grazed surrounding thicket vegetation.

Sexual reproduction

Inflorescence and flowers: Inflorescence ascending to spreading; corolla white, attracting the right pollinating flying insect in summer (December–February).

Fruit/Seed

Size: Seed small, ideal for establishment in crevices.

Dispersal: Light, angular seeds shaken from the capsules and dispersed by wind.

Time: Seeds ripening in late summer and autumn, coinciding with the autumn rains. Germination within 14–21 days.

Vegetative reproduction: *Haworthia angustifolia* var. *baylissii* suckers freely from the base, forming dense, rounded clusters. Continual sprouting from the base represents an efficient vegetative backup dispersal strategy for this harsh cliff-face environment. Detached clusters or heads will also root if they fall into a crevice.

CONSERVATION STATUS

A local endemic, not threatened.

ADDITIONAL NOTES

Horticulture: Best grown in a sandy, slightly acid soil mixture. Feed in spring and summer and keep dry in winter. Plants easily grown by division, thriving in cultivation but in shady places. Outside its thicket habitat, is best grown under controlled conditions in a greenhouse. Plants rapidly dividing, forming clusters. Its very easy growing nature maximises survival rate.

VOUCHER

Van Jaarsveld 16038 (NBG).

ILLUSTRATIONS AND MAP

Figures 50a & 50b, Map 50.

51. *Haworthia attenuata* (Haw.) Haw. var. *attenuata*, Haworth, Synopsis plantarum succulentarum: 92 (1812). (Enon form.)

Cremonophyte growth form: Cluster-forming, rosulate (of light to medium weight, cliff hugger).

Growth form formula: A:S:Lper:R:C:La (vb)

Etymology: The epithet *attenuata*, tapering, pertains to the tapering leaves.

DESCRIPTION AND HABITAT

Plants dwarf-sized, rosulate, prolific from base, forming rounded clusters up to 200 mm in diameter and 70 mm high consisting of many heads. Rosettes 80–100 mm in diameter. Roots grey, terete. Leaves firm, light to dark green, often reddish, triangular-lanceolate, 40–50 × 15–18 mm, erect at first becoming spreading and somewhat recurved under shady conditions; upper side flat, convex to slightly channelled depending on moisture state, smooth or with few white cartilaginous tubercles, lower surface convex, distinctly keeled towards apex, rarely densely tuberculate; tubercles cartilaginous, often in white horizontal bars; margin tuberculate, tubercles about 3 mm apart; apex acute, aristate. Inflorescence racemose, up to 300 mm long, occasionally branched in distal half, 12–18-flowered in distal half; bracts 3 mm long, clasping, ovate-acuminate; pedicels 2–7 mm long. Perianth tubular, curved, ascending-spreading, 14–18 mm long, white with purplish green midstripe. Capsule 12–14 × 3–4 mm. Seed 3 × 1–2 mm, greyish black, angular.

Phenology: Flowering mainly from spring to early summer (October–November). Seeds dispersed by wind in summer and early autumn.

Pollinators: Insects.

Habitat and aspect: South-facing cliffs, the plants firmly rooted in crevices, and size often depending on the growing space allowed by the crevice. Temperature high in summer (35–40°C). Winters are cooler but frost is absent. Rainfall throughout the year but mostly in summer, ranging from 300–400 mm per annum (thunder showers or cyclonic winter rain).

Altitude: 400 m.

Associated vegetation: Sundays Thicket of the Albany Thicket Biome (Mucina *et al.* 2005)

Associated cremonophytes: *Adromischus sphenophyllus*, *Anacampseros arachnoidea*, *Crassula cultrata*, *C. lactea* and *C. perforata*.

Geology: Enon Conglomerate cliffs. The cliff substrate has sufficient crevices and fissures and is ideal for the establishment of plants.

DISTRIBUTION

This cremonophilous form of *Haworthia attenuata* is confined to the Enon Conglomerate cliffs near the town of Enon in the Eastern Cape.

RELATED SPECIES

Related to *Haworthia glabrata* which occurs on cliffs to the east and lacks the distinct large, white tubercles in horizontal bars of *H. attenuata*.

ADAPTATIONS TO THE CLIFF ENVIRONMENT

Habit and presentation: Conspicuous compact, globose clusters, suggesting a xeromorphic adaptation, maximising tolerance to drought.

Size and weight: Plants dwarf-sized with small rosettes, of light weight.

Leaves

Orientation: Ascending-spreading, becoming somewhat recurved, an adaptation maximising light absorption on the shady cliff face.

Colour: Green, becoming reddish owing to production of anthocyanins during dry periods, reducing photosynthesis.

Age and persistence: Plants slow-growing, long-lived, with firm leaves withering from the base. The fleshy leaves becoming turgid after rain, but channelled during dry periods, an adaptation to the dry habitat. The slow growth rate and long-lived leaves can be viewed as an adaptation to mineral-poor soil.

Armament: The leaves of this Enon form of *Haworthia attenuata* are more triangular and shorter, with a reduction in tubercles and often with a smooth surface, adaptations to the shady south-facing cliff environment.

Sexual reproduction

Inflorescence and flowers: Inflorescence ascending to spreading; corolla white, attracting the right pollinating flying insect.

Fruit/Seed

Size: Seed small and angular, ideal for establishment in crevices.

Dispersal: Light seeds shaken from the capsules and dispersed by wind.

Time: Seeds ripening in summer and autumn, coinciding with the rainy season. Germination after 14–21 days.

Vegetative reproduction: *Haworthia attenuata* (Enon Form) suckers freely from the base, forming dense clusters. Continual sprouting from the base represents an efficient vegetative backup dispersal strategy for this harsh cliff-face environment.

CONSERVATION STATUS

Classified as endangered (Raimondo *et al.* 2009). A local endemic, not threatened.

ADDITIONAL NOTES

Horticulture: Best for thicket gardens and plants are easily grown by division, doing well in cultivation. Plants can be grown in rockeries, in a shady corner, but also thrive in small containers (Van Jaarsveld 2010). It is best kept in partial shade in a sandy, well-drained mixture. Plants rapidly divide, forming mats or rounded clusters. Sow seed in summer or autumn.

VOUCHER

Van Jaarsveld 17833 (NBG).

ILLUSTRATIONS AND MAP

Plate 51, Figures 51a–51c, Map 51.

52. *Haworthia cymbiformis* (Haw.) Duval var. *ramosa* (G.G.Sm.) M.B.Bayer, *Haworthia* revisited: 60 (1999).

Cremonophyte growth form: Cluster-forming, rosulate (of light weight, cliff hugger).

Growth form formula: A:S:Lper:R:C:La (vb)

Etymology: The name *cymbiformis*, boat-shaped, pertains to the leaves; *ramosa*, bearing branches.

DESCRIPTION AND HABITAT

Plants dwarf-sized, neatly rosulate, prolific from base, forming small rounded clusters up to 80 mm in diameter and consisting of up to and more than 25 heads and bearing leafy branches up to 150 mm long; branches grey, up to 7 mm in diameter. Rosettes 40–130 mm in diameter. Roots grey, terete, up to 4 mm in diameter. Leaves up to 25, soft, broadly ovate to oblanceolate, amplexicaul at base and partly imbricate, patent with spreading to incurved translucent and striate apices; upper side flat to channelled or slightly convex, lower side cymbiform; surface smooth, green, becoming pinkish green to yellowish during dry periods; margin entire or with soft teeth; apex obtuse or acute, mucronate. Inflorescence racemose, up to 250 mm long, 10–20-flowered in distal half; bracts white, clasping, up to 3 mm long, ovate-acuminate; pedicels 2 mm long. Perianth tubular, curved, ascending-spreading, 15 mm long, white with purplish green midstripe. Capsule 5 × 2 mm. Seed 2.5 × 1.5 mm.

Phenology: Flowering mainly from spring to early summer (October–November). Seeds dispersed by wind in summer and early autumn.

Pollinators: Insects.

Habitat and aspect: Cliffs (all aspects but more so on open, shady, south-facing aspects). Plants are rooted in crevices and size often depends on the growing space allowed by the crevice. Temperature high in summer (28–40°C). Winters are cooler but frost is absent. Rainfall occurs throughout the year but with a peak in spring and summer, ranging from 250–400 mm per annum (thunder showers or cyclonic winter rain).

Altitude: 400–500 m.

Associated vegetation: Great Fish Thicket of the Thicket Biome (Mucina *et al.* 2005).

Associated cremnophytes: *Bulbine natalensis*, *Crassula cordata*, *C. intermedia*, *C. muscosa*, *C. perfoliata* var. *minor*, *C. spathulata*, *Ornithogalum longibracteatum* and *Plectranthus verticillatus*.

Geology: Plants are found on sandstone and mudstone cliffs (Adelaide Subgroup) of the Karoo Supergroup. The cliff substrate has many ledges, crevices and fissures, ideal for establishment of plants.

DISTRIBUTION

Haworthia cymbiformis var. *ramosa* is confined to a cliff near Wooldridge (Peddie district) in the Eastern Cape.

RELATED SPECIES

Haworthia cymbiformis var. *ramosa* is distinguished mainly by the formation of short stems. However, as Bayer (1999) stated, the plants are variable and some populations do not have stems. Related to *H. cooperi* and *H. retusa*, both usually flat-ground species, well camouflaged, with a sunken growth and difficult to detect. They often occur under the protection of thorny nurse shrubs. Their leaves generally have a firmer texture.

ADAPTATIONS TO THE CLIFF ENVIRONMENT

Habit: Conspicuous globose clusters, the plants often bearing short, flaccid, leafy stems, suggesting an adaptation to maximise light absorption in its environment.

Size and weight: Rosettes small and light, but large clusters of medium weight.

Leaves

Orientation: Very fleshy, soft, in dense leafy stems and rosettes, the leaves spreading as an adaptation to regulate excessive absorption of light. The leaves are amplexicaul at the base and partly imbricate, the arrangement minimising water loss and exposure to excessive radiation on the exposed cliff faces.

Colour: Green, becoming yellowish to pinkish during dry periods as the plants aestivate, blocking out excessive light and reducing photosynthesis.

Presentation: Conspicuous globose clusters.

Age and persistence: Plants long-lived, with soft leaves withering from the base. The very fleshy leaves are soft, becoming turgid after rain, but channelled during dry periods, an adaptation to the extreme, dry habitat.

Armament and camouflage: Leaves soft, the margin varying from entire to softly dentate. Compared to their relatives, there is a reduction in armament and camouflage in response to the undisturbed cliff habitat in contrast to the thorny but heavily grazed surrounding thicket.

Sexual reproduction

Inflorescence and flowers: Inflorescence ascending to spreading; corolla white, attracting the right pollinating flying insect.

Fruit/Seed

Size: Seed small, ideal for establishment in crevices.

Dispersal: Light, angular seeds shaken from the capsules and dispersed by wind.

Time: Seeds ripening in summer and autumn, coinciding with the rainy season. Germination within 14–21 days.

Vegetative reproduction: *Haworthia cymbiformis* var. *ramosa* suckers freely from the base, forming dense, rounded clusters. Continual sprouting from the base represents an efficient vegetative backup dispersal strategy for this harsh cliff-face environment. Detached clusters or heads will also root if they fall into a crevice.

CONSERVATION STATUS

A local endemic, not threatened.

ADDITIONAL NOTES

Variability: *Haworthia cymbiformis* var. *ramosa* is one of seven recognised varieties (Bayer 1999). They include *H. cymbiformis* var. *cymbiformis*, var. *incurvula*, var. *obtusata*, var. *ramosa*, var. *reddii*, var. *setulifera* and var. *transiens*. The genetic variability or plasticity reflects its ability to adapt to local conditions and colonisation, should the opportunity of new habitats arise. Most varieties are found predominantly on cliffs but *H. cymbiformis* var. *ramosa* and var. *setulifera* are strictly confined to cliff faces.

Horticulture: Plants doing well in cultivation and are best for containers and miniature succulent gardens (Van Jaarsveld 2010). This is an adaptable plant, suitable for thicket and subtropical coastal gardens. Its very easy growing nature maximises survival rate. Plants are rapid-growing and respond well to watering and feeding, soon filling a container. Water can be given throughout the year, but sparingly in winter.

VOUCHER

Van Jaarsveld 16829 (NBG).

ILLUSTRATIONS AND MAP

Figures 52a & 52b, Map 52.

53. *Haworthia cymbiformis* (Haw.) Duval var. *setulifera* (Poelln.) M.B.Bayer, *Haworthia* revisited: 62 (1999).

Cremonophyte growth form: Cluster-forming, rosulate (of light to medium weight, cliff hugger).

Growth form formula: A:S:Lper:R:C:La (vb)

Etymology: The epithet *setulifera* refers to small bristles on the leaf margins.

DESCRIPTION AND HABITAT

Plants dwarf-sized, neatly rosulate, prolific from base, forming small rounded clusters up to 80 mm in diameter and consisting of up to 25 heads. Rosettes about 45 mm in diameter. Roots grey, terete, up to 4 mm in diameter. Leaves up to 25, soft, oblanceolate, patent with spreading to incurved translucent and striate apices; upper side flat to channelled or slightly convex, lower surface cymbiform; surface smooth, green, becoming pinkish green during dry periods; margin with soft bristle-like teeth; apex obtuse or acute, mucronate. Inflorescence racemose, 170 mm long, 12–20-flowered in distal half; bracts white, clasping, up to 3 mm long, ovate-acuminate; pedicels 2 mm long. Perianth tubular, curved, ascending-spreading, 15 mm long, white with purplish green midstripe. Capsule 8 × 3 mm. Seed 2.5 × 1.5 mm, angular, grey-black.

Phenology: Flowering mainly from spring to early summer (October–November). Seeds dispersed by wind in summer and early autumn.

Pollinators: Insects.

Habitat and aspect: South-facing cliffs on the upper portion of the cliff face. Plants are firmly rooted in crevices. Temperature high in summer (35–40°C). Winters are cooler but frost is absent. Rainfall occurs mainly in summer and ranges from 800–1250 mm per annum (thunder showers or cyclonic winter rain) towards the east, with rain almost absent in winter.

Altitude: 400–1500 m.

Associated vegetation: Eastern Valley Bushveld of the Savanna Biome (Mucina *et al.* 2005).

Associated cremonophytes: *Albuca batteniana*, *Aptenia cordifolia*, *Bulbine natalensis*, *Cotyledon orbiculata*, *Crassula cordata*, *C. lactea*, *C. perfoliata* var. *minor*, *C. perforata*, *Delosperma* sp., *Ornithogalum longibracteatum* and *Trichodiadema* sp.

Geology: Sandstone and mudstone of the Emakwezini Formation (Beaufort Group) of the Karoo Supergroup. Substrate has many ledges, crevices and fissures that are ideal for establishment of plants.

DISTRIBUTION

Haworthia cymbiformis var. *setulifera* is a quartzitic sandstone endemic, confined to the coastal river valleys in the Transkei region of the Eastern Cape, from the Bashee River in the north to the Kei River in the south.

RELATED SPECIES

Related to *Haworthia retusa* and *H. arachnoidea*, which are flat-ground species with firmer leaves, well sunken into the ground and well camouflaged in their habitats.

ADAPTATIONS TO THE CLIFF ENVIRONMENT

Habit: Globose clusters on shady cliffs, suggesting an adaptation to maximise light absorption in its environment.

Size and weight: Heads small, of light to medium weight (fully grown, globose, turgid clusters).

Leaves

Orientation: Flattened and distinctly incurved, an adaptation to the dry cliff habitat and also regulating excessive absorption of light.

Colour: Green, becoming pinkish during dry periods as the plants aestivate, blocking out excessive light and reducing photosynthesis.

Presentation: Conspicuous globose clusters.

Age and persistence: Plants long-lived, with soft leaves withering from the base. The very fleshy leaves are soft, becoming turgid after rain, but channelled during dry periods, an adaptation to the extreme, dry habitat.

Armament: The soft leaf texture and soft teeth on the margins suggest a reduction in armament in response to the undisturbed cliff habitat in contrast to the thorny but heavily grazed surrounding thicket vegetation.

Sexual reproduction

Inflorescence and flowers: Inflorescence ascending to spreading; corolla white, attracting the right pollinating flying insect.

Fruit/Seed

Size: Seed small, ideal for establishment in crevices.

Dispersal: Light, angular seeds shaken from the capsules and dispersed by wind.

Time: Seeds ripening in summer and autumn, coinciding with the rainy season. Germination within 14–21 days.

Vegetative reproduction: *Haworthia cymbiformis* var. *setulifera* suckers freely from the base, forming dense, rounded clusters. Continual sprouting from the base represents an efficient vegetative backup dispersal strategy for this harsh cliff-face environment. Detached clusters or heads will also root if they fall into a crevice.

CONSERVATION STATUS

A local endemic, not threatened.

ADDITIONAL NOTES

Variability: *Haworthia cymbiformis* var. *setulifera* is one of seven recognised varieties (Bayer 1999). They include *H. cymbiformis* var. *cymbiformis*, var. *incurvula*, var. *obtusa*, var. *ramosa*, var. *reddii*, var. *setulifera* and var. *transiens*. The genetic variability or plasticity reflects its ability to adapt to local conditions and colonisation, should the opportunity of new habitats arise. Most varieties are found predominantly on cliffs but *H. cymbiformis* var. *ramosa* and var. *setulifera* are strictly confined to cliff faces.

Horticulture: Plants do well in cultivation and are best for containers and miniature succulent gardens. It is best kept in partial shade. It is a rapid grower, soon filling its container and forming rounded clusters. It responds rapidly to watering and feeding. It is adaptable but best suited as a pot plant. It is ideal for thicket and subtropical coastal gardens (Van Jaarsveld 2010). It grows easily, maximising its survival rate.

VOUCHER

Van Jaarsveld 17578 (NBG).

ILLUSTRATIONS AND MAP

Figures 53a–53c, Map 53.

54. *Haworthia glabrata* (Salm-Dyck) Baker in Journal of the Linnean Society, Botany 18: 206 (1880).

Cremonophyte growth form: Cluster-forming, rosulate (mainly of light to medium weight, cliff hugger).

Growth form formula: A:S:Lper:R:C:La (vb)

Etymology: The epithet *glabrata* refers to the smooth leaves.

DESCRIPTION AND HABITAT

Plants dwarf-sized, rosulate, prolific from base, forming rounded clusters up to 220 mm in diameter and up to a 100 mm high, consisting of many heads. Rosettes 50–120 mm in diameter. Roots grey, terete. Leaves firm, triangular-lanceolate to attenuate, 75 × 20 mm, erect at first becoming spreading and recurved under shady conditions; upper side flat, convex to slightly channelled depending on moisture state, lower surface convex, keeled towards apex; surface scabrid, green, becoming purplish green during dry periods; margin entire; apex acute, aristate. Inflorescence racemose, 340–400 mm long, occasionally branched from base, 18–25-flowered in distal half; bracts white, clasping, up to 3 mm long, ovate-acuminate; pedicels up to 5 mm long. Perianth tubular, curved, ascending-spreading, 18 mm long, white with purplish green midstripe.

Phenology: Flowering mainly from spring to early summer (October–November). Seeds dispersed by wind in summer and early autumn.

Pollinators: Insects.

Habitat and aspect: Vertical north-facing cliffs, plants firmly rooted in crevices. Temperature high in summer (35–40°C). Winters are cooler but frost is absent. Rainfall mainly in spring and summer, ranging from 800–1250 mm per annum (thunder showers or cyclonic winter rain).

Altitude: 500–1000 m.

Associated vegetation: Eastern Valley Bushveld of the Savanna Biome (Mucina *et al.* 2005).

Associated cremnophytes: *Aloe reynoldsii*, *Crassula lactea*, *C. perfoliata* var. *minor*, *C. planifolia*, *Ophioglossum* sp. and *Ornithogalum juncifolium*.

Geology: Shale cliffs of the Beaufort Group, Adelaide Subgroup (Karoo Supergroup). The cliff substrate has many ledges, crevices and fissures, ideal for establishment of plants.

DISTRIBUTION

Haworthia glabrata is confined to the southern Transkei (northern Eastern Cape), from the Bashee River in the south to near Mthatha in central Transkei (Eastern Cape).

RELATED SPECIES

Haworthia glabrata is related to *H. radula* and *H. attenuata*, which occur further west in a mosaic of Thicket (*H. radula*), Nama-Karoo and grassy Fynbos (*H. attenuata*). Both have distinct white tubercles and grow on undulating to flat terrain.

ADAPTATIONS TO THE CLIFF ENVIRONMENT

Habit and presentation: Conspicuous globose clusters on sunny north-facing slopes, the firm thick epidermis suggesting adaptation to the hot, dry, exposed, sunny habitat. By contrast, *H. cymbiformis* var. *setulifera* occurs on cliffs on south-facing slopes, the leaves soft and with a more translucent appearance, maximising light absorption in the shady environment.

Size and weight: Heads small, of light to medium weight.

Leaves

Orientation: Ascending, triangular-lanceolate, an adaptation to the exposed, sunny situation.

Colour: Green, becoming purplish during dry periods as the plants aestivate, blocking out excessive light and reducing photosynthesis.

Age and persistence: Plants long-lived with a firm texture, leaves withering from the base. The fleshy leaves become turgid after rain, but channelled during dry periods, an adaptation to the dry habitat.

Armament: The leaf colour (in contrast to that of related species) is uniform, the leaves with a scabrid texture and entire margin, suggesting a reduction in armament in response to the undisturbed cliff habitat in contrast to the thorny but heavily grazed surrounding thicket.

Sexual reproduction

Inflorescence and flowers: Inflorescence ascending to spreading; corolla white, attracting the right pollinating flying insect.

Fruit/Seed

Size: Seed small, ideal for establishment in crevices.

Dispersal: Light, angular seeds shaken from the capsules and dispersed by wind.

Time: Seeds ripening in summer and autumn, coinciding with the rainy season. Germination within 14–21 days.

Vegetative reproduction: *Haworthia glabrata* suckers freely from the base, forming dense, rounded clusters. Continual sprouting from the base represents an efficient vegetative backup dispersal strategy for this harsh cliff-face environment. Detached clusters or heads will also root if they fall into a crevice.

CONSERVATION STATUS

Classified as vulnerable (Raimondo *et al.* 2009). A local endemic, not threatened.

ADDITIONAL NOTES

Horticulture: Although rare in its native habitat, it is one of the many examples of cremnophytes well established in cultivation. Plants thrive in cultivation (containers, miniature succulent gardens), are very easily grown and are best propagated by division (Van Jaarsveld 2010). Owing to its ease of growth and ornamental features, it is probably one of the most widely cultivated succulents in the world today, a great survivor. This ease of cultivation reflects its shale cliff habitat where plants may fall and re-root in crevices.

VOUCHER

Van Jaarsveld 16840 (NBG).

ILLUSTRATIONS AND MAP

Figures 54a & 54b, Map 54.

55. *Haworthia gracilis* Poelln. var. *picturata* M.B.Bayer, *Haworthia revisited*: 78 (1999).

Creemnophyte growth form: Cluster-forming, rosulate (of light weight, cliff hugger).

Growth form formula: A:S:Lper:R:C:La (vb)

Etymology: The epithet *picturata* pertains to the leaf ornamentation.

DESCRIPTION AND HABITAT

Plants dwarf-sized, neatly rosulate, prolific from base, forming small rounded clusters up to 80 mm in diameter and consisting of up to 12 heads. Rosettes about 35 mm in diameter. Roots grey, terete, up to 4 mm in diameter. Leaves up to 25, soft, oblanceolate, ascending-spreading; apices translucent, striate, obtuse or acute, mucronate; upper side flat to channelled or slightly convex, lower surface cymbiform; surface smooth, green, becoming pinkish green during dry periods; margin entire. Inflorescence racemose, 150–350 mm long, 8–12-flowered in distal half; bracts white, clasping, up to 3 mm long, ovate-acuminate; pedicels 2 mm long. Perianth tubular, curved, ascending-spreading, 15 mm long, white purplish with green midstripe. Fruit 8×2.5 mm. Seed oblong, 2×1 mm, grey brown.

Phenology: Flowering mainly from spring to early summer (October–November). Seeds dispersed by wind in summer and early autumn.

Pollinators: Insects.

Habitat and aspect: Mainly south-facing cliffs. Plants are firmly rooted in crevices and their growth size often depends on the growing space allowed by the crevice. Temperature high in summer (35–40°C). Winters are cooler but frost is absent. The average daily maximum temperature is about 27°C and the average daily minimum is about 12°C. Rainfall occurs throughout the year but with a peak in spring and summer, ranging from 300–400 mm per annum (thunder showers or cyclonic winter rain).

Altitude: 400–1000 m.

Associated vegetation: Gamtoos Thicket of the Albany Thicket Biome (Mucina *et al.* 2005).

Associated cremnophytes: *Albuca batteniana*, *Bulbine cremnophila*, *Cotyledon tomentosa*, *Crassula perfoliata* var. *minor*, *C. perforata*, *Cyrtanthus labiatus*, *C. montanus* and *Gasteria rawlinsonii*.

Geology: Quartzitic sandstone (light-coloured and smooth-textured), Peninsula Formation (Cape Supergroup). Substrate has sufficient ledges, crevices and fissures and is ideal for establishment of plants.

DISTRIBUTION

Haworthia gracilis var. *picturata* is a quartzitic sandstone endemic, confined to the Baviaanskloof and surrounding region of the Eastern Cape.

RELATED SPECIES

Haworthia gracilis var. *picturata* is related to the *H. retusa*, an often a well-camouflaged geophyte or chasmophyte occurring in conglomerate and soil.

ADAPTATIONS TO THE CLIFF ENVIRONMENT

Habit: Globose clusters in shady cliffs, suggesting an adaptation to maximise light absorption in its shady environment.

Size and weight: Rosettes small, of light weight.

Leaves

Orientation: Flattened, compact and distinctly incurved, an adaptation to the semi-arid environment and also regulating excessive absorption of light.

Colour: Green, becoming purplish during dry periods as the plants aestivate, blocking out excessive light and reducing photosynthesis. The windows on the leaf surface allow for penetration of light to the inner tissue, aiding in effective photosynthesis in the shady cliff environment.

Presentation: Conspicuous globose clusters.

Age and persistence: Long-lived, succulent, with a soft texture, withering from the base. After rain, the leaves becoming turgid, but channelled during dry periods, an adaptation to the extreme dry habitat.

Armament: The soft leaf texture and entire margin (occasionally ciliate) suggest a reduction in armament in response to the undisturbed cliff habitat in contrast to the thorny but heavily grazed surrounding thicket vegetation.

Sexual reproduction

Inflorescence and flowers: Inflorescence ascending to spreading; corolla white, attracting the right pollinating flying insect.

Fruit/Seed

Size: Seed small, ideal for establishment in crevices.

Dispersal: Light, angular seeds shaken from the capsules and dispersed by wind.

Time: Seeds ripening in summer and autumn, coinciding with the rainy season. Germination within 14–21 days.

Vegetative reproduction: *Haworthia gracilis* var. *picturata* suckers freely from the base, forming dense clusters. Continual sprouting from the base represents an efficient vegetative backup dispersal strategy for this harsh cliff-face environment. Heads blown from the cliff will root where they land.

CONSERVATION STATUS

A local endemic, not threatened.

ADDITIONAL NOTES

Horticulture: *Haworthia gracilis* var. *picturata* is easily grown by division and thrives in cultivation (Van Jaarsveld 2010). Suitable for small containers (full sun or partial shade). Outside its habitat it is best grown under controlled conditions in a greenhouse. Its very easy growing nature maximises survival rate. It is best grown in sandy, well-drained soil. Plants rapidly enlarge and will soon fill their container. Feed in spring and summer. Popular in cultivation and cultivated worldwide.

VOUCHER

Van Jaarsveld 17101 (NBG).

ILLUSTRATIONS AND MAP

Figures 55a & 55b, Map 55.

56. *Haworthia marumiana* Uitewaal var. *batesiana* (Uitewaal) M.B.Bayer, *Haworthia* revisited: 105 (1999).

Cremnophyte growth form: Cluster-forming, rosulate (of light weight, cliff hugger).

Growth form formula: A:S:Lper:R:C:La (vb)

Etymology: After J.T. Bates, London trolley bus conductor and collector of succulent plants.

DESCRIPTION AND HABITAT

Plants stemless, rosulate succulents up to 45 mm in diameter, proliferating from base to form large clusters. Leaves up to 23 × 6 mm, ascending (outer spreading and incurved), green, incurved, flattened, lanceolata to ovate lanceolate; upper surface flat to subconvex, lower surface convex, with centric keel towards tip, both surfaces with 6–8 pellucid longitudinal lines; margin entire; apex acuminate-aristate. Inflorescence an erect raceme up to about 310 mm long. Flowers about 12; pedicels up to 4 mm long, erect; perianth white, up to 11 mm long; tube compressed at base, 4 mm in diameter, curved, funnel-shaped; segments free, with green keels, bilabiate, posterior segments erect, slightly recurved. Stamens 7–8 mm long. Ovary 5 × 2 mm; style 1,5 mm long, capitate.

Phenology: Flowering mainly from spring (September–October). Seeds dispersed by wind in summer and early autumn.

Pollinators: Insects.

Habitat and aspect: Vertical south-facing cliffs. Plants are firmly rooted in crevices and size often depends on the growing space allowed by the crevice. Temperature high in summer (35–40°C). Winters are cooler but frost is absent or limited to flat terrain. The average annual daily maximum temperature is about 24°C and the average annual daily minimum temperature about 9°C. Rainfall occurs mainly in summer, ranging from 300–400 mm per annum (thunder showers or cyclonic winter rain).

Altitude: 500–1500 m.

Associated vegetation: Camdebo Escarpment Thicket of the Albany Thicket Biome (Mucina *et al.* 2005).

Associated cremnophytes: Observations at the Valley of Desolation include the following species: *Cotyledon orbiculata* var. *orbiculata*, *Crassula exilis* subsp. *cooperi*, *C. lanceolata* subsp. *lanceolata*, *C. nemorosa*, *C. perforata*, *Delosperma* spp., *Drimia uniflora* and *Haemanthus humilis* subsp. *hirsutus*.

Geology: Beaufort shales, Adelaide Subgroup (Karoo Supergroup). Substrate with many ledges, crevices and fissures and ideal for establishment of plants.

DISTRIBUTION

Haworthia marumiana var. *batesiana* is endemic to the higher-lying cliff faces around Graaff-Reinet (Eastern Cape).

RELATED SPECIES

Haworthia marumiana var. *batesiana* is related to *H. arachnoidea*, a well-camouflaged succulent plant or chasmophyte of the flats that grows in various soil types under karoo shrubs in Succulent Karoo. The latter has firm leaves with dense marginal cilia and dry tips, providing camouflage and protection from the sun.

ADAPTATIONS TO THE CLIFF ENVIRONMENT

Habit: Globose clusters in shady cliffs, suggesting an adaptation to maximise light absorption in its shady environment.

Size and weight: Rosettes small, of light weight.

Leaves

Orientation: In tight rosettes, becoming incurved under dry conditions. This is an adaptation to the semi-arid environment and also helps with adjustment to the available light.

Colour: Green, becoming purplish during dry periods as the plants aestivate, blocking out excessive light and reducing photosynthesis.

Presentation: Conspicuous globose clusters.

Age and persistence: Plants long-lived, with soft leaves withering from the base. The very fleshy leaves are soft, becoming turgid after rain, but channelled during dry periods, an adaptation to the extreme, dry habitat.

Armament: The soft leaf texture and entire margin suggest a reduction in armament in response to the undisturbed cliff habitat in contrast to the thorny but heavily grazed surrounding Nama-Karoo vegetation.

Sexual reproduction

Inflorescence and flowers: Inflorescence ascending to spreading; corolla white, attracting the right pollinating flying insect.

Fruit/Seed

Size: Seed small, ideal for establishment in crevices.

Dispersal: Light, angular seeds shaken from the capsules and dispersed by wind.

Time: Seeds ripening in summer and autumn, coinciding with the rainy season. Germination after 14–21 days.

Vegetative reproduction: *Haworthia marumiana* var. *batesiana* suckers freely from the base, forming dense, rounded clusters. Continual sprouting from the base represents an efficient vegetative backup dispersal strategy for this harsh cliff-face environment. Detached clusters or heads will also root if they fall into a crevice.

CONSERVATION STATUS

A local endemic, not threatened.

ADDITIONAL NOTES

Horticulture: *Haworthia marumiana* var. *batesiana* is easily grown by division and does well in cultivation. It should preferably be kept in a partially shady place. Feed in spring and summer. Its ease of growth maximises its survival rate. Best for dry summer-rainfall karoo gardens grown as a pot plant. Keep dry during the winter months. Outside its habitat it should be grown under controlled conditions in a greenhouse.

VOUCHER

Van Jaarsveld 16590 (NBG).

ILLUSTRATIONS AND MAP

Figure 56a, Map 56.

57. *Haworthia marumiana* Uitewaal var. *marumiana*, Uitewaal in Cactussen en Vetplanten 6: 33 (1940).

Cremonophyte growth form: Cluster-forming, rosulate (of light weight, cliff hugger).

Growth form formula: A:S:Lper:R:C:La (vb)

Etymology: After Dr N. van Marum, collector of succulent plants.

DESCRIPTION AND HABITAT

Plants stemless, rosulate succulents up to 30 mm in diameter, proliferating from base to form large clusters. Leaves up to 20 × 8 mm, ascending (outer spreading), light top dark to brownish-green, flattened, ovate-lanceolate; upper surface flat to subconvex, lower surface convex, with centric keel towards tip, both surfaces with 3–6 pellucid longitudinal lines; margin and keel with soft spines; apex acuminate-aristate. Inflorescence an erect raceme up to about 230 mm long. Flowers about 10; pedicels up to 3 mm long, erect; perianth white, up to 11 mm long; tube compressed at base, 4 mm long, curved, funnel-shaped; segments free, with green keels, bilabiate, posterior segments erect, slightly recurved. Stamens 7–8 mm long. Ovary 4 mm long; style 1 mm long, white, not capitate.

Phenology: Flowering mainly during summer (January-February). Seeds dispersed by wind in summer and early autumn.

Pollinators: Insects.

Habitat and aspect: Mainly south-facing cliffs. Plants are firmly rooted in crevices and size often depends on the growing space allowed by the crevice. Temperature high in summer (35–40°C). Winters are cooler but frost is absent or limited to flat terrain. The average annual daily maximum temperature is about 24°C and the average annual daily minimum temperature about 10°C. Rainfall throughout the year but with a peak in spring and summer, 300–400 mm per annum (thunder showers or cyclonic winter rain).

Altitude: 1300–2000 m.

Associated vegetation: Grootrivier Quartzite Fynbos of the Fynbos Biome as well as Camdeboo Escarpment Thicket of the Albany Thicket Biome (Mucina *et al.* 2005).

Associated cremnoophytes: The following species occur at Aasvoëlberg, northwest of Willowmore where the plants are very common: *Adromischus subdistichus*, *Cotyledon orbiculata* var. *orbiculata*, *Crassula montana* subsp. *quadrangularis*, *C. orbicularis*, *C. pellucida* subsp. *marginalis*, *C. perforata* and *Delosperma esterhuyseniae*.

Geology: Quartzitic sandstone (Witteberg quartzite) and Beaufort shales, Adelaide Subgroup (Karoo Supergroup). Substrate has many ledges, crevices and fissures, ideal for establishment of plants.

DISTRIBUTION

Widely distributed, from the escarpment mountains near Graaff-Reinet to Queenstown in the east, and southwards to Willowmore and westwards to Beaufort West.

RELATED SPECIES

Haworthia marumiana var. *marumiana* is related to *H. arachnoidea*, a well-camouflaged succulent plant or chasmophyte of the flats that grows in various soil types under karoo shrubs in Succulent Karoo. The latter has firm leaves with dense marginal cilia and dry tips, providing camouflage and protection from the sun. *Haworthia marumiana* var. *batesiana* does not have soft spines on the leaf margins.

ADAPTATIONS TO THE CLIFF ENVIRONMENT

Habit: Globose clusters in shady cliffs, suggesting an adaptation to maximise light absorption in its shady environment.

Size and weight: Rosettes small, of light weight.

Leaves

Orientation: In tight rosettes, but becoming incurved in under dry conditions. This is an adaptation to the semi-arid environment and also helps with adjustment to the available light.

Colour: Dark to lighter green, becoming purplish during dry periods as the plants aestivate, blocking out excessive light and reducing photosynthesis.

Presentation: Conspicuous globose clusters.

Age and persistence: Plants long-lived, with soft leaves withering from the base. The very fleshy leaves are soft, becoming turgid after rain, but channelled during dry periods, an adaptation to the extreme, dry habitat.

Armament: The soft leaf texture and soft spines on the keel and margin suggest a reduction in armament in response to the undisturbed cliff habitat in contrast to the thorny but heavily grazed surrounding Nama-Karoo vegetation.

Sexual reproduction

Inflorescence and flowers: Inflorescence ascending to spreading; corolla white, attracting the right pollinating flying insect.

Fruit/Seed

Size: Seed small, ideal for establishment in crevices.

Dispersal: Light, angular seeds shaken from the capsules and dispersed by wind.

Time: Seeds ripening in summer and autumn, coinciding with the rainy season. Germination after 14–21 days.

Vegetative reproduction: *Haworthia marumiana* var. *marumiana* suckers freely from the base, forming dense, rounded clusters. Continual sprouting from the base represents an efficient vegetative backup dispersal strategy for this harsh cliff-face environment. Detached clusters or heads will also root if they fall into a crevice.

CONSERVATION STATUS

A local endemic, not threatened.

ADDITIONAL NOTES

Horticulture: Plants are easily grown by division and do well in cultivation, but rather in small containers kept in partial shade. Plants rapidly proliferate and are best propagated by division. Feed in spring and summer and water sparingly in winter. Outside its habitat, it is best suited to a greenhouse where conditions can be controlled. Its very easy growing, adaptable nature maximises its survival rate.

VOUCHER

Van Jaarsveld 20050 (NBG).

ILLUSTRATIONS AND MAP

Figures 57a & 57b, Map 57.

58. *Haworthia mirabilis* (Haw.) Haw. var. *consanguinea* M.B.Bayer, *Haworthia revisited*: 111 (1999).

Crempnophyte growth form: Cluster-forming, rosulate (of light weight, cliff hugger).

Growth form formula: A:S:Lper:R:C:La (vb)

Etymology: Latin *consanguinea*, kindred or related to, pertains to its superficial likeness to the small mountain form of *Haworthia turgida*.

DESCRIPTION AND HABITAT

Plants dwarf-sized, rosulate, prolific from base, forming small rounded clusters up to 50 mm in diameter and consisting of up to 12 heads. Rosettes 30–50 mm in diameter. Roots grey, terete. Leaves up to 35, soft, triangular, ascending-spreading to patent, with translucent linear markings; upper surface rounded, lower surface cymbiform, surface smooth, green, becoming brownish red during dry periods; margin entire; apex acute to acuminate, mucronate (shiny and pellucid). Inflorescence racemose, up to 150 mm long, 10-flowered in distal half; bracts white, clasping, up to 3 mm long, ovate-acuminate; pedicels 2 mm long. Perianth tubular, curved, ascending-spreading, 15 mm long, white with purplish green midstripe.

Phenology: Flowering mainly from spring to early summer (October–November). Seeds dispersed by wind in summer and early autumn.

Pollinators: Insects.

Habitat and aspect: Mainly south-facing cliffs. Plants are rooted in crevices and size often depends on the growing space allowed by the crevice. Temperature high in summer (28–34°C). Winters are cooler but frost is absent. Rainfall occurs throughout the year but mainly in winter, ranging from 600–800 mm per annum (cyclonic winter rain or thunder showers).

Altitude: 1000–1500 m.

Associated vegetation: North Sonderend Sandstone Fynbos of the Fynbos Biome (Mucina *et al.* 2005).

Associated cremnophytes: *Cotyledon orbiculata*, *Crassula dejecta*, *C. nudicaulis* and *C. perforata*.

Geology: Plants are found on quartzitic sandstone, Peninsula Formation (Cape Supergroup), but also on shale (Bokkeveld Group, Ceres Subgroup of the Cape Supergroup). The rocky cliff substrate has many ledges, crevices and fissures, ideal for establishment of plants.

DISTRIBUTION

Confined to the mountains near McGregor and Greyton (Western Cape).

RELATED SPECIES

Haworthia mirabilis var. *consanguinea* differs from the other four level-ground varieties in its softer, less retuse leaves. The others are well camouflaged, with a sunken growth and are difficult to detect. They often occur under the protection of thorny nurse shrubs.

ADAPTATIONS TO THE CLIFF ENVIRONMENT

Habit: Small globose clusters on shady cliffs.

Size and weight: Rosettes small, of light weight.

Leaves

Orientation: In dense rosettes, spreading, maximising absorption of light.

Colour: Green, becoming brownish red during dry periods, reducing absorption of light. Windows on upper leaf surface allowing deep penetration of light. Compared to its inconspicuous relatives, these plants occur as conspicuous globose clusters on the cliff face.

Age and persistence: Plants long-lived, with soft leaves withering from the base. The very fleshy leaves are soft, becoming turgid after rain, but channelled during dry periods, an adaptation to the extreme dry habitat.

Armament and camouflage: The leaves have a soft texture and entire margin. Compared to their relatives, there is a reduction in armament and camouflage in response to the undisturbed cliff habitat in contrast to accessible fynbos and thicket vegetation.

Sexual reproduction

Inflorescence and flowers: Inflorescence ascending to spreading; corolla white, attracting the right pollinating flying insect.

Fruit/Seed

Size: Seed small, ideal for establishment in crevices.

Dispersal: Light, angular seeds shaken from the capsules and dispersed by wind.

Time: Seeds ripening in summer and autumn, coinciding with the rainy season. Germination within 14–21 days.

Vegetative reproduction: *Haworthia mirabilis* var. *consanguinea* suckers freely from the base, forming dense, rounded clusters. Continual sprouting from the base is an efficient vegetative backup dispersal strategy for this harsh cliff-face environment. Detached clusters or heads will also root if they fall into a crevice.

CONSERVATION STATUS

Classified as rare (Raimondo *et al.* 2009). A local endemic, not threatened.

ADDITIONAL NOTES

Variability: This variety belongs to a genotypically extremely variable complex of *Haworthia mirabilis* with many local variants. Bayer (1999) recognises five varieties, the other all level-ground taxa. The genetic variability or plasticity reflects its ability to adapt to local conditions and colonisation, should the opportunity of new habitats arise.

Horticulture: Best suited to fynbos gardens. Grow in small containers in slightly acidic, sandy soil and feed in autumn. Keep in dappled shade. Plants are easily propagated by division, doing well in cultivation. Water should be provided throughout the year, but sparingly in summer. A rapidly dividing plant, forming clusters.

VOUCHER

Van Jaarsveld 18443 (NBG).

ILLUSTRATIONS AND MAP

Figures 58a–58c, Map 58.

59. *Haworthia scabra* Haw. var. *starkiana* (Poelln.) M.B.Bayer in *Haworthia revisited*: 197 (1999).

Crempnophyte growth form: Cluster-forming, rosulate (of medium weight, cliff hugger).

Growth form formula: A:S:Lper:R:C:La (vb)

Etymology: In honour of Professor Peter Stark.

DESCRIPTION AND HABITAT

Plants rosulate, prolific from base, forming rounded clusters up to 500 mm in diameter and consisting of up to 10 heads. Rosettes up to 150 mm in diameter. Roots grey, terete. Leaves up to 30, firm, falcate, ovate to triangular-lanceolate, attenuate, ascending-spreading, laterally

incurved (towards apex), up to 70 × 20 mm; surface yellowish green, smooth, shiny green; apex mucronate. Inflorescence racemose, up to 370 mm long, 18-flowered in distal half; bracts white, clasping, up to 3 mm long, ovate-acuminate; pedicels 2 mm long. Perianth tubular, 14–15 mm long, curved, ascending-spreading, white with purplish green midstripe.

Phenology: Flowering mainly from early autumn (March–April). Seeds dispersed by wind in summer and early autumn.

Pollinators: Insects.

Habitat and aspect: Mainly north-facing cliffs. Plants are rooted in crevices and size often depends on the growing space allowed by the crevice. Temperature high in summer (28–38°C). Winters are cooler but frost is absent. The average daily maximum temperature is about 25°C and the annual daily minimum about 8°C. Rainfall occurs throughout the year, ranging from 200–300 mm per annum (cyclonic winter rain or thunder showers).

Altitude: 500–1500 m.

Associated vegetation: Gamka Thicket of the Thicket Biome (Mucina *et al.* 2005).

Associated cremnophytes: *Cotyledon orbiculata*, *Crassula perforata* and *Portulacaria afra*.

Geology: Plants are found on quartzitic sandstone, Peninsula Formation (Cape Supergroup). Substrate has many ledges, crevices and fissures, ideal for establishment of plants.

DISTRIBUTION

Haworthia scabra var. *starkiana* is confined to the northern Little Karoo adjacent to the Groot Swartberg Mountains, from Cango to near De Rust (Western Cape).

RELATED SPECIES

Haworthia scabra var. *starkiana* differs from *H. scabra* var. *scabra* (level-ground species) in its conspicuous, smooth, yellowish green leaves. *Haworthia scabra* var. *scabra* has rough (scabrid), dark green leaves and is well camouflaged.

ADAPTATIONS TO THE CLIFF ENVIRONMENT

Habit: Large conspicuous clusters on exposed cliffs.

Size and weight: Heads medium-sized, of medium weight in fully turgid adult plants.

Leaves

Orientation: Spirally twisted, shading out copious amounts of sunlight from the inner parts.

Colour: Conspicuous, yellowish green. The leaves of its relative, *Haworthia scabra* var. *scabra*, are dark, with a rough texture.

Age and persistence: Plants long-lived, with hard, firm leaves withering from the base. The fleshy leaves become turgid after rain, storing sufficient moisture for dry periods, an adaptation to the extreme, dry habitat.

Armament and camouflage: The leaves have an entire leaf margin, ending in a hard point that would deter cliff-adapted animals such as the rock dassie (*Procavia capensis*) and chacma baboon (*Papio ursinus*). Compared to *Haworthia scabra* var. *scabra*, there is some reduction in armament (conspicuous clusters, glabrous leaves, entire margin) and camouflage (the non-cremophilous *H. scabra* is well camouflaged) in response to the undisturbed cliff habitat in contrast to accessible fynbos and succulent karoo vegetation.

Sexual reproduction

Inflorescence and flowers: Inflorescence ascending to spreading; corolla white, attracting the right pollinating flying insect.

Fruit/Seed

Size: Seed small, ideal for establishment in crevices.

Dispersal: Light, angular seeds shaken from the capsules and dispersed by wind.

Time: Seeds ripening in winter, coinciding with the cool period of winter rains, a good time for effective establishment. Germination after 14–21 days.

Vegetative reproduction: *Haworthia scabra* var. *starkiana* suckers freely from the base, forming dense, rounded clusters. Continual sprouting from the base represents an efficient vegetative backup dispersal strategy for this harsh cliff-face environment. Detached clusters or heads will also root if they fall into a crevice.

CONSERVATION STATUS

Classified as vulnerable (Raimondo *et al.* 2009). A local endemic, not threatened.

ADDITIONAL NOTES

Variability: Although it has a limited distribution, *Haworthia scabra* var. *starkiana* is very variable, with local forms and showing genotypic plasticity. This is reflected in the work of Bayer (1999) who recognises four varieties of a variable *H. scabra* (*H. scabra* var. *scabra*, var. *morrisiae*, var. *lateganiae* and var. *starkiana*). *Haworthia scabra* var. *scabra* is not a cremnophyte and the others are regarded here as local variants of *H. scabra* var. *starkiana*. This genetic variability reflects its evolutionary ability to adapt to local conditions and colonisation of new habitats, should the opportunity arise. However, plants are not as easily grown as other *Haworthia* species, reflecting the narrow adaptation to the extreme, exposed conditions.

Horticulture: It is best grown in dry succulent karoo and thicket gardens, in full sun or partial shade and propagated from seed or division. Outside its habitat, it should preferably be grown under controlled conditions in a greenhouse. Plants should be watered sparingly in winter and summer.

VOUCHER

Van Jaarsveld 16720 (NBG).

ILLUSTRATIONS AND MAP

Figures 59a & 59b, Map 59.

60. *Haworthia turgida* Haw. var. *turgida*, Haworth, Supplementum plantarum succulentarum: 52 (1819).

Cremonophyte growth form: Cluster-forming, rosulate (of light weight, cliff hugger).

Growth form formula: A:S:Lper:R:C:La (vb)

Etymology: The epithet *turgida*, swollen, pertains to the leaves.

DESCRIPTION AND HABITAT

Plants dwarf-sized, rosulate, prolific from base, forming dense rounded clusters up to 15 mm in diameter and consisting of up to and more than 25 heads. Rosettes 20–30(–80) mm in diameter. Roots grey, terete. Leaves up to 40, soft, oblanceolate, somewhat retuse at apices, somewhat recurved, turgid, ascending-spreading, with somewhat translucent reticulation; upper side flat to convex, lower surface rounded, surface smooth, bright green, becoming pinkish green to purplish green during dry periods; margin entire or with soft sparse teeth; apex obtuse or acute (shiny and pellucid), mucronate. Inflorescence racemose, up to 200 mm long, 10–20-flowered in distal half; bracts white, clasping, up to 3 mm long, ovate-acuminate; pedicels 2 mm long. Perianth tubular, curved, ascending-spreading, 15 mm long, white with purplish green midstripe.

Phenology: Flowering mainly from in summer and early autumn (February–April). Seeds dispersed by wind in autumn.

Pollinators: Insects.

Habitat and aspect: Cliffs and all aspects, but more on open, shady, south-facing aspects. Plants are rooted in crevices and size often depends on the growing space allowed by the crevice. Temperature high in summer (28–40°C). Winters are cooler but frost is absent. Rainfall occurs throughout the year but more so in winter, 250–500 mm per annum (thunder showers or cyclonic winter rain).

Altitude: 500–1500 m.

Associated vegetation: South Langeberg Sandstone Fynbos and southern Cape Valley Thicket of the Thicket Biome (Mucina *et al.* 2005).

Associated cremonophytes: *Cotyledon eliseae*, *C. orbiculata*, *Crassula perforata*, *C. rupestris*, *Drimia anomala* and *Ornithogalum longibracteatum*.

Geology: Plants are found on quartzitic sandstone of the Peninsula Formation (Cape Supergroup), but also on shale and mudstone (Ceres Group, Bokkeveld Formation) of the same supergroup. Substrate has many ledges, crevices and fissures, ideal for establishment of plants.

DISTRIBUTION

Haworthia turgida is a Western Cape endemic confined to an area from Mossel Bay in the east to the mountains north of Bredasdorp in the west.

RELATED SPECIES

Haworthia turgida var. *turgida* is related to *H. mirabilis*, *H. magnifica*, *H. retusa*, *H. reticulata* and *H. herbacea*, all of them usually flat-ground species, well camouflaged, with a sunken growth and inconspicuous. They often occur under the protection of thorny nurse shrubs and their leaves have a firmer texture. *Haworthia turgida* var. *suberecta* does not occur in cliff habitats and has distinctly retuse leaves with markings. *Haworthia turgida* var. *longibracteata* is much larger, occurring on steep, rocky slopes near Still Bay.

ADAPTATIONS TO THE CLIFF ENVIRONMENT

Habit: Conspicuous globose clusters, in contrast to the cryptic sunken habit of its relatives.

Size and weight: Rosettes small, of light weight.

Leaves

Orientation: In dense rosettes, ascending-spreading to almost recurved, with slightly retuse but pellucid to distinctly translucent apices. This appears to be an adaptation to maximise distribution of light within the leaf tissue on the shady cliff face. The very swollen nature of the leaves reflects their ability to store moisture on the extreme, well-drained cliffs.

Colour: Bright to greyish green, becoming pinkish to purplish green under dry conditions, minimising absorption of light under dry conditions.

Presentation: Conspicuous clusters. Leaves tightly arranged, ascending-spreading and can be almost recurved compared to those of its relatives, which are inconspicuous in their habitat.

Age and persistence: Long-lived, with soft leaves withering from the base. The very fleshy leaves becoming turgid after rain, but less so during dry periods, an adaptation to the extreme, dry habitat.

Armament and camouflage: The leaves are unarmed or have a soft texture, the margin varying from entire to softly dentate. Compared to their relatives, there is a reduction in armament and camouflage in response to the undisturbed cliff habitat in contrast to the thorny but heavily grazed surrounding thicket vegetation.

Sexual reproduction

Inflorescence and flowers: Inflorescence ascending to spreading; corolla white, attracting the right pollinating flying insect.

Fruit/Seed

Size: Seed small, ideal for establishment in crevices.

Dispersal: Light, angular seeds shaken from the capsules and dispersed by wind.

Time: Seeds ripening in summer and autumn, coinciding with the rainy season.
Germination within 14–21 days.

Vegetative reproduction: *Haworthia turgida* var. *turgida* suckers freely from the base, forming dense, rounded clusters. Continual sprouting from the base represents an efficient vegetative backup dispersal strategy for this harsh cliff-face environment. Detached clusters or heads will also root if they fall into a crevice.

CONSERVATION STATUS

A local endemic, not threatened.

ADDITIONAL NOTES

Variability: This is an extremely variable taxon (genotypic variation), with many local variants. Bayer (1999) recognises three varieties, var. *turgida*, var. *longibracteata* and var. *suberecta*, reflecting its variability. The genetic variability or plasticity reflects its ability to adapt to local conditions and colonisation, should the opportunity of new habitats arise.

Horticulture: Plants are easily grown from stolons or division and thrive in cultivation. It is best grown in partial shade in a sandy, well-drained soil in succulent karoo gardens. Plants rapidly respond to water, becoming turgid, and should be fed with an organic fertiliser sparingly throughout the year. Its very easy growing nature maximises its survival rate. Well-established in cultivation throughout the world. Plants do well in containers.

VOUCHER

Van Jaarsveld 17715 (NBG).

ILLUSTRATIONS AND MAP

Figures 60a–60c, Map 60.

61. *Haworthia zantneriana* Poelln. in *Cactus Journal*, British 5: 35 (1936).

Cremonophyte growth form: Cluster, mat-forming (of light weight, cliff hugger).

Growth form formula: A:S:Lper:R:C:La (vb)

Etymology: After a Major Alfred Zantner (?–1953).

DESCRIPTION AND HABITAT

Plants dwarf-sized, rosulate, prolific from base, forming clusters up to 60 mm in diameter and consisting of up to 12 heads. Rosettes about 30 mm in diameter. Roots grey, terete. Leaves up to 40, triangular to linear-lanceolate, attenuate, soft, with entire white margin, at first erect becoming ascending-spreading; abaxial surface keeled, green becoming purplish during dry periods; apex mucronate. Inflorescence racemose, up to 250 mm long; 17–35-flowered in distal half. Perianth tubular, curved, ascending-spreading, 15–18 mm long, white with green midstripe. Ovary tubular, 2 × 1.5 mm, green; stigma 1 mm long, widening and truncate at apex.

Phenology: Flowering mainly from spring to early summer (October–November). Seeds dispersed by wind in summer and early autumn.

Pollinators: Insects.

Habitat and aspect: Cliffs of narrow shady kloofs, mainly on southern aspects. Plants firmly rooted in crevices and size often depends on the growing space allowed by the crevice. Temperature high in summer (35–40°C). Winters are cooler but frost is absent. Rainfall throughout the year, ranging from 250–400 mm per annum (thunder showers or cyclonic winter rain).

Altitude: 600–1500 m.

Associated vegetation: Mainly Groot Thicket of the Albany Thicket Biome (Mucina *et al.* 2005).

Associated cremnohytes: *Bulbine latifolia*, *Crassula perfoliata* var. *minor*, *Haworthia glauca*, *Lampranthus affinis*, *Ledebouria ensifolia* and *Ornithogalum juncifolium*.

Geology: Quartzitic sandstone (light-coloured and smooth-textured), Witteberg Group, Witpoort Formation (Cape Supergroup). Cliff substrate has many ledges, crevices and fissures, ideal for establishment of plants.

DISTRIBUTION

Haworthia zantneriana appears to be a quartzitic sandstone endemic, confined to the mountains north of the Little Karoo, from Willowmore in the west to Camphor's Poort in the east (Eastern Cape). The plants are chasmophytes, occurring on rock slabs and inaccessible vertical cliff faces.

RELATED SPECIES

Its soft leaves with an entire margin separate it from related flat-ground *Haworthia* species, the latter with firm leaves and some densely covered with hairs, suggesting some herbivory defence strategies.

ADAPTATIONS TO THE CLIFF ENVIRONMENT

Habit: Small clusters in shady cliffs, suggesting an adaptation to maximise light absorption in its shady environment.

Size and weight: Rosettes dwarf-sized, of light weight.

Leaves

Orientation: Flattened, becoming more spreading in shadier environments, an adaptation to maximise absorption of light.

Colour: Green, becoming purplish during dry periods, reducing absorption of light and slowing down photosynthesis.

Presentation: Fairly inconspicuous clusters.

Age and persistence: Plants long-lived, with soft leaves withering from the base. The very fleshy leaves are soft, becoming turgid after rain, but channelled during dry periods, an adaptation to the extreme dry habitat.

Armament: The soft leaf texture and entire margin suggest a reduction in armament in response to the undisturbed cliff habitat in contrast to the thorny but heavily grazed surrounding thicket vegetation.

Sexual reproduction

Inflorescence and flowers: Inflorescence ascending to spreading; corolla white, attracting the right pollinating flying insect.

Fruit/Seed

Size: Seed small, ideal for establishment in crevices.

Dispersal: Light, angular seeds shaken from the capsules and dispersed by wind.

Time: Seeds ripening in early autumn (March, April), coinciding with the cooler winter-rainfall season, a good time for successful establishment. Germination within 14–21 days.

Vegetative reproduction: *Haworthia zantneriana* suckers freely from the base, forming dense, rounded clusters. Continual sprouting from the base represents an efficient vegetative backup dispersal strategy for this harsh cliff-face environment. Detached clusters or heads will also root if they fall into a crevice.

CONSERVATION STATUS

Classified as critically rare (Raimondo *et al.* 2009). A local endemic, not threatened.

ADDITIONAL NOTES

Horticulture: It is best grown in dry thicket gardens. The soil should be sandy and slightly acid, the plants kept in small containers in partial shade. Plants are easily grown by division and thrive in cultivation. Its very easy growing nature maximises survival rate. Plants within

reach of herbivores such as the rock dassie (*Procavia capensis*) are grazed in habitat, as seen at Camphor's Poort.

VOUCHER

Van Jaarsveld 16596 (NBG).

ILLUSTRATIONS AND MAP

Figures 61a–61c, Map 61.

TRACHYANDRA Kunth

62. *Trachyandra tabularis* (Baker) Oberm. in *Bothalia* 7: 730 (1962). (Table Mountain cliff-face form.)

Cremonophyte growth form: Cluster-forming, long pendent leaves (of medium weight, cliff hanger).

Growth form formula: A:B:Lper:C:Lp (e) (vb)

Etymology: The epithet *tabularis*, flat-topped, from Table Mountain, pertains to its mountain habitat.

DESCRIPTION AND HABITAT

Plants at first solitary, dividing to form dense clusters. Rhizome herbaceous, subterranean, wiry, up to 300 mm long. Roots yellow. Leaves 1–5, succulent, pendent, terete in young plants, becoming flat in mature plants, 750 × 2.5–7.0 mm, drooping from basal rosette; surface smooth, faintly striate, slightly translucent; margin entire to obscurely denticulate. Inflorescence solitary, few-branched to simple; scape arcuate, up to 0.5 m long, curved upwards; pedicels 5–7 mm long. Perianth white, sweetly scented, segments 14 mm long. Capsule globose, 5 mm in diameter. Seed black, angular, 2.5–3.0 mm in diameter.

Phenology: Flowering in summer, capsule ripening from March–April. Perianth opening in the late morning, sweetly scented, attracting insect pollinators.

Pollinators: Insects.

Habitat and aspect: Vertical cliffs, at altitudes of about 500–1000 m, in narrow, shady kloofs (mainly southern and eastern aspects) and where temperatures are mild. Plants are firmly rooted among moss in crevices. Winters are cool, with occasional snow. Rainfall mainly in autumn, winter and spring, 2000–3000 mm per annum (cyclonic winter rain).

Altitude: 500–1000 m.

Associated vegetation: Peninsula Sandstone Fynbos of the Fynbos Biome (Mucina *et al.* 2005).

Associated cremnophytes: At Window Gorge, plants grow with *Crassula atropurpurea* var. *anomala*, *C. coccinea*, *C. nudicaulis*, *Disa uniflora*, *Elaphoglossum* sp. and species of moss. On the back table of Table Mountain, *Trachyandra tabularis* shares its habitat with *Cotyledon orbiculata* var. *orbiculata*, *Crassula nudicaulis*, *C. pellucida* subsp. *alsinoides*, *Erepsia falciformis* and *Ornithogalum juncifolium*.

Geology: Quartzitic sandstone (light-coloured and smooth-textured), Peninsula Formation (Cape Supergroup). Substrate has sufficient fissures, ledges and crevices, ideal for establishment of plants.

DISTRIBUTION

Trachyandra tabularis is a quartzitic sandstone endemic, confined to the narrow kloofs and sheer south-facing rock faces of Table Mountain and adjacent areas.

RELATED SPECIES

Trachyandra tabularis is related to *T. hirsuta*, a species with firm leaves, a hairy, woody inflorescence and occurring on mountain slopes and flats.

ADAPTATIONS TO THE CLIFF ENVIRONMENT

Habit: Plants with drooping, subterete to dorsiventrally flattened leaves.

Size and weight: Plants cluster-forming, of medium weight.

Stem: Short subterranean rhizome.

Leaves

Orientation: Pendulous (positively geotropic).

Colour and texture: Dark to light green, with a soft texture. The slight translucent nature allows light to penetrate deeply, an adaptation helping the plants to cope with the shady cliff environment.

Age and persistence: Plants evergreen, leaves persistent, long-lived.

Armament: The entire to minutely denticulate margin and softer leaf texture suggest a reduction in armament in response to the undisturbed cliff habitat.

Sexual reproduction

Inflorescence and flowers: Inflorescence ascending to spreading; flowers scented, conspicuous, white, attracting insects.

Fruit/Seed

Size: Seed small.

Dispersal: Angular seeds shaken from the capsules and dispersed by wind.

Time: Seeds ripening in autumn, coinciding with the start of the rainy season.

Vegetative reproduction: Plants divide, forming dense clusters. Continual sprouting from the base represents an efficient vegetative backup dispersal strategy for this cliff-face environment.

CONSERVATION STATUS

A local endemic, not threatened (Hilton-Taylor 1996).

ADDITIONAL NOTES

Cremnophilous *Trachyandra*: This is the only known member of *Trachyandra* that grows only on cliffs. Plants are locally abundant but confined to moist southern and southeastern cliffs. On Table Mountain, plants have been observed on the lower and upper cliffs above 'The Aloes'.

Horticulture: Plants require cool, moist conditions throughout the year. Best grown in a warm temperate climate, under cool, moist conditions. Propagation is by seed or division.

VOUCHER

Van Jaarsveld 22891 (NBG).

ILLUSTRATIONS AND MAP

Plate 62, Figures 62a & 62b, Map 62.

HYACINTHACEAE

Albuca L.

- 63. *A. batteniana* Hilliard & B.L.Burt
- 64. *A. cremnophila* Van Jaarsv. & A.E.van Wyk
- 65. *A. crudenii* Archibald
- 66. *A. kirstenii* (J.C.Manning & Goldblatt) J.C.Manning & Goldblatt
- 67. *A. shawii* Baker
- 68. *A. thermarum* Van Jaarsv.

Drimia Jacq.

- 69. *D. cremnophila* Van Jaarsv.
- 70. *D. flagellaris* T.J.Edwards, D.Styles & N.R.Crouch
- 71. *D. loedolffiae* Van Jaarsv.
- 72. *D. mzimvubuensis* Van Jaarsv.
- 73. *D. uniflora* J.C.Manning & Goldblatt

Ledebouria Roth

- 74. *L. concolor* (Baker) Jessop
- 75. *L. cremnophila* S.Venter & Van Jaarsv.
- 76. *L. venteri* Van Jaarsv. & A.E.van Wyk

Ornithogalum L.

- 77. *O. juncifolium* Jacq. var. *emsii* Van Jaarsv. & A.E.van Wyk
- 78. *O. longibracteatum* Jacq.
- 79. *O. pendens* Van Jaarsv.

Schizobasis Baker

- 80. *S. intricata* (Baker) Baker

ALBUCA L.

63. *Albuca batteniana* Hilliard & B.L.Burt in Notes from the Royal Botanical Garden Edinburgh 42,2: 247–249 (1985).

Cremnophyte growth form: Cluster-forming geophyte, with rosulate subpendent leaves (of medium weight to heavy, cliff hugger).

Growth form formula: A:B:Lper:C:La (e) (vb) (r)

Etymology: After Auriol Batten (née Taylor) (1918–), well-known South African botanical artist and teacher.

DESCRIPTION AND HABITAT

Plants cluster-forming, glabrous, evergreen and bulbous. Bulbs epigeous, ovoid to 50 × 30 mm; tunics fleshy, imbricate, truncate at top, green. Roots fleshy, white, up to 2 mm diameter. Leaves

10–70 × 20–30 mm, in apical rosette, soft to firm, oblong, canaliculate, linear-attenuate, faintly lineate; apex acute. Inflorescence a spreading raceme, up to 800 mm long; scape 6–10 mm in diameter at base; peduncle up to 250 mm long; pedicels erect, up to 120 mm long at base, becoming smaller distally, up to 35 mm long near tip. Flowers erect, white with green median stripe; outer tepals 30–42 × 7 mm, oblong, green with white margins, apex cucullate, inner tepals 25–30 × 7 mm, oblong, green with white margins, apex cucullate. Filaments 15–20, white, flattened at base; anthers oblong, versatile, outer 4 × 1 mm, inner 7 × 2.5 mm. Ovary 8–12 mm long, obtuse-trigonous; style 10–13 mm long; stigma trilobate, white. Capsule ovoid, 20 × 14 mm. Seed flat, 5 mm long.

Phenology: Flowering in winter (July–August). Seed released in spring (September–November).

Pollinators: Insects.

Habitat and aspect: Sea-facing coastal cliffs where plants are firmly rooted in crevices on the cliff faces and on the talus slopes below. Winters are cool but frost is absent. Average daily maximum temperature is about 23°C, but daily temperatures can reach 35°C under hot berg wind conditions. Rainfall mainly in summer and winter, ranging from 700–800 mm per annum (thunder showers and cyclonic winter rain).

Altitude: 25–800 m.

Associated vegetation: Albany Coastal Belt of the Albany Thicket Biome (Mucina *et al.* 2005).

Associated cremnophytes: Associated species include *Aptenia cordifolia*, *Bulbine natalensis*, *Crassula multicava*, *C. orbicularis*, *C. pellucida* subsp. *marginalis*, *Gasteria excelsa* and *Haemanthus albiflos*.

Geology: Mudstone, Emakwezini Formation, Adelaide Subgroup (Beaufort Group of the Karoo Supergroup).

DISTRIBUTION

Albuca batteniana is distributed along the coastal region from Oribi Gorge in southern KwaZulu-Natal to the Bashee River and East London in the southwest (Eastern Cape).

RELATED SPECIES

Related to *A. cremnophila*, both species with imbricate leaf bases and similar secundly arranged flowers. The flowers of *A. cremnophila* are smaller and more densely arranged and yellow-tipped. *Albuca cremnophila* differs further in its larger, very firm, drooping, canaliculate leaves up to 1 m and drooping inflorescence up to 2 m long. *Albuca batteniana* has a rosette of recurved leaves, with a more robust inflorescence and larger flowers (30–42 mm long), which are not yellow-tipped. It is winter-flowering while *A. cremnophila* flowers in spring (October–November). Both are related to *A. nelsonii*, a non-cremnophilous species with soft, erect leaves and inflorescence.

ADAPTATIONS TO THE CLIFF ENVIRONMENT

Habit: Plants forming clusters of epigeous bulbs with rosulate, spreading, recurved to subpendulous leaves and ascending-spreading inflorescence.

Size and weight: Bulbs medium-sized, of medium weight to heavy in large clusters.

Bulb: Bulbs epigeous, forming dense clusters, tunics succulent, imbricate and an adaptation to the dry cliff environment.

Leaves

Orientation: In apical rosette, recurved to spreading, pendulous.

Colour and texture: Dark green, with soft to firm texture.

Age and persistence: Evergreen, long-lived, with basal abscission layer.

Armament: Leaves channelled and without obvious armament.

Sexual reproduction

Inflorescence and flowers: Inflorescence horizontally presented, the conspicuous white flowers attracting insects.

Fruit/Seed

Size: Seed flat, shiny, 5 mm in diameter, an ideal size for establishment in crevices.

Dispersal: Seeds shaken or blown from the erect capsules and dispersed by wind.

Time: Seeds ripening at the end of December and dispersed in summer and autumn, coinciding with autumn rains. Germination after 21 days.

Vegetative reproduction: *Albuca batteniana* proliferates from the base, forming dense clusters. When bulbs become detached, they will re-root and continue growth. This vegetative regeneration can be seen as a backup ensuring survival in the harsh cliff-face environment.

CONSERVATION STATUS

Local endemic, not threatened (Hilton-Taylor 1996).

ADDITIONAL NOTES

Horticulture: *Albuca batteniana* is an ornamental species best for subtropical coastal gardens. Ideal for embankments, gabions or terraforce walls, also well suited to hanging baskets and large containers. Plants can be grown in full sun or partial shade and should be well watered during their summer growing season. Plants easily grown from seed or division and thrive in cultivation. Its very easy growing nature maximises survival rate.

VOUCHERS

Van Jaarsveld 16617, 16815, 16885 (NBG).

ILLUSTRATIONS AND MAP

Plate 63, Figures 63a–63d, Map 63.

64. *Albuca cremnophila* Van Jaarsv. & A.E.van Wyk in *Aloe* 36,4: 71–74 (1999).

Cremonophyte growth form: Cluster-forming geophyte, with rosulate pendent leaves (of medium weight to heavy, cliff hanger).

Growth form formula: A:B:Lper:C:La (e) (vb) (r)

Etymology: Greek *kremnos*, cliff, and Greek *phileein*, to love, pertaining to its cliff habitat.

DESCRIPTION AND HABITAT

Evergreen, epigeous (rarely hypogeous), bulbous plants, solitary or dichotomously dividing forming small, dense clusters. Bulb ovoid, 90 × 50–60 mm; tunics fleshy, imbricate, truncate at top, green-grey. Roots fleshy, white, up to 3 mm in diameter. Leaves 30–70 × 20–30 mm, in apical rosette, firm, oblong, canaliculate, linear-attenuate, drooping, succulent, dark green, glabrous, becoming terete towards tip; apex acute. Inflorescence a spreading to pendulous raceme, up to 2 m long; peduncle up to 250 mm long; bracts acuminate, membranous, margin translucent, basal bracts up to 110 × 13 mm, gradually becoming smaller distally; pedicels erect, 35–50(–80) mm long (exceptionally 120 mm), becoming shorter distally (35 mm). Flowers secundly arranged, 20–25 mm long, dense, erect, white with green median stripe; outer tepals linear-obovate, 20–25 × 7–8 mm, green with green median portion, inner tepals 18–20 × 8–10 mm, ovate with hooded yellowish apex. Filaments 13 mm long, 2.5 mm in diameter at base. Ovary stipitate for 1 mm, 6 mm long, 4 mm in diameter at base, narrowing to 3 mm, 3-angular, basally each angle with raised twin tubercles; stigma linear-trigonous, 10 × 2 mm. Capsule 15 × 9 mm. Seed flat, 4 × 3 mm.

Phenology: Flowering in spring (October–November) or after sufficient rainfall. Seed released towards end of November, early December.

Pollinators: Insects.

Habitat and aspect: Cliffs in dry river valleys and dark, narrow kloofs at all aspects but more on the cooler south-facing ones. Plants firmly rooted in crevices. Winters are cool but frost is a rarity or absent. Average daily maximum temperature is about 27°C and the average daily minimum about 9°C. Rainfall mainly in summer and winter, ranging from 200–300 mm per annum (thunder showers and cyclonic winter rain).

Altitude: 300–600 m.

Associated vegetation: Gamtoos Thicket of the Albany Thicket Biome (Mucina *et al.* 2005).

Associated cremonophytes: *Adromischus cristatus* var. *zeyheri*, *Cotyledon tomentosa* subsp. *tomentosa*, *Cyrtanthus flammosus*, *C. labiatus*, *C. montanus*, *Delosperma elsieae*, *Gasteria*

rawlinsonii, *Haworthia gracilis* var. *picturata*, *H. viscosa*, *Othonna lobata* and *Plectranthus verticillatus*.

Geology: Quartzitic sandstone, Peninsula Formation (Cape Supergroup). Substrate with sufficient ledges and crevices for establishment of plants.

DISTRIBUTION

Albuca cremnophila is distributed in Baviaanskloof and the Kouga Dam region west of Hankey (Eastern Cape).

RELATED SPECIES

Albuca cremnophila is related to *A. batteniana*.

ADAPTATIONS TO THE CLIFF ENVIRONMENT

Habit: Plants solitary or forming small clusters of epigeous bulbs with pendulous leaves up to 1 m long and a pendulous inflorescence up to 2 m long. The pendent nature and epinastic growth are retained in cultivation, an adaptation related to its cliff habit. The bulbs are succulent, with truncate tunics.

Size and weight: Heads of medium weight but heavy in large clusters.

Bulb: Bulb solitary or dividing dichotomously, forming small, dense clusters. Tunics fleshy, green, an adaptation to the dry cliff environment.

Leaves

Orientation: In apical rosette, pendulous, with positive geotropic growth.

Colour and texture: Dark green. The firm, succulent texture and terete apices can be seen as an adaptation to the dry habitat.

Age and persistence: Leaves evergreen, long-lived.

Armament: Leaves channelled and without obvious armament.

Sexual reproduction

Inflorescence and flowers: Inflorescence pendulous to horizontally presented, the conspicuous, erect, white flowers attracting insects.

Fruit/Seed

Size: Seed flat, shiny, 3 × 4 mm, an ideal size for establishment in crevices.

Dispersal: Seeds shaken from the capsules and dispersed by wind.

Time: Seeds ripening at the end of December and dispersed in summer and autumn, coinciding with autumn rains. Germination after 21 days.

Vegetative reproduction: *Albuca cremnophila* sometimes divides dichotomously to form small, dense clusters. When bulbs become detached, they will re-root and continue growth. This vegetative regeneration can be seen as a backup ensuring survival in the harsh cliff-face environment.

CONSERVATION STATUS

A local endemic, not threatened (Hilton-Taylor 1996).

ADDITIONAL NOTES

Horticulture: *Albuca cremnophila* is easily grown from seed or division and does well in cultivation. It is best grown in thicket gardens and is suited to sheer embankments, gabions and rockeries. It can be grown in dappled shade or full sun. Its very easy growing nature maximises its survival rate. The plants retain their pendent growth in cultivation and plants in the Botanical Society conservatory at Kirstenbosch have positively geotropic rosettes.

VOUCHER

Van Jaarsveld 12171 (NBG).

ILLUSTRATIONS AND MAP

Plate 64, Figures 64a–64c, Map 64.

65. *Albuca crudenii* Archibald in *Bothalia* 6: 542–544 (1956).

Cremonophyte growth form: Cluster-forming bulbous plant, with linear drooping leaves (of light weight, cliff hugger).

Growth form formula: A:B:D:C:Lp (e) (vb) (eg)

Etymology: After Frank Cruden (date of birth and death unknown), schoolmaster at Grahamstown in the Eastern Cape during the 1920s and collector of plants who collected this species near Alicedale in September 1917.

DESCRIPTION AND HABITAT

Summer-deciduous, semi-epigeous (rarely hypogeous), glabrous, bulbous plants, sprouting from base, forming small clusters up to 80 mm in diameter. Bulb globose, up to 30 mm in diameter; scales tunicate, outer tunics thin, papery, grey-green, clasping, withering and exposing green tissue. Roots white, 0.5 mm in diameter, fibrous. Leaves 1, rarely 2, green, flaccid, slightly fleshy, linear-lanceolate; surface flat to channelled, up to 450 × 19 mm, striate; tip subulate in young leaf; margin with single row of minute, glandular, transparent, erect hairs. Inflorescence lax, secund, racemose, up to 450 mm long; scape up to 260 × 3 mm; surface minutely sparsely glandular hairy; raceme up to 70 mm long; bracts puberulous, deltoid, apiculate, up to 9 mm

long, 8 mm broad at base, membranous, translucent; pedicels cernuous, becoming erect after fruiting. Flowers 3–10, pendulous, with faint vanilla scent; outer tepals 15×6 mm, patent, oblong, with very slightly cucullate apex, bright yellow, with narrow green median stripe, inner segments up to 12×5 mm, erect, connivent, ovate, pale yellow, with narrow green median stripe, apex cucullate, 1 mm long. Androecium of 3 sterile and 3 fertile stamens; outer filaments ovate-lanceolate, 9×1.5 mm, mucronate, with sterile tip, inner filaments spade-shaped, basal part 1.5×1.5 mm, distal part 5.5×1 mm; anthers 4 mm long, apex rectangular, base spreading. Gynoecium glabrous; ovary ellipsoidal; style oblong, slightly narrower in distal third, triquetrous, 5×1 mm, yellow; stigma convex, 3-lobed, lobes simple, each with row of minute papillae, green. Fruit a trilocular capsule, 13 mm long. Seed flat, 3×1.5 mm, black.

Phenology: Flowering from end of October–November. Seed released in summer.

Pollinators: Insects.

Habitat and aspect: South-facing sandstone cliffs. Plants rooted in crevices and on ledges. The average daily maximum temperature is about 24°C and average daily minimum about 10°C . Rainfall in summer and winter, ranging from 400–600 mm per annum (mainly thunder showers and cyclonic winter rain).

Altitude: 350–400 m.

Associated vegetation: Bisho Thornveld of the Sub-Escarpment Savanna Bioregion of the Savanna Biome (Mucina *et al.* 2005).

Associated cremnophytes: *Aloe arborescens*, *Bowiea volubilis*, *Bulbine natalensis*, *Crassula orbicularis*, *C. perforata*, *Ophioglossum nudicaule* and *Plectranthus strigosus*.

Geology: Witteberg quartzite (Cape Supergroup). Substrate with sufficient ledges and crevices for establishment of plants.

DISTRIBUTION

Albuca crudenii is known only from the Grahamstown district (Eastern Cape).

RELATED SPECIES

Albuca crudenii is related to *A. glandulosa*, immediately distinguished by its more than one leaf and white flowers with glandular hairs on the perianth segments.

ADAPTATIONS TO THE CLIFF ENVIRONMENT

Habit: Plants form small clusters of epigeous bulbs, with narrow, flaccid, drooping leaves.

Size and weight: Clusters small, of light weight.

Bulb: The bulbs are photosynthetically functional. The small clusters of epigeous succulent bulbs are an adaptation to the dry vertical habitat. Its prolific vegetative reproductive nature (sprouting bulbils) from the base acts as a backup and ensures small mats. Deciduous during the summer months.

Leaves

Orientation: Soft flaccid, drooping, grooved on upper surface, suggesting adaptation to the sheer cliff habitat.

Colour and texture: Light green. Texture succulent, flaccid and channelled at the base, suggesting xeromorphic adaptation to the dry vertical habitat.

Age and persistence: Plants evergreen and leaves gradually replaced.

Armament: Leaves without obvious armament.

Sexual reproduction

Inflorescence and flowers: Inflorescence ascending, the conspicuous yellow flowers attracting insects.

Fruit/Seed

Size: Seed 3×1.5 mm.

Dispersal: Flat, black seeds shaken or blown from the erect, dehiscent capsules and dispersed by wind.

Time: Seeds ripening in the summer, coinciding with summer rains.

Vegetative reproduction: *Albuca crudenii* proliferates, forming small, dense clusters. When bulbs become detached, they will re-root and continue growth. This vegetative regeneration can be seen as a backup ensuring survival in the harsh cliff-face environment.

CONSERVATION STATUS

Classified as rare (Raimondo *et al.* 2009). A local endemic, not threatened.

ADDITIONAL NOTES

Horticulture: Plants of *Albuca crudenii* are easily grown by division or from seed. However, owing to their small stature and little appeal, they are not grown much. Best for containers, in a sandy mixture and in dappled shade. Outside its habitat, it is best grown under controlled conditions in a greenhouse. It is not shy to flower.

VOUCHER

Cruden 14a (ALB).

ILLUSTRATIONS AND MAP

Plate 65, Figures 65a & 65b, Map 65.

66. *Albuca kirstenii* (J.C.Manning & Goldblatt) J.C.Manning & Goldblatt in *Taxon* 58: 97 (2009).

Cremonophyte growth form: Cluster-forming geophyte, with terete leaves (of light weight, cliff hugger).

Growth form formula: A:B:D:C:Lp (e) (vb)

Etymology: After the late Kirsten Louw.

DESCRIPTION AND HABITAT

Summer-deciduous, epigeous (rarely hypogeous), bulbous plants forming small clusters up to 80 mm in diameter. Bulb globose to ovoid, up to 20 × 18 mm; outer tunics thin, papery, grey-green, clasping, withering, exposing green tissue. Roots white, 0.5 mm in diameter, fleshy. Leaves 1 or 2, linear, succulent, inrolled with margins often touching and appearing terete, 50–100 × 1.5–2.0 mm; surface smooth, glaucous; margin entire: apex acute. Inflorescence ascending, up to 140 mm high, enclosed in basal half of youngest leaf; peduncle smooth, glaucous, 0.8 mm in diameter at base, enlarging to 1.5 mm in diameter in distal half; raceme up to 50 mm long; bracts ovate-acuminate, thin, papery, 7 × 3 mm, base clasping; pedicels 3 mm long, bending down. Flowers yellow with green median stripe, 30 mm in diameter; outer tepals spreading, linear-obovate, 12 × 3 mm, pale yellow with green median portion, inner tepals 11 × 5 mm, ovate, with hooded apex. Filaments 9 mm long, 1 mm in diameter, canaliculate at base, white; anthers 1.5 mm long, oblong, white; pollen yellowish. Ovary stipitate for 1 mm, 4–6 mm long, 2–3 mm in diameter, green, grooved, 3-angular; style trigonous, 6 × 1 mm, yellowish; stigma capitate. Capsule dehiscent, 12 × 6 mm. Seed black, flattish 3 × 2 mm.

Phenology: Flowering in autumn (end March–April). Seed released towards end of April.

Pollinators: Insects.

Habitat and aspect: Southeast-facing cliffs overlooking Gourits River. Plants rooted in crevices and on ledges. On hot days with berg wind conditions, temperatures can go up to 40°C. Average daily maximum about 23°C, average daily minimum about 11°C. Rainfall mainly in winter and in summer, 300–400 mm per annum (thunder showers and cyclonic winter rain).

Altitude: 200–300 m.

Associated vegetation: Southern Cape Valley Thicket of the Albany Thicket Biome (Mucina *et al.* 2005).

Associated cremonophytes: *Cotyledon elisae*, *Crassula atropurpurea*, *C. lactea* and *Haworthia turgida*.

Geology: Quartzitic sandstone, Peninsula Formation (Cape Supergroup).

DISTRIBUTION

Albuca kirstenii is known only from the Breede and lower Gourits Rivers in the Western Cape.

RELATED SPECIES

Albuca kirstenii is related to *A. crudenii*, the latter with a solitary dorsiventrally flattened leaf.

ADAPTATIONS TO THE CLIFF ENVIRONMENT

Habit: Plants form small clusters of epigeous bulbs, with ascending, narrow leaves. The bulbs are photosynthetically functional.

Size and weight: Clusters small, of light to medium weight in large clusters.

Bulb: The small clusters of epigeous succulent bulbs are an adaptation to the dry vertical habitat.

Leaves

Orientation: Ascending, only 1 or 2 terete leaves, blocking out minimum light from the photo-active bulbs.

Colour and texture: Glaucous. Texture succulent and channelled, suggesting xeromorphic adaptation to the dry vertical habitat.

Age and persistence: Plants becoming deciduous in summer.

Armament: Leaves without obvious armament.

Sexual reproduction

Inflorescence and flowers: Inflorescence ascending, conspicuous yellow flowers attracting insects.

Fruit/Seed

Size: Seed small and light.

Dispersal: Seeds blown and shaken from the erect capsules and dispersed by wind.

Time: Seeds ripening and dispersed at end of autumn, coinciding with first winter rains.

Vegetative reproduction: *Albuca kirstenii* proliferates, forming small, dense clusters. When bulbs become detached, they will re-root and continue growth. This vegetative regeneration can be seen as a backup ensuring survival in the harsh cliff-face environment.

CONSERVATION STATUS

Classified as rare (Raimondo *et al.* 2009). A local endemic, not threatened.

ADDITIONAL NOTES

Horticulture: Easily grown by division or from seed. However, owing to their small stature and little appeal, they are not grown much. Best for containers, in a sandy mixture and in dappled shade. Outside its habitat, it is best grown under controlled greenhouse conditions.

VOUCHER

Van Jaarsveld 16718 (NBG).

ILLUSTRATIONS AND MAP

Figures 66a & 66b, Map 66.

67. *Albuca shawii* Baker in Journal of Botany 12: 367 (1874). (Cliff-face form.)

Cremonophyte growth form: Cluster-forming geophyte, with linear drooping leaves (of light weight, cliff hanger).

Growth form formula: A:B:Lper:C:Lp (vb) (eg)

Etymology: After John Shaw (1837–1890), Scotsman, geologist and naturalist.

DESCRIPTION AND HABITAT

Evergreen, hypogeous, bulbous plants proliferating from base, forming small clusters up to 120 mm in diameter. Bulb globose to ovoid, up to 20 × 18 mm; outer tunics thin, papery, grey-green, clasping, withering, exposing green tissue. Roots white, 0.5 mm in diameter, fleshy. Leaves up to 12, in a rosette, often drooping from cliff face, linear-lanceolate, succulent, 150–400 × 1.5–6.0 mm; surface slightly hairy, green; margin ciliate; apex acuminate; young leaves terete. Inflorescence ascending, racemose, 200 mm high; surface beset with short translucent hairs; peduncle 3 mm in diameter at base, green; raceme up to 80–100 mm long; bracts ovate-acuminate, thin, papery, 16 × 4 mm, base clasping; pedicels 20 mm long, ascending. Flowers nodding, yellow with green median stripe, 18 mm in diameter; outer tepals spreading, linear-lanceolate, 7 × 3.5 mm, pale yellow with green median portion, apices obtuse, incurved, inner tepals 11 × 4 mm, linear-ovate, with hooded incurved apex. Filaments 9 mm long, 1 mm in diameter, outer 1.5 mm in diameter at base, hyaline, abruptly constricted, canaliculate at base, white. Anthers 15 × 1 mm, oblong, white; pollen yellowish. Ovary stipitate for 1 mm, 4 mm long, 2 mm in diameter, green, grooved, 3-angular. Style 5 mm long, 1 mm in diameter expanding to 2 mm, yellow; stigma 3-lobed, truncate. Capsule and seed not seen.

Phenology: Flowering in spring (October–November). Seed released towards summer and early autumn.

Pollinators: Insects.

Habitat and aspect: South- and southeast-facing quartzitic sandstone cliffs or large boulders. Plants rooted in crevices and on ledges. Average daily maximum temperature is about 23°C and average daily minimum 12°C. Rainfall occurs mainly in summer, ranging from 800–1500 mm per annum (thunder showers).

Altitude: 533–2400 m.

Associated vegetation: Zululand Lowveld of the Savanna Biome as well as many regions within the Grassland Biome (Mucina *et al.* 2005).

Associated cremnophytes: Along the White Mfolozi, it shares its habitat with *Aloe arborescens*, *Crassula orbicularis*, *C. expansa* subsp. *fragilis* and *Delosperma lebomboensis*.

Geology: Varied, but mainly sandstone such as quartzitic sandstone of the Moodies Group (Barberton Supergroup) (Keyser 1997).

DISTRIBUTION

Albuca shawii is widely distributed from the Eastern Cape to Limpopo Province in the north, confined to mountain slopes and river valleys. This cliff-face form appears to be confined to the White Mfolozi.

RELATED SPECIES

Albuca shawii is related to *A. crudenii* but is immediately distinguished by its much narrower leaves in a central rosette.

ADAPTATIONS TO THE CLIFF ENVIRONMENT

Habit: Small clusters of hypogeous bulbs, with drooping linear-lanceolate leaves. The succulent leaves are an adaptation to dry conditions in the vertical habitat.

Size and weight: Clusters of light to medium weight in large clusters.

Bulb: Hypogeous, prolific from the base and forming dense clusters.

Leaves

Orientation: Drooping, up to 12, canaliculate; young leaves terete.

Colour and texture: Light to dark green. Texture succulent and channelled, suggesting xeromorphic adaptation to the dry vertical habitat.

Age and persistence: Plants evergreen, leaves seasonally replaced.

Armament: Leaves soft and without obvious armament.

Sexual reproduction

Inflorescence and flowers: Inflorescence ascending, nodding yellow flowers attracting insects.

Fruit/Seed

Size: Not seen.

Dispersal: Seeds shaken from the erectly orientated capsules and dispersed by wind.

Time: Seeds ripening in summer and autumn and dispersed in late autumn, coinciding with the first winter rains.

Vegetative reproduction: *Albuca shawii* proliferates, forming small, dense clusters. When bulbs become detached, they will re-root and continue growth. This vegetative regeneration can be seen as a backup ensuring survival in the harsh cliff-face environment.

CONSERVATION STATUS

A local endemic, not threatened.

ADDITIONAL NOTES

General: *Albuca shawii* is not an obligate cremnophyte and has many forms. This form from the White Mfolozi River appears to be obligate.

Horticulture: Plants of *Albuca shawii* are easily grown by division or from seed and thrive in cultivation. It is best for bushveld and subtropical coastal gardens, grown in dappled shade. Water well in summer and feed with an organic fertiliser. It does well in rockeries and containers. Its very easy growing nature maximises its survival rate.

VOUCHERS

Van Jaarsveld 18708, 19379 (NBG).

ILLUSTRATIONS AND MAP

Figures 67a–67c, Map 67.

68. *Albuca thermarum* Van Jaarsv., in Van Jaarsveld & Van Wyk in *Bothalia* 33,1: 116 (2003e).

Cremonophyte growth form: Solitary geophyte, with pendent leaves (of medium weight, cliff hanger).

Growth form formula: A:B:Lper:C:Lp (e) (vb) (eg)

Etymology: After the thermal springs at Calitzdorp.

DESCRIPTION AND HABITAT

Evergreen, hypogeous (rarely epigeous), solitary, bulbous plants. Bulb ovoid, 70 × 55 mm; tunics fleshy, imbricate, persistent, drying grey and with fibrous network. Roots fleshy, white, up to 3 mm in diameter. Leaves oblong, linear-attenuate, 300–550 × 20–30 mm, in apical rosette, drooping, succulent, firm, dark green, glabrous, channelled for most of their length; apex acute. Inflorescence a spreading to pendulous raceme, 400–600 mm long; peduncle up to 260 mm long; bracts acuminate, 45 × 8 mm, green with white translucent margin; scape 8–10 mm in diameter at base; pedicels ascending to erect, up to 105 mm long at base, becoming

shorter, up to 35 mm long near tip. Flowers erect; tepals yellowish green, tips yellow to yellowish green, becoming white proximally but with distinct green midstripe (about 3 mm wide), outer tepals 25×7 mm, strap-shaped, apex cucullate, inner tepals ovate, 20–12 mm long. Stamens: filaments 15 mm long, 2 mm in diameter at base (flattened); inner 13 mm long, with distinct short channelled constriction 4.5 mm from base, basal third broadly triangular-ovate (3mm wide at base), margin membranous, apices of both inner and outer filaments projected forward and adpressed against style; anthers oblong, versatile, outer 2.5×1.5 mm, inner 3.5×2.5 mm. Ovary oblong, 3-angled, 7×4 mm, stipitate for 1.5 mm, each angle with raised emarginate base; style linear-trigonous, clavate, 9×2 mm; stigma yellowish green. Capsule 18×10 mm, grey-brown, valves splitting in distal quarter. Seeds flat, 6×3 mm, angular, distinctly wrinkled, blackish brown.

Phenology: Flowering October–November. Seed released towards end of November, early December.

Pollinators: Insects.

Habitat and aspect: South- and east-facing cliffs at altitude of about 500–1000 m (Badspoot, Olifantsrivier in the southern Little Karoo) near Calitzdorp. Plants firmly rooted in crevices. Temperature high in summer, 28–38°C. Winters are cooler but frost is absent. The average daily maximum temperature is about 26°C and the average daily minimum about 9°C. Rainfall occurs in summer and winter, ranging from 200–300 mm per annum (thunder showers and cyclonic winter rain).

Altitude: 400–800 m.

Associated vegetation: Western Gwarrieveld of the Rainshadow Valley Karoo Bioregion, Succulent Karoo (Mucina *et al.* 2005).

Associated cremnoophytes: Associated species include *Aloe comptonii*, *Cotyledon tomentosa* subsp. *tomentosa*, *Crassula badspootense*, *C. perforata*, *C. rupestris*, *Haworthia integra* var. *rycroftiana* and *Senecio ficoides*.

Geology: Quartzitic sandstone of the Nardouw Subgroup, Table Mountain Group (Cape Supergroup).

DISTRIBUTION

Albuca thermarum is a quartzitic sandstone endemic, confined to the mountains of the southern Little Karoo at Calitzdorp Spa.

RELATED SPECIES

Albuca thermarum is related to *A. papyracea*, both with fibrous sheaths but the latter with shorter leaves that are not drooping.

ADAPTATIONS TO THE CLIFF ENVIRONMENT

Habit: Plants with drooping leaves and inflorescence.

Size and weight: Heads medium-sized, of medium weight.

Bulb: Hypogeous, tunics fleshy, imbricate, persistent.

Leaves

Orientation: Pendulous (positively geotropic).

Colour and texture: Dark green, with a firm texture.

Armament: Leaves without obvious armament.

Sexual reproduction

Inflorescence, flowers and fruit: Inflorescence horizontally presented to drooping, the conspicuous white flowers attracting insects. Fruit a dehiscent capsule becoming erect once fertilised.

Fruit/Seed

Size: Seed 6×3 mm, an ideal size for establishment in crevices.

Dispersal: Seed blown and shaken from the erect infructescence and dispersed by wind.

Time: Seeds ripening at the end of December and dispersed in summer and autumn, coinciding with autumn rains. Germination after 21 days.

Vegetative reproduction: Absent.

CONSERVATION STATUS

Classified as critically rare (Raimondo *et al.* 2009). A local endemic, not threatened.

ADDITIONAL NOTES

Horticulture: Plants of *Albuca thermarum* are easily grown from seed, doing well in cultivation. Its very easy growing nature maximises its survival rate. It is best grown in succulent karoo gardens. Water sparingly throughout the year. Suitable for embankments. Also thriving in containers.

VOUCHER

Van Jaarsveld 14152 (NBG).

ILLUSTRATIONS AND MAP

Plate 68, Figures 68a–68e, Map 68.

DRIMIA Jacq.

69. Van Jaarsv., in Van Jaarsveld & Van Wyk in *Aloe* 42,4: 53–55 (2005d).

Cremonophyte growth form: Cluster-forming, epigeous bulbs (of medium weight, cliff hanger).

Growth form formula: A:B:Lper:C:Lp (e) (vb)

Etymology: Greek *kremnos*, cliff, and Greek *phileein*, to love, pertaining to its cliff habitat.

DESCRIPTION AND HABITAT

Semi-evergreen, epigeous, bulbous geophytes. Roots white, fleshy, 2 mm in diameter. Bulbs ovoid, up to 30 mm high, forming loose clusters of up to 4 heads and about 80 mm in diameter; tunics (scales) loose, thick, succulent, oblong-clavate, 15–45 × 5–12 mm; stalk flattened, up to 20 mm long, up to 4 mm in diameter; distal part of tunic oval-depressed; adaxial side flat, grooved to convex, abaxial side cymbiform to convex; apex truncate to obtuse; surface dark purplish. Leaves linear, amplexicaul at base, 100–200 × 3–8 mm, dark green; petiole short, indistinct, purplish; adaxial surface with 3–5 shallow grooves, abaxial surface with distinct midrib; margin entire. Inflorescence spreading, ascending, racemose, 250–300 mm long; scape 1.5 mm in diameter, dark green, terete, glabrous; racemes 50–80 mm long, bearing 4–8 pendent flowers; pedicels 7–8 mm long, curving down; bracts 3.5–4.0 mm long, white, linear-lanceolate, ascending, not clasping; spur 6 mm long, linear-lanceolate, adpressed to peduncle. Perianth white, 15–16 mm in diameter, opening in the morning; tepals oblanceolate-oblong, 7 × 2 mm, white with dull purplish centric stripes, apices obtuse to acute. Stamens adpressed to ovary into an erect cone-like structure, 11 mm high, with an acute apex; filaments short, 1.5 mm long, flattened at base (diameter of about 0.5 mm), tapering to 0.25 mm, white, translucent; anthers linear-lanceolate, 6 mm long, introrse, erectly projected, apex acute, opening by means of an apical pore. Ovary ovoid, 3.5 × 1.8 mm, 6-grooved, green, shortly stipitate; stipe black; style 3 mm long; stigma capitate.

Phenology: Flowering mainly in early summer (December–January). Seeds dispersed by wind from summer onwards. Flowers opening acroptally from below, promoting cross pollination, in the morning and lasting for two days.

Pollinators: Insects, pollen released by vibration of insect wings.

Habitat and aspect: Shale cliffs, mainly on shady south-facing ones. Plants firmly rooted in crevices, size often depending on the growing space allowed by the crevice. Winters are cool but frost is absent. The average daily maximum temperature is about 23°C and average daily minimum 14°C, but extremes of up to 40°C have been recorded in the region. Rainfall mainly in summer, ranging from 800–1000 mm per annum (thunder showers or cyclonic winter rain), occasionally in winter.

Altitude: 50–600 m.

Associated vegetation: Eastern Valley Bushveld of the Sub-Escarpment Savanna Bioregion, Savanna Biome (Mucina *et al.* 2005).

Associated cremnophytes: Near Ludonga (Mzimvubu River) it is associated with *Adromischus cristatus* var. *mzimvubuensis*, *Bulbine natalensis*, *Crassula cordata*, *C. cultrata*, *C. multicava* subsp. *floribunda*, *C. orbicularis*, *Cyanotis speciosa*, *Ornithogalum longibracteatum*, *Peperomia blanda* and *Plectranthus mzimvubuensis*.

Geology: Ecca shale (Karoo Supergroup).

DISTRIBUTION

From the lower Mzimvubu River (Transkei, Eastern Cape) and also on cliffs from the Kei Mouth. The plants occur mainly on south-facing shale cliffs.

RELATED SPECIES

Drimia cremnophila is related to *D. haworthioides* of the Eastern Cape from East London westwards, which has similar loose, bulbous scales but that is where the resemblance ends. The leaves of *D. haworthioides* have a ciliate margin, the flowers are spreading and not pendent and the plants occur in thicket among rocks, usually not on cliffs. It also resembles *D. mzimvubuensis* but the latter has terete leaves and a distinct staminal column in the flowers.

ADAPTATIONS TO THE CLIFF ENVIRONMENT

Habit: Plants forming loose, globose clusters, exploiting the vertical cliff-face habitat and absence of disturbance by larger herbivores. A fairly slow-growing, long-lived perennial.

Size and weight: Heads of medium and average weight.

Bulb: Bulb epigeous with loose, fleshy, club-shaped scales, slightly compressed and tolerant of warm, dry, vertical conditions. It is photosynthetically active, maximising absorption of light. The succulent nature suggests an adaptation to the xeric habitat.

Leaves

Orientation: Mainly drooping, but varying according the crevice location. Long, flat, pendent, not shading out the bulb.

Succulence: The succulent bulb scales well adapted to the dry habitat. The succulent nature of the leaves is an adaptation to the xeric cliff-face habitat.

Colour: Dark green, immaculate.

Age and persistence: Semi-evergreen species, reflecting the climatic pattern of almost year-round rainfall.

Armament and camouflage: Lack of a camouflage defence strategy and the conspicuous clustered habit suggest adaptation to the safe cliff habitat in the absence of disturbances.

Sexual reproduction

Inflorescence and flowers: Inflorescence spreading-ascending, racemose, with conspicuous, drooping, white flowers, maximising visibility from below, an adaptation to the cliff-face dwelling.

Fruit/Seed

Size: Not seen.

Dispersal: Capsules ripening in summer, the flat, winged seeds wind-dispersed.

Time: Seeds ripening in summer and autumn, coinciding with the rainy season.

Vegetative reproduction: Plants proliferate, forming clusters. The vegetative clusters actively occupy crevices by growth and should any bulb or bulb scale become dislodged and fall onto ledges below, it will root—a prolific vegetative dispersal strategy ensuring long-term survival on the cliffs.

CONSERVATION STATUS

A local endemic, not threatened.

ADDITIONAL NOTES

Horticulture: Plants easily grown by division, from bulb scales or from seed, doing well in cultivation. Its very easy growing nature maximises survival rate on the cliff face. It is best for thicket and subtropical gardens, suitable for rockeries and containers.

VOUCHER

Van Jaarsveld, Xaba & Harrower 97 (NBG).

ILLUSTRATIONS AND MAP

Plate 69, Figures 69a–69c, Map 69.

70. *Drimia flagellaris* T.J.Edwards, D.Styles & N.R.Crouch in *South African Journal of Botany* 71,1: 122–126 (2005).

Cremonophyte growth form: Cluster-forming (hugging), epigeous bulbs, with spreading to pendent linear-terete leaves (of medium weight, cliff hanger).

Growth form formula: A:B:Lper:C:Lp (e) (vb)

Etymology: The epithet *flagellaris*, like a flagellum, pertains to the leaves.

DESCRIPTION AND HABITAT

Plants evergreen, with epigeous bulbs proliferating from base, forming tight round clusters up to 100 mm in diameter and consisting of up to 14 bulbs. Bulbs ovoid, up to 20–30 × 15–20 mm, each with a solitary leaf; tunics grey-brown, leathery, exposing green to purplish green lower tissue. Leaf synanthous, 100–250 × 2 mm, linear, filiform, tapering towards apex, withering from tip, green. Inflorescence 10–25-flowered, 18–250 mm high; scape terete, erect; racemes 80–90 mm long; bracts deltoid-cymbiform, 1 × 1 mm, white, slightly translucent, basal bracts spurred, up to 3.5 mm long; pedicels (8–)10–12 mm long. Perianth stellate, up to 14 mm in diameter, white; outer tepals linear-obovate, 5–8 × 1.8–3.0 mm, acute, inner tepals narrowly elliptic, 5–8 × 2–3 mm, obtuse, white with red-brown keel. Stamens 4.5 mm long; filaments linear, inner slightly shorter; anthers 0.7 mm long, versatile; pollen yellow. Ovary ovoid, tapering towards apex, 2.2 × 1.8 mm, green, shortly stipitate; style erect, 3 mm long. Capsule obovoid, 4 mm long. Seed oblong, angular, 3.5–4.0 × 1 mm, black.

Phenology: Flowering mainly from early spring to spring (end July–October). Seeds dispersed by wind in summer.

Pollinators: Insects.

Habitat and aspect: South- and east-facing cliffs. Plants firmly rooted in crevices. Temperature high in summer (35–40°C). Winters are cooler but frost is absent. The average daily maximum temperature is about 24°C and the average daily minimum about 16°C. Rainfall occurs mainly in summer and ranges from 1000–1250 mm per annum.

Altitude: 250–800 m.

Associated vegetation: Mainly KwaZulu-Natal Coastal Belt of the Indian Ocean Coastal Belt (Mucina *et al.* 2005). The local vegetation consists of short forest, thicket and grassland and margin of grassland.

Associated cremnophytes: *Aloe arborescens*, *Bulbine natalensis*, *Crassula perfoliata* var. *minor*, *Gasteria pendulifolia*, *Peperomia blanda* and *Plectranthus purpuratus*.

Geology: Quartzitic sandstone (light-coloured and smooth-textured), Natal Group (Cape Supergroup).

DISTRIBUTION

Drimia flagellaris is confined to quartzitic sandstone gorges from Durban (KwaZulu-Natal) to Fraser Gorge in the Eastern Cape.

RELATED SPECIES

Related to both *Drimia loedolffiae* and *D. anomala*. *Drimia loedolffiae* has yellowish green flowers and the bulbs are not angular (also see under *D. loedolffiae*). *Drimia anomala* is a widespread species that occurs on shale or sandstone; the solitary plants are much larger and robust, each with a single terete leaf.

ADAPTATIONS TO THE CLIFF ENVIRONMENT

Habit: Small, globose, often pendent to vertically orientated clusters of green (photosynthetically active) bulbs, each with spreading-ascending to pendent, filiform leaves, suggesting an adaptation to shady cliffs and the thin leaves allowing optimum penetration of light to the bulbs in this environment.

Size and weight: Heads in clusters of medium weight.

Bulb: Bulb epigeous, succulent, proliferating from base, forming tight clusters, an adaptation to the xeric environment.

Leaves

Orientation and presentation: Spreading, becoming pendent from cliff face, numerous, filiform (2 mm), an adaptation to the dry cliff conditions.

Colour: Green, withering from the apices during dry periods, the bulbs enveloped in grey tunics blocking much light.

Age and persistence: Plants long-lived, with the dry leaves persistent, withering from the base.

Armament and camouflage: Clusters conspicuous and without any obvious armament.

Sexual reproduction

Inflorescence and flowers: Inflorescence spreading-ascending, the white corolla attracting the right pollinating flying insect. The inflorescence remains persistent, green and alive for some time after flowering, thus contributing to photosynthesis on the shady southern aspects, suggesting an adaptation to the harsh environment.

Fruit/Seed

Size: Seed 4×1 mm, ideal for establishment in crevices.

Dispersal: Light, black, angular, oblong seeds shaken from the capsules and dispersed by wind.

Time: Seeds ripening in summer, which coincides with the rainy season.

Vegetative reproduction: Plants proliferate, forming dense clusters. The vegetative clusters actively occupy crevices by growth and should any bulb or bulb scale become dislodged and fall onto ledges below, it will root—a prolific vegetative dispersal strategy ensuring long-term survival on the cliffs. Plants of the Fraser Falls collection (*Van Jaarsveld, Bellstedt & Dekker 16371*) are smaller, producing basal stolons and bulbils, very much in the same manner as *Ornithogalum longibracteatum*, but to a lesser degree. It can be seen as a vegetative backup dispersal method often associated with succulent cremophilous bulbs and succulent plants.

CONSERVATION STATUS

Classified as rare (Raimondo *et al.* 2009). A local endemic, not threatened.

ADDITIONAL NOTES

Horticulture: Best for subtropical coastal gardens and ideal for steep embankments. It also thrives in containers. It is best grown by division and does well in cultivation. Its very easy growing nature maximises its survival rate.

VOUCHERS

Van Jaarsveld 16731, 17456 (NBG).

ILLUSTRATIONS AND MAP

Figures 70a–70f, Map 70.

71. *Drimia loedolffiae* Van Jaarsv., in Van Jaarsveld & Van Wyk in *Aloe* 43,2 & 3: 49–51 (2006b).

Cremonophyte growth form: Cluster-forming, epigeous bulbs, with spreading to pendent linear-terete leaves (of medium weight, cliff hugger).

Growth form formula: A:B:Lper:C:Lp (e) (vb)

Etymology: Named after Jeanette Loedolff, botanical artist at the former National Botanical Institute for 20 years (1982–2002).

DESCRIPTION AND HABITAT

Evergreen plants forming tight, round clusters up to 150 mm in diameter and consisting of up to 15 bulbs. Bulbs epigeous, ovoid to globose, 40–45 × 25–50 mm, each bulb with up to 3 or 4 leaves; outer tunics greyish white, papery, exposing purplish green inner tunics. Leaves flaccid, linear, terete, tapering towards apex, 200–260 × 1–4 mm, surface striate, bright green, withering from tip. Inflorescence racemose, 350–400 mm long, initially erect, becoming decumbent; flowers 1–3 mm apart, densely arranged in distal quarter; scape erect, terete, 200–270 mm long, 1.5 mm in diameter; racemes 60–65-flowered, 120–150 mm long; bracts deltoid-cymbiform, 2 × 0.5 mm, purplish white, slightly translucent, basal bracts caudate, spur up to 4 × 1 mm, distal bracts becoming smaller; pedicels 1.5–2.5 mm long, enlarging to 4–5 mm in fruit. Perianth rotate, cream-coloured, up to 12 mm in diameter; tepals linear-elliptic to linear-obovate, inner 5 × 1.5 mm, outer 5.5 × 1.75 mm, with dark brownish median stripe on abaxial surface. Stamens 2.5 mm long; filaments linear, inner slightly shorter; anthers 1 mm long, versatile; pollen yellow. Ovary ovoid, 3-lobed, tapering towards apex, 1.5–2.0 × 1.5 mm, green, shortly stipitate; style erect, 2 mm long; stigma minute, truncate. Capsule ovoid, 5 × 2.5–4 mm. Seed flattened, sickle-shaped, 2.5–3.0 × 1.0–1.8 mm, black.

Phenology: Flowering October–February, flowers opening late in the afternoon.

Pollinators: Insects.

Habitat and aspect: South- and east-facing cliffs. Plants firmly rooted in crevices. Winters are cool but frost is absent. Average daily maximum temperature is about 22°C and the average minimum about 14°C. Rainfall occurs mainly in summer, but some also occurs in the winter months. It ranges from 600–1250 mm per annum.

Altitude: 300–500 m.

Associated vegetation: Mainly subtropical short forest, thicket and grassland vegetation, and on the margin of grassland.

Associated cremnophytes: *Cotyledon orbiculata*, *Crassula cultrata*, *C. orbicularis*, *C. perforata*, *Gasteria excelsa*, *Ornithogalum juncifolium*, *Peperomia blanda*, *Plectranthus spicatus*, *P. strigosus*, *Pyrrhosia africana* and *Senecio aizoides*.

Geology: Mainly Beaufort shales of the Emakwezini Formation (Beaufort Group, Karoo Supergroup). Also on dolerite cliffs (intrusions).

DISTRIBUTION

Drimia loedolffiae has been found only in Buffels Thicket of the Albany Thicket Biome (Mucina *et al.* 2005), on sheer shale or rarely dolerite cliffs of dry river valleys. At the type locality near the Kei River, it grows in clusters on exposed south-facing aspects.

RELATED SPECIES

Both *Drimia loedolffiae* and *D. flagellaris* are cluster-forming, with semi-epigeous, somewhat similar bulbs and pendent, terete leaves. However, that is where the resemblance ends as *D. loedolffiae* is at once distinguished by its floral features and shape of the seeds. In *D. loedolffiae* the bulb is ovoid to globose, never angular as in *D. flagellaris*. *Drimia loedolffiae* has densely arranged, cream-coloured flowers (distal quarter of inflorescence) on short pedicels (1.5–2.5 mm) and ovoid capsules 5 × 2.5 mm, with sickle-shaped seeds 2–3 × 1.0–1.8 mm. The inflorescence is not persistent and soon withers after the capsules have dried. *Drimia flagellaris* has laxly arranged, white flowers (distal half of inflorescence) on longer pedicels (17–25 mm). Its slender seeds are 3–5 mm long, a distinctive character. The somewhat persistent inflorescence remains alive and green after the capsules have been shed.

ADAPTATIONS TO THE CLIFF ENVIRONMENT

Habit: Small, globose, often pendent to vertically orientated clusters of green (photosynthetically active) bulbs, each with spreading-ascending to pendent filiform leaves, suggesting an adaptation to shady cliffs and the thin leaves allowing optimum light exposure of the bulbs in this environment.

Size and weight: Heads small, of light weight.

Bulb: Bulbs epigeous, succulent, forming tight clusters and an adaptation to the dry cliff environment.

Leaves

Orientation and presentation: Spreading, becoming pendent from cliff face, numerous, filiform (2 mm), an adaptation to the dry cliff conditions.

Colour: Green, withering from the apices during dry periods, bulbs enveloped in grey tunics blocking much light.

Age and persistence: Plants long-lived, dry leaves persisting and withering from the base.

Armament and camouflage: Conspicuous clusters lacking in armament and camouflage characters. They are less firm than those of the typical chasmophytic relatives, suggesting a reduction in armament in response to the less disturbed environment.

Sexual reproduction

Inflorescence and flowers: The solitary inflorescence is spreading-ascending, the cream-coloured corolla attracting the right pollinating flying insect. Flowers open in succession from below (acropetally), with only a few flowers on an inflorescence open at the same time, thus promoting cross pollination.

Fruit/Seed

Size: Seed 2.5–3.0 mm long, ideal for establishment in crevices.

Dispersal: Light, black, angular, sickle-shaped seeds shaken from the capsules and dispersed by wind.

Time: Seeds ripening in summer, which coincides with the rainy season.

Vegetative reproduction: Plants proliferate, forming clusters. The vegetative clusters actively occupy crevices by growth and should any bulb become dislodged and fall onto ledges below, it will root—a prolific vegetative dispersal strategy ensuring long-term survival on the cliffs.

CONSERVATION STATUS

A local endemic, not threatened.

ADDITIONAL NOTES

Horticulture: Plants of both *Drimia loedolffiae* and *D. flagellaris* have been grown at Kirstenbosch for a number of years and both are easily propagated by division and thrive in cultivation. They are slow-growing and divide to form dense, small clusters. It is best for thicket gardens and ideal for steep embankments. *Drimia loedolffiae* flowers from the end of October to January (February) while *D. flagellaris* flowers from the end of July to October.

VOUCHER

Van Jaarsveld & Voigt 17914 (NBG).

ILLUSTRATIONS AND MAP

Plate 71, Figures 71a–71e, Map 71.

72. *Drimia mzimvubuensis* Van Jaarsv. in *Aloe* 42,4: 53–55 (2005d).

Cremonophyte growth form: Cluster-forming (hugging) epigeous bulbs, with drooping leaves (of medium weight, cliff hanger).

Growth form formula: A:B:Lper:C:Lp (e) (vb)

Etymology: After the Mzimvubu River in the Eastern Cape Province.

DESCRIPTION AND HABITAT

Evergreen, bulbous geophytes. Roots white, fleshy, 2 mm in diameter. Bulbs epigeous, ovoid, up to 50 mm high, forming loose clusters of up to 6 heads and about 100 mm in diameter; tunics (scales) loose, club-shaped, 18–30 × 15–23 mm, thick and succulent, maroon-brown, stalked, apex obtuse; stalk flattened, up to 4 mm in diameter, maroon-brown. Leaves linear, subterete, amplexicaul at base, 47–50 × 5–3 mm, leathery, dark green; adaxial surface shallowly channelled, abaxial surface 12–14-grooved, minutely ciliate on angles (short translucent hairs). Inflorescence spreading, ascending, racemose, 340–380 mm long; scape 3 mm in diameter, dark green, terete, glabrous; racemes 60–120 mm long, bearing 20–30 pendent flowers; pedicels 15–18 mm long, curving down; bracts 8 mm long, white, linear-lanceolate, ascending, not clasping; spur 10 mm long, linear-lanceolate, adpressed to peduncle. Perianth white, 22–24 mm in diameter, opening at noon; tepals white with green centric stripes, 9 × 3 mm, lanceolate to strap-shaped, green at base; apices obtuse. Anthers 3 mm long, erectly projected, sagittate; filaments fused into a central cylindrical staminal column 2.5 mm high and 2 mm wide; apices free, triangular, 1 × 1 mm, together tapering into a cone-like structure consisting of acute adpressed introrse anthers and exposing centric white stigma for 0.5 mm. Ovary green, ovate-tapering, 6-grooved, 3 × 1.5 mm; style 4.5 mm long, white; stigma capitate. Capsule 3-locular, 10 × 7.5 mm, loculicidal. Seed 7 × 3 mm, oblong, flat, surface angular, black.

Phenology: Flowering mainly in early summer (end of November–December). Flowers open in succession acropetally from below, encouraging cross pollination. Seeds dispersed by wind from summer onwards.

Pollinators: Insects.

Habitat and aspect: Shale cliffs, mainly shady south-facing aspects. Plants firmly rooted in crevices, size often depending on the growing space allowed by the crevice. Temperature in summer may go up to 40°C. Winters are cooler but frost is absent. The average daily maximum temperature is about 23°C and the average daily minimum about 15°C. Rainfall occurs mainly in summer, ranging from 600–1250 mm per annum (thunder showers or occasional cyclonic winter rain), occasionally in winter.

Altitude: 300–500 m.

Associated vegetation: Eastern Valley Bushveld of the Sub-Escarpment Savanna Bioregion, Savanna Biome (Mucina *et al.* 2005).

Associated cremnophytes: Near Lutengele (Mzimvubu River) it is associated with *Adromischus cristatus*, *Bulbine natalensis*, *Crassula multicava*, *C. perforata*, *C. spathulata*, *Ornithogalum longibracteatum* and *Peperomia blanda*.

Geology: Ecce shale (Karoo Supergroup). Substrate with ledges, crevices and fissures ideal for establishment of plants.

DISTRIBUTION

Known only from the lower Mzimvubu River (Transkei, Eastern Cape). Mainly shale cliffs along river.

RELATED SPECIES

Drimia mzimvubuensis is related to *D. cremnophila* of the same river system in the Eastern Cape from East London westwards, which has similar loose bulbous scales but the leaves of *D. cremnophila* are dorsiventrally compressed, not terete.

ADAPTATIONS TO THE CLIFF ENVIRONMENT

Habit: Plants forming loose, globose clusters, thus exploiting the vertical cliff-face habitat and the absence of disturbance by larger herbivores. It is a fairly slow-growing, long-lived perennial.

Size and weight: Heads of medium weight.

Bulb: Bulb epigeous with loose, fleshy, club-shaped scales slightly compressed and tolerant of warm, dry, vertical conditions. Bulb scales are purplish green and photosynthetically active, optimising absorption of light. The succulent nature suggests an adaptation to the xeric habitat.

Leaves

Orientation: Mainly spreading to drooping but varying according the crevice location. Extended terete nature minimising transpiration.

Succulence: Fleshy, grooved, an adaptation to the xeric cliff-face habitat.

Colour: Dark green, without markings.

Age and persistence: Evergreen condition reflecting the climatic pattern of almost year-round rainfall. Evergreen and persistent leaves maximising absorption of light.

Armament and camouflage: Lack of a camouflage defence strategy and the conspicuous clustered growth suggest adaptation to the safe cliff habitat in the absence of disturbances.

Sexual reproduction

Inflorescence and flowers: Inflorescence spreading-ascending, racemose, the conspicuous, drooping, white flowers maximising visibility from below, an adaptation to the cliff-face dwelling.

Fruit/Seed

Size: Capsule 3-locular, 10×7.5 mm, loculicidal. Seed 7×3 mm, oblong.

Dispersal: Capsules ripening in summer and the flat, black, angular, winged seeds dispersed by wind.

Time: Seeds ripening in summer and autumn, coinciding with the rainy season.

Vegetative reproduction: Plants proliferate, forming small clusters. The vegetative clusters actively occupy crevices by growth and should any bulb or bulb scale become dislodged and fall onto ledges below, it will root—a prolific vegetative dispersal strategy ensuring long-term survival on the cliffs.

CONSERVATION STATUS

A local endemic, not threatened.

ADDITIONAL NOTES

Horticulture: *Drimia mzimvubuensis* is easily grown and thrives in cultivation, but requires well-drained soil and is best for containers. Feed in spring and keep dry for its winter resting season. It is best grown in partial shade. Plants easily grown by division, from bulb scales or from seed. Its very easy growing nature maximises its survival rate on the cliff face.

VOUCHER

Van Jaarsveld, Xaba, Harrower & Styles 58 (NBG).

ILLUSTRATIONS AND MAP

Plate 72, Figures 72a–72c, Map 72.

73. *Drimia uniflora* J.C.Manning & Goldblatt in *Strelitzia* 9: 712 (2000) (= *Litanthus pusillus*)

Cremnophyte growth form: Cluster-forming, miniature bulbs (of light weight, cliff hugger, in fact, the smallest of all cremnophytes and the smallest bulb in the world!).

Growth form formula: A:Lper:C:La (vb)

Etymology: The epithet *uniflora* pertains to the solitary flower. The older Greek generic name *Litanthus* is derived from *litos*, plain or simple, and *anthos*, flower (Jackson 1971); *pusillus*, very small, refers to its small stature.

DESCRIPTION AND HABITAT

Plants bulbous (epigeous to hypogeous), forming inconspicuous dwarf-sized clusters up to 25 mm in diameter. Bulbs up to 13 mm in diameter, globose-conical; outer tunics imbricate, grey. Roots fibrous. Leaves 1–3, hysteranthous, filiform, up to 70 mm long, ascending to spreading, pendulous. Inflorescence reduced to a 1 (rarely 2)-flowered raceme, up to 17–55 mm long; bracts 2, up to 1 mm long, spurred. Perianth pendulous, white to pink, tubular, up to 4 × 2 mm; lobes fused for two thirds. Stamens fused to perianth tube; anthers dorsifixed. Ovary sessile, ellipsoid. Capsule loculicidal, 3 × 2.5 mm, slightly transparent. Seeds angular, up to 1 × 0.4 mm, flattened, black.

Phenology: Flowering summer and midsummer. Perianth opening day and night, attracting insect pollinators.

Pollinators: Insects.

Habitat and aspect: Cliffs, in rock crevices at altitudes of about 500–3000 m in exposed to sheltered kloofs (all aspects). Plants are rooted among moss and other succulent plants in crevices. Temperature warm to cool. Winters are cool, with frost at higher altitudes. Rainfall occurs at any time of the year in the south, but mainly in summer in the northeast, ranging from 100–1250 mm per annum.

Altitude: 650–3000 m.

Associated vegetation: Mainly Fynbos, Albany Thicket, Nama-Karoo and Succulent Karoo Biomes and afroalpine vegetation (Mucina *et al.* 2005).

Associated cremnophytes: *Cotyledon orbiculata* var. *orbiculata*, *Crassula nemorosa*, *C. nudicaulis*, *C. pellucida* subsp. *marginalis* and *Ornithogalum juncifolium*.

Geology: Shale (Phanerozoic Emakwezini Formation) or quartzitic sandstone (light-coloured and smooth-textured), Peninsula Formation (Cape Supergroup).

DISTRIBUTION

Drimia uniflora is widespread throughout South Africa, occurring on vertical cliffs and rock crevices.

RELATED SPECIES

Without any close relatives. The smallest bulbous plant in South Africa. Easily overlooked.

ADAPTATIONS TO THE CLIFF ENVIRONMENT

Habit: Dwarf-sized cluster form with ascending to drooping, filiform leaves.

Size and weight: Plants miniature, small and of light weight.

Bulb: Bulbs succulent, proliferating and forming clusters, an adaptation to the dry cliff habitat.

Leaves

Orientation: Ascending or subpendulous, orientation maximising absorption of light.

Colour and texture: Dark green, with a soft texture. The slight translucent nature allows light to penetrate deeply, an adaptation helping plants to cope with the shady to sunny cliff environment.

Age and persistence: Plants evergreen, leaves continuously replaced.

Armament: The filiform leaves without any armament, perhaps a response to the undisturbed cliff habitat.

Sexual reproduction

Inflorescence, flowers and fruit: Raceme ascending and the small, white, pendulous perianth attracting insects. Fruit becoming erect.

Fruit/Seed

Size: Seed 1×0.4 mm, an ideal size for establishment in crevices.

Dispersal: Seed blown or shaken from the erect capsules and dispersed by wind.

Time: Seeds ripening in summer and autumn.

Vegetative reproduction: *Drimia uniflora* proliferates from the base, forming small, dense clusters. When bulbs become detached, they will re-root and continue growth. This vegetative regeneration can be seen as a backup ensuring survival in the harsh cliff-face environment.

CONSERVATION STATUS

A local endemic, not threatened.

ADDITIONAL NOTES

General: Plants very small and easily overlooked.

Horticulture: Best grown in small containers. Not popular owing to its minute size. Plants easily grown from seed or division, doing well in cultivation. Its very easy growing nature maximises survival rate. Plants are often unwittingly or accidentally introduced with other bulb or succulent clusters and are often found among clusters of *Conophytum* or other succulents.

VOUCHER

Van Jaarsveld & Nordenstam 20041 (NBG).

ILLUSTRATIONS AND MAP

Plate 73, Figures 73a–73d, Map 73.

LEDEBOURIA Roth

74. *Ledebouria concolor* (Baker) Jessop in Journal of South African Botany 36: 254 (1970). (Suurberg cliff form.)

Cremnophyte growth form: Cluster-forming, epigeous bulbs, rosulate leaves (of medium weight, cliff hugger).

Growth form formula: B:Lper:C:La (e) (vb) (rd)

Etymology: The epithet *concolor*, uniform in colour, refers to the uniform leaf colour in contrast to most other *Ledebouria* species which have characteristic leaf markings.

DESCRIPTION AND HABITAT

Epigeous, cluster-forming, bulbous plants. Roots succulent, 2 mm in diameter. Bulb conical to 40–60 × 55 mm, purplish green, proliferating from base, forming rounded clusters on cliffs; tunics tight, withering grey. Leaves 5–10 per plant, ovate-lanceolate to ovate, 80–110 × 45–60 mm, green, fleshy, not spotted, obscurely striate, younger leaves ascending, older drooping. Inflorescence up to 200 mm long, ascending; raceme 140 mm long; peduncle 3–4 mm long; bracts small, ovate. Perianth, cup-shaped, greenish white, 5 mm in diameter, 3 mm deep, becoming purplish, drooping; pedicels white, up to 7 mm long, becoming purple; tepals greenish, with broad white margins, outer surface purplish at base, 6 × 2.5 mm. Ovary globose, 6-lobed. Stamens 6 mm long; filaments white, collected into a cone; anthers 0.5 long, oblong, versatile. Stigma 3 mm long, lengthening to 5 mm at maturity, subulate, white. Fruit and seed not seen.

Phenology: Flowering mainly from end of October–November.

Pollinators: Insects.

Habitat and aspect: Mainly south-facing cliffs in protected river gorges. Plants firmly rooted in crevices, size often depending on the growing space allowed by the crevice. Summers are hot and temperatures of up to 35°C are not uncommon. Winters are cooler but frost is absent. The average daily maximum temperature is about 22°C and average daily minimum about 12°C. Rainfall can occur throughout the year, but with a peak in spring and summer, ranging from 300–500 mm per annum (thunder showers or cyclonic winter rain).

Altitude: 300–800 m.

Associated vegetation: Sundays Thicket of the Albany Thicket Biome (Mucina *et al.* 2005).

Associated cremnophytes: *Bulbine latifolia*, *Crassula intermedia*, *C. perfoliata* var. *minor*, *Haworthia angustifolia* var. *baylissii*, *Lampranthus affinis*, *Ornithogalum juncifolium* and *O. longibracteatum*.

Geology: Quartzitic sandstone (light-coloured and smooth-textured), Witteberg Group, Witpoort Formation (Cape Supergroup).

DISTRIBUTION

Ledebouria concolor is confined to the Eastern Cape, and this form is endemic to the narrow kloofs of the Witrivier in the Suurberg. Larger forms of the same species occur on the flats near Uitenhage and Port Elizabeth.

RELATED SPECIES

Ledebouria concolor is one of the larger *Ledebouria* species and is without leaf markings. It is related to *L. socialis*, another species with epigeous bulbs but with silvery green, mottled leaves occurring in shade of thickets.

ADAPTATIONS TO THE CLIFF ENVIRONMENT

Habit: Plants forming globose clusters, exploiting the vertical cliff-face habitat. A fairly rapid-growing, fairly long-lived perennial.

Size and weight: Heads of medium weight.

Bulb: Bulb globose, fleshy and tolerant of warm, dry, vertical conditions.

Leaves

Orientation: Spreading, in an apical rosette, maximising absorption of light

Succulence: Fleshy, tolerant of the dry habitat.

Colour: Light to dark green. Unlike leaves of most *Ledebouria* species in which the mottling provides the ideal camouflage, leaves of this species are without leaf spots, suggesting an adaptation to the absence of herbivory.

Age and persistence: Evergreen condition reflecting the rainfall patterns.

Armament and camouflage: Lack of a camouflage defence strategy suggests adaptation to the safe cliff habitat.

Sexual reproduction

Inflorescence and flowers: Ascending racemes of whitish green flowers.

Fruit/Seed

Size: Fruit and seed not seen.

Dispersal: Seeds locally dispersed.

Time: Seeds ripening in summer and autumn, coinciding with the rainy season.

Vegetative reproduction: Plants proliferate, forming clusters. The vegetative clusters actively occupy crevices by growth and should any bulb become dislodged and fall onto ledges below, it will root—a prolific vegetative dispersal strategy ensuring long-term survival on the cliffs.

CONSERVATION STATUS

A local endemic, not threatened.

ADDITIONAL NOTES

Horticulture: *Ledebouria concolor* is easily propagated by division. Plants are best grown on steep embankments, gabions, rockeries or terraforce and can be grown in full sun or dappled shade. They require a well-drained soil. They also thrive in containers. Its very easy growing nature maximises survival rate.

VOUCHER

Van Jaarsveld 19229 (NBG).

ILLUSTRATIONS AND MAP

Figures 74a–74c, Map 74.

75. *Ledebouria cremnophila* S.Venter & Van Jaarsv., in Venter *et al.* in *Aloe* 43,4: 78–79 (2007).

Cremnophyte growth form: Cluster-forming, epigeous bulbs, rosulate leaves (of medium weight, cliff hugger).

Growth form formula: B:Lper:C:La (e) (vb) (rd)

Etymology: Greek *kremnos*, cliff, and Greek *phileein*, to love, pertaining to its cliff habitat.

DESCRIPTION AND HABITAT

Plants solitary. Bulb epigeous to semi-epigeous, 90–120 × 30–40 mm, cylindrical; dry bulb scales dark brown and hard, live bulb scales tightly arranged with visible threads when torn. Leaves 6–8, fully emerged at anthesis, spreading, lanceolate, 80–130 × 20–40 mm, with threads when torn, fleshy; surfaces dull green with purple blotches, venation sunken on adaxial surface; margin smooth but wavy; leaf base shallowly canaliculate; apex acute. Inflorescence 1, rarely 2, flaccid, lax, 50–120-flowered, longer than leaves, with a pronounced coma when young; peduncle terete at base, green fused purple, glabrous, 50–110 mm long; rachis shallowly ridged, 80–140 mm long; raceme lax, oblong, 130–250 × 20–30 mm; bracts and bracteoles always present, membranous, 5–8 × 0.25–0.50 mm, linear, white; pedicels

spreading, 8–12 mm long, pink turning olive-green. Tepals initially spreading then strongly recurved, equal, linear-oblong, 5–6 × 1.5 mm, olive-green on abaxial surface, green fused purple on adaxial surface; apex acute. Stamens erect, 3–4 mm long; filaments pink with white base, epitepalous; anthers 0.75 mm long, orange-yellow. Ovary depressed, ovate, 6-lobed, 1 × 2 mm; lobes obtusely deltate, apical shoulders not raised, basal lobes absent; style 2.5–3.0 mm long, terete, pink with white apex and base; stipe 0.25 × 0.25 mm. Capsule clavate, base tapering. Seed not seen

Phenology: Flowering November–January.

Pollinators: Insects.

Habitat and aspect: Wooded shady south-facing cliffs. Plants are firmly rooted in crevices, size often depending on the growing space allowed by the crevice. Summers are hot, with temperatures up to 35°C. Winters are cooler but frost is absent. Temperatures are high in summer, the average daily temperature in summer is about 27°C and average daily minimum about 13°C. Rainfall mainly in summer, 500–700 mm per annum (mainly thunder showers).

Altitude: 400–600 m.

Associated vegetation: Barberton Serpentine Sourveld of the Lowveld Bioregion, Savanna Biome (Mucina *et al.* 2005).

Associated cremnophytes: *Aloe arborescens*, *Cotyledon barbeyi*, *Crassula perfoliata*, *Cyanotis speciosus*, *Delosperma lebomboensis*, *Haemanthus paucifolius*, *Plectranthus verticillatus* and *Portulacaria afra*.

Geology: Quartzitic sandstone, Moodies Group (Barberton Supergroup).

DISTRIBUTION

Ledebouria cremnophila appears to be confined to the mountains along the Honeybird Creek (Noordkaap east of Barberton) in Mpumalanga. It occurs on high quartzite cliffs in humus-filled rock cracks, but sometimes in humus-rich lithosols.

RELATED SPECIES

Ledebouria cremnophila is related to the widespread *L. revoluta*, but it is at once distinguished by three prominent features. Firstly, the bulbs are cylindrical, with hard, dark brown bulb scales. Secondly, the bulbs are semi-epigeous to epigeous. The third feature is the filiform floral bracts that form a distinct coma, which is very prominent in the young inflorescence.

ADAPTATIONS TO THE CLIFF ENVIRONMENT

Habit: Plants forming epigeous clusters, exploiting the vertical cliff-face habitat. A fairly rapid-growing, fairly long-lived perennial.

Size and weight: Heads of medium weight.

Bulb: Bulb cylindrical, oblong, fleshy, photosynthetically active and tolerant of warm, dry, vertical conditions.

Leaves

Orientation: Spreading, in apical rosette, maximising absorption of light.

Succulence: Fleshy, tolerant of the dry habitat.

Colour: Dull green, with purple blotches.

Age and persistence: Evergreen condition reflecting the warm climate.

Camouflage: *Ledebouria cremnophila* is well camouflaged, perhaps indicating that it is a recent cliff neo-endemic.

Sexual reproduction

Inflorescence and flowers: Spreading to pendent racemes.

Fruit/Seed

Size: Fruit and seed not seen.

Dispersal: Seeds are released and then presumably locally dispersed when the capsules split open.

Time: Seeds ripening in summer and autumn, coinciding with the rainy season.

Vegetative reproduction: Plants proliferate, forming clusters. The vegetative clusters actively occupy crevices by growth and should any bulb become dislodged and fall onto ledges below, it will root—a prolific vegetative dispersal strategy ensuring long-term survival on the cliffs.

CONSERVATION STATUS

Classified as rare (Raimondo *et al.* 2009). A local endemic, not threatened.

ADDITIONAL NOTES

General: *Ledebouria cremnophila* is one of four species commonly associated with cliff faces. The others are *L. concolor*, *L. ensifolia* and *L. venterii*. All of them have bulbs that are epigeously produced. *Ledebouria concolor* and *L. venterii* have spreading, fleshy leaves without spots and are cluster-forming, while *L. ensifolia* and *L. cremnophila* have spotted leaves. *Ledebouria ensifolia* is also cluster-forming, the smallest of the group. The epigeous nature makes them vulnerable to fire, a character perhaps adopted as a result of to the safer, fire-free cliff-face environment. The fleshy leaves are an efficient adaptation to the dry conditions on the cliff face.

Horticulture: *Ledebouria cremnophila* is best grown in bushveld gardens, on steep embankments in dappled shade. It also does well in containers. Keep dry in winter and feed in spring. Plants are easily propagated by division or from seed and thrive in cultivation. Its very easy growing nature maximises its survival rate.

VOUCHER

Van Jaarsveld 19372 (NBG).

ILLUSTRATIONS AND MAP

Plate 75, Figures 75a–75c, Map 75.

76. *Ledebouria venteri* Van Jaarsv. & A.E.van Wyk in *Aloe* 43,4: 75–77 (2007b).

Cremnophyte growth form: Cluster-forming, epigeous bulbs, rosulate leaves (of medium weight, cliff hugger).

Growth form formula: B:Lper:C:La (e) (vb) (rd)

Etymology: After Stefanus Venter (1953–) botanist formerly at the University of the North who revised the genus *Ledebouria*.

DESCRIPTION AND HABITAT

Bulbs globose, up to 50 × 45 mm, at first solitary, becoming small, epigeous or semi-epigeous clusters of up to 14 individuals, 220 mm in diameter, covered in dense, dry tunic remains; tunics thin, papery, brownish, translucent, with indistinct, transverse abscission layer. Roots fleshy, up to 1.5 mm long. Leaves succulent, 6–12, spreading, linear-lanceolate to ovate-lanceolate, 55–100 × 15–35 mm, green, glabrous, obscurely striate, with thread-like strings when severed; abaxial surface suffused with purple streaks in centre and towards base; apex acute, becoming slightly channelled; base amplexicaul; margin white, minutely denticulate. Inflorescence 70–100 mm long; scape terete, 50 mm long, 3 mm in diameter at base; raceme 40–50 mm long, with up to 14 flowers open at the same time; rachis angular; bracts small, subulate, curving upwards, up to 1 × 0.3 mm, base ending in a decurrent ridge and resulting in angular floral axis. Flowers spreading, nodding; stalks 14–15 mm long, maroon-mottled; tepals triangular-ovate, 5 × 1.5 mm, purplish green, soon becoming reflexed, apices acute. Stamens 3.0–3.5 mm long, purplish, base green; anthers 0.75 mm long; pollen yellowish. Ovary 1 × 2.5 mm, 6-lobed, grooved, green, stipitate for 0.5 mm. Capsule obovoid, 6 mm long. Seed obovoid-oblong, 5 × 2.5 mm.

Phenology: Flowering November–December.

Pollinators: Insects.

Habitat and aspect: Cliffs, at altitudes of about 300 m. Plants firmly rooted in crevices, size often depending on the growing space allowed by the crevice. Summers are hot, with temperatures up to 35°C. Winters are cooler but frost is absent. The average maximum

temperature is about 24°C and average minimum about 12°C. Rainfall throughout the year, ranging from 300–400 mm per annum (thunder showers or cyclonic winter rain).

Altitude: 600–800 m.

Associated vegetation: North Langeberg Sandstone Fynbos and Southern Cape Valley Thicket of the Albany Thicket Biome (Mucina *et al.* 2005).

Associated cremnophytes: Associated species include *Albuca tortuosa*, *Bulbine aloides*, *Crassula orbicularis*, *C. perforata*, *C. rupestris*, *Haworthia chloracantha* var. *chloracantha*, *Litanthus pusillus*, *Ornithogalum longibracteatum*, *Othonna carnosa* and *Scopelogena verruculata*.

Geology: Quartzitic sandstone, Table Mountain Group (Cape Supergroup).

DISTRIBUTION

Ledebouria venterii is at present known only from between the Gourits River Poort and near the Gourits Bridge (N2 between Albertinia and Mossel Bay) where it grows on ledges of east-facing cliffs and steep embankments. The Langeberg habitat consists of dry fynbos and at the confluence with the Vals River it grows in thicket vegetation with a high proportion of succulent plants.

RELATED SPECIES

Ledebouria venterii is related to *L. concolor*. Both are evergreen species, with epigeous bulbs and fleshy leaves without spots, usually confined to cliff faces and steep slopes. *Ledebouria venterii* is at once distinguished by its succulent, unspotted, linear-lanceolate leaves with a white, minutely denticulate margin and tepals that are free and fully reflexed. The flowers are much smaller than those of *L. concolor* and the flower stalks, stamens and stigma are distinctly maroon-red. *Ledebouria concolor*, in contrast, is a much larger species, the leaves are ovate-lanceolate, with a distinctly undulating margin, and the tepals are much larger, fused at the base.

ADAPTATIONS TO THE CLIFF ENVIRONMENT

Habit: Plants forming globose clusters, exploiting the vertical cliff-face habitat. A slow-growing fairly long-lived perennial.

Size and weight: Heads of medium and average weight.

Bulb: Bulb globose, fleshy and tolerant of warm, dry, vertical conditions.

Leaves

Orientation: Spreading, in apical rosette, maximising absorption of light.

Succulence: Fleshy, tolerant of the dry habitat.

Colour: Light to dark green. Unlike leaves of most *Ledebouria* species in which the mottling provides the ideal camouflage, leaves of this species are without leaf spots, suggesting an adaptation to the absence of herbivory.

Age and persistence: Evergreen condition reflecting the rainfall patterns.

Armament and camouflage: Lack of a camouflage defence strategy suggests an adaptation to the safe cliff habitat.

Sexual reproduction

Inflorescence and flowers: Ascending racemes of whitish green flowers.

Fruit/Seed

Size: Capsule obovoid, 6 mm long. Seed obovoid-oblong, 5 × 2.5 mm.

Dispersal: Seeds released and locally dispersed when the capsules split open.

Time: Seeds ripening in summer and autumn, coinciding with the rainy season.

Vegetative reproduction: Plants proliferate, forming clusters. The vegetative clusters actively occupy crevices by growth and should any bulb or bulb scale become dislodged and fall onto ledges below, it will root—a prolific vegetative dispersal strategy ensuring long-term survival on the cliffs.

CONSERVATION STATUS

A local endemic, not threatened.

ADDITIONAL NOTES

Horticulture: Plants of *Ledebouria venterii* are best suited to fynbos and thicket gardens and are ideal for dry rockeries or containers. They are best grown in well-drained soil with ample compost added. The plants can be propagated by division and can be grown in full sun or light shade.

VOUCHERS

Harrower 2115, Van Jaarsveld 17633, 19247 (NBG).

ILLUSTRATIONS AND MAP

Plate 76, Figure 76a, Map 76.

ORNITHOGALUM L.

77. *Ornithogalum juncifolium* Jacq. var. *emsii* Van Jaarsv. & A.E.van Wyk in *Bothalia* 35,1: 82–84 (2005e).

Cremonophyte growth form: Cluster-forming, epigeous bulbs, with spreading linear leaves (of light weight, cliff hugger).

Growth form formula: A:B:Lper:C:La (e) (vb)

Etymology: After Paul Ems, botanist, who first noticed the population on the cliff face.

DESCRIPTION AND HABITAT

Plants bulbous, epigeous, forming round clusters up to 100 mm in diameter and consisting of many bulbs and bulbils. Bulbs globose, 15–20 mm in diameter and high; tunics grey, papery, exposing green live tissue, basal part of bulb continuously proliferating, forming many ovate to rounded bulbils up to 5 mm in diameter. Leaves 2 or 3, synanthous, linear, half-terete, 95–150 × 1.5 mm; apex acute, dark green; adaxial surface shallowly canaliculate, abaxial surface rounded; base sheathing, tubular, with short membranous neck 5–8 mm long, 2–3 mm in diameter; margin minutely ciliolate. Raceme 100–200 mm long, 8–12-flowered; scape terete, erect; bracts deltoid-cuspidate, auriculate, up to 6 × 2 mm; pedicel up to 4–5 mm long, lengthening to up to 6–7 mm in fruit. Perianth stellate, white, up to 20–24 mm in diameter; tepals linear-lanceolate, 3 inner 10.0–12.0 × 3.0–3.5 mm, white, with green median stripe. Stamens 5 mm long; outer filaments flattened, linear-acuminate, 1 mm in diameter at base, inner filaments shorter, ovate-triangular, up to 1.5 mm long; anthers 0.8 mm long, yellow. Ovary ovate, 3 × 2 mm, green, shortly stipitate; style erect, 4 mm long; stigma capitate. Capsule ovoid, 5–7 × 3–4 mm. Seeds 24 per capsule, triangular-ovate, 1.5 × 0.8 mm, black, denticulate.

Phenology: Flowering mainly in summer (from early December–January). Seeds dispersed by wind in summer and early autumn (October onwards).

Pollinators: Insects.

Habitat and aspect: Mainly south-facing shale cliffs. Plants firmly rooted in crevices. Temperature high in summer (35–40°C). Winters are cooler but frost is absent. Rainfall throughout the year but with a peak in spring and summer, ranging from 300–400 mm per annum (thunder showers or cyclonic winter rain).

Altitude: 500–600 m.

Associated vegetation: Mainly Great Fish Noorsveld of the Albany Thicket Biome (Mucina *et al.* 2005).

Associated cremonophytes: The plants at the type locality share their habitat with others such as *Bulbine latifolia*, *Crassula cultrata*, *C. perfoliata* var. *minor*, *C. socialis*, *Haworthia angustifolia* var. *baylissii* and *Ledebouria concolor*.

Geology: Dark-coloured and smooth-textured Ecce shale (Fort Brown Formation) of the Karoo Supergroup. Substrate with sufficient ledges, crevices and fissures for establishment of plants.

DISTRIBUTION

Ornithogalum juncifolium var. *emsii* is a shale endemic, confined to the Kei River (north of Grahamstown) Eastern Cape.

RELATED SPECIES

Related to *Ornithogalum juncifolium* var. *juncifolium*, which is also encountered on cliffs but does not have the prolific nature of producing small bulblets.

ADAPTATIONS TO THE CLIFF ENVIRONMENT

Habit: Small, globose clusters of green (photosynthetically active) and (2 or 3 active) spreading, pendulous, linear leaves, an adaptation to shady cliffs and the thin leaves allowing optimum absorption of light by the bulbs in this environment.

Size and weight: Bulbs small, of light weight, cliff hugger.

Bulb: Bulb tunics becoming dry and grey, protecting the bulb from excessive light.

Leaves

Orientation and presentation: Grouped and bundled together at base, very thin, allowing maximum light reaching the bulbs. The leaves are spreading, becoming subpendent.

Colour: Dark green.

Age and persistence: Plants long-lived, with dry leaves persistent, withering from the base.

Armament: Without obvious defence characters.

Sexual reproduction

Inflorescence and flowers: Inflorescence spreading, the apices drooping and the white corolla attracting the right pollinating flying insect.

Fruit/Seed

Size: Seed 1.5×0.8 mm, 24 per capsule.

Dispersal: Seeds light, triangular-ovate, denticulate, ideal for dispersal by wind and easily becoming stuck in crevices after release from the capsules.

Time: Seeds ripening in summer and autumn, coinciding with the rainy season.

Vegetative reproduction: Plants continuously forming bulbils at the base of the mother bulb and these spilling over, filling crevices and thus maximising survival. It is a prolific vegetative dispersal strategy that ensures continued existence on the cliffs.

CONSERVATION STATUS

A local endemic, not threatened.

ADDITIONAL NOTES

Horticulture: Plants best grown in small containers and miniature succulent gardens. It is easily propagated by division, thriving in cultivation. Outside the thicket habitat it is best grown under controlled conditions in a greenhouse. Its very easy growing nature maximises its survival rate.

VOUCHER

Van Jaarsveld 16808 (NBG).

ILLUSTRATIONS AND MAP

Figures 77a & 77b, Map 77.

78. *Ornithogalum longibracteatum* Jacq., Hortus botanicus vindobonensis 3: t. 29 (1776). (Bashee form.)

Cremonophyte growth form: Cluster-forming, epigeous bulbs, with recurved spreading subpendent leaves (of medium weight, cliff hugger).

Growth form formula: A:B:Lper:C:La (e) (vb)

Etymology: Latin *longi*, long, and *bracteatum*, bract, referring to the long bracts on the inflorescence.

DESCRIPTION AND HABITAT

Plants glabrous, bulbous, epigeous and cluster-forming. Bulbs globose, up to 80 mm in diameter, bulbiferous; tunics succulent, green, withering grey, exposing green live tissue; vegetative bulbils 6–8 × 6–7 mm, grey-green. Roots white, terete, succulent. Leaves synanthous, 200–1000 × 20–50 mm, rosulate, flaccid, ascending to curving, linear, succulent, channelled, withering from apex. Raceme up to 1 m high, densely flowered; scape terete, erect; bracts filiform, broadening at base to 40 mm long; pedicels up to 5 mm long, lengthening to 15 mm in fruit. Perianth stellate; tepals linear-elliptic, 9 × 2.5 mm, green with white margins. Ovary spherical. Capsule trigonous, 10 × 6 mm. Seeds oblong, angular, 4 × 1.5 mm, black.

Phenology: Flowering mainly from spring to early summer but in some populations to autumn, and occasionally throughout the year. Seeds are dispersed by wind in summer and early autumn.

Pollinators: Insects.

Habitat and aspect: Cliffs and steep slopes, often south-facing but also in other habitats. Plants firmly rooted in crevices. Temperature moderate to high in summer. Winters are cooler but frost is absent. Average daily maximum temperature about 24°C and average daily minimum about 11°C. Rainfall throughout the year but with a peak in spring and summer, ranging from 300–1000 mm per annum (thunder showers or cyclonic winter rain). In the north the rainfall occurs mainly in summer, with dry winters.

Altitude: 300–500 m.

Associated vegetation: Mainly thicket and subtropical coast vegetation.

Associated cremnophytes: On the Suurberg, the following plants grow with *Ornithogalum longibracteatum*: *Bulbine latifolia*, *Crassula intermedia*, *C. perfoliata* var. *minor*, *Haworthia angustifolia* var. *baylissii*, *H. glauca*, *Lampranthus affinis* and *Ledebouria concolor*.

Geology: Occurs on various rock formations such as shale, mudstone, sandstone and quartzitic sandstone belonging to the Karoo and Cape Supergroup.

DISTRIBUTION

Ornithogalum longibracteatum is widely distributed from Mossel Bay in the Western Cape to southeastern Africa. The Bashee form is confined to the lower Bashee River.

RELATED SPECIES

Not closely related to other species of *Ornithogalum*.

ADAPTATIONS TO THE CLIFF ENVIRONMENT

Habit: Globose clusters of epigeous bulbs.

Size and weight: Heads of medium weight.

Bulb: Bulbs green (photosynthetically active), an adaptation to shady cliffs and exposing the surface to the light source.

Leaves

Orientation and presentation: Rosulate, flaccid and recurved, exposing maximum surface for absorption of light during the rainy season. Leaves are spreading, fleshy and sometimes pendulous. Apices are terete, an adaptation to the dry cliff face. Forms from the lower Bashee cliffs with much-reduced, narrow, almost terete leaves.

Colour: Light green and smooth, becoming dry during dry periods, the bulbs enveloped in grey tunics protecting them from excessive rays of the sun.

Age and persistence: Plants long-lived, evergreen leaves withering from below.

Armament and camouflage: Clusters conspicuous, less firm than those of the typical chasmophytic relatives, suggesting a reduction in armament in response to the less disturbed environment. Leaf sap causing tremendous itching and hence the Afrikaans name *jeukbol*. The leopard tortoise (*Testudo pardalis*) is very fond of the leaves and bulbs, and whenever the plants occur in accessible areas they are immediately demolished.

Sexual reproduction

Inflorescence and flowers: Inflorescence spreading, the apices drooping, the white corolla attracting the right pollinating flying insect.

Fruit/Seed

Size: Seed 4×1 mm, an ideal size for establishment in crevices.

Dispersal: Light, black, angular seeds shaken from the capsules and dispersed by wind.

Time: Seeds ripening in summer and autumn, coinciding with the rainy season. Germination after 21 days.

Vegetative reproduction: The very prolific nature of continuous production of bulbils has led to the common name ‘pregnant onions’. This prolific vegetative reproductive strategy ensures long-term survival and represents adaptation to the cliff environment. Bulbils are continuously dispersed and will root if they fall into a crevice. The grey-green bulbils are $6\text{--}8 \times 6\text{--}7$ mm and brittle and are therefore easily detached, a vegetative reproductive backup ensuring a hold on the cliff face.

CONSERVATION STATUS

A local endemic, not threatened.

ADDITIONAL NOTES

Horticulture: *Ornithogalum longibracteatum*, also known as ‘pregnant onions’, is one of the most commonly grown *Ornithogalum* species, popular as a pot plant worldwide. It is mainly grown for its ornamental green, photosynthetically active bulbs. It will do best in thicket gardens, on steep embankments, gabions or terraforce concrete walls. It thrives in dappled shade but also in full sun. It is easily propagated by division or seed and does well in cultivation. Its very easy growing nature maximises survival rate.

VOUCHER

Van Jaarsveld 16636 (NBG).

ILLUSTRATIONS AND MAP

Plate 78, Figures 78a–78c, Map 78.

79. *Ornithogalum pendens* Van Jaarsv., in Van Jaarsveld & Van Wyk in Aloe 46,2: 30–32 (2009a).

Cremonophyte growth form: Cluster-forming, hypogeous bulbs, with pendent linear leaves (of light weight, cliff hanger).

Growth form formula: A:B:D:C:Lp (vb)

Etymology: The epithet *pendens* refers to the pendent leaves.

DESCRIPTION AND HABITAT

Plants bulbous, hypogeous, forming dense clusters up to 100 mm in diameter and consisting of many bulbs and bulbils. Bulbs globose-ovoid, up to 5–10 × 5–8 mm; tunics white, lightly translucent. Roots whitish, less than 1 mm in diameter. Leaves 2, synanthous, 50–100 × 10–16 mm, pendent, linear, fleshy, channelled; surface glaucous, somewhat translucent, smooth, striate, lower surface with slight keel; margin entire. Inflorescence 1 per plant; 50–70 mm long; raceme subcorymbose, 25–30 mm long, 3–6-flowered; scape terete, 1 mm in diameter at base, erect, same colour as leaves; bracts ascending, lanceolate to linear-lanceolate, cymbiform, same colour as leaves, clasping pedicel, channelled, 10–14 × 2–4 mm, becoming smaller distally; pedicel up to 12–20 × 0.5–0.7 mm. Perianth stellate, white, 15–18 mm in diameter; tepals white, ovate-elliptic, 7–12 × 3–4 mm. Stamens 4–7 mm long; filaments white, linear, inner flattened, up to 1 mm in diameter at base; anthers 1.4 mm long. Ovary oblong, abruptly tapering at apex, 3.5 × 2 mm, green, 3-ridged, sessile; style erect, 1.2 mm long, yellowish; stigma capitate. Capsule and seed not seen.

Phenology: Flowering in spring (September). Seeds dispersed by wind in summer.

Pollinators: Insects.

Habitat and aspect: South-facing quartzitic sandstone cliffs. Plants occur in crevices, on ledges and in shady rock veins on southern aspects. Summers are warm to hot, winters are cooler but frost is absent. The average daily maximum temperature ranges from 22–24°C and the average daily minimum for the region is between 10–12°C. Rainfall mainly in winter and autumn, 100–250 mm per annum (mainly cyclonic winter rain). Occasional fog provides extra moisture.

Altitude: 400–600 m.

Associated vegetation: Namaqualand Shale Shrubland of the Succulent Karoo Biome (Mucina *et al.* 2005).

Associated cremonophytes: *Bulbine pendens*, *Colpias molle*, *Ornithogalum pendens* and *Ornithogalum* sp.

Geology: Quartzitic sandstone cliffs (Kuibus Formation) of the Nama Group.

DISTRIBUTION

Ornithogalum pendens is known only from the Skaaprivierspoort northwest of Springbok (Northern Cape).

RELATED SPECIES

Related to *Ornithogalum puberulum*, differs from that species by its glabrous leaves. *Ornithogalum pendens* is at once distinguished by its proliferous production of bulbils at the base of the bulb, by the two distichous, succulent, grey-green leaves becoming pendent and by the subcorymbose racemes of white flowers. The plants grow in dense clusters. It belongs to subgenus *Aspasia* characterised by leafy cymbiform bracts and a style as long as or shorter than the ovary (Obermeyer 1978).

ADAPTATIONS TO THE CLIFF ENVIRONMENT

Habit: Small, dense clusters of grey-green (photosynthetically active) and (2 active) pendulous linear leaves. Plants become deciduous after flowering in spring.

Size and weight: Heads small, of light weight.

Bulb: Hypogeous and prolific from the base, filling crevices.

Leaves

Orientation and presentation: Dense owing to the clustered growth, channelled and slightly translucent, allowing maximum penetration of light. Leaves soon becoming pendent.

Colour and texture: Grey-green, succulent, soft-textured.

Age and persistence: Plants long-lived perennials, becoming deciduous in late spring.

Armament: Without obvious defence characters.

Sexual reproduction

Inflorescence and flowers: Ascending subcorymbose raceme.

Fruit/Seed

Size: Seed not seen.

Dispersal: Light, angular seeds shaken from the capsules and dispersed by wind.

Time: Seeds ripening in summer and autumn.

Vegetative reproduction: Plants continuously form bulbils at the base of the mother bulb, these spilling over and filling crevices, thus maximising survival. It is a prolific vegetative dispersal strategy ensuring continued existence on the cliffs.

CONSERVATION STATUS

A local endemic, not threatened.

ADDITIONAL NOTES

Horticulture: Plants best grown in small containers and miniature succulent gardens. It is easily propagated by division, thriving in cultivation. Outside its succulent karoo habitat, it is best grown under controlled conditions in a greenhouse. It grows very easily, maximising survival rate.

VOUCHER

Van Jaarsveld 21108 (NBG).

ILLUSTRATIONS AND MAP

Plate 79, Figures 79a–79c, Map 79.

SCHIZOBASIS Baker

80. *Schizobasis intricata* (Baker) Baker in *Journal of Botany, British and Foreign* 12: 368 (1874).

Cremonophyte growth form: Solitary, bulbous (of light to medium weight, cliff hugger).

Growth form formula: A:B:D:C:La (e) (vb)

Etymology: The epithet *intricata* pertains to the ‘intricate’ inflorescence.

DESCRIPTION AND HABITAT

Bulb solitary or dividing to form small groups, epigeous, pear-shaped, 50–70 × 40–60 mm; tunics fleshy, reddish to greyish green, soft. Leaf rudimentary, filiform, soon deciduous. Inflorescence (stem) erect to spreading, up to 300 mm long, leafless, persistent, green (functioning as assimilating organ), forming loose panicles up to 150 × 150 mm; scape 120–150 mm × 1.5 mm at base; bracts 2 × 1 mm, triangular, soon withering, acute, spurred at base; spur 2.5 mm long; pedicels 2 mm long. Perianth campanulate, drooping, yellowish cream to greenish, 6 × 3 mm; segments 6, subequal, 1-nerved. Stamens arising from base of segments; anthers oblong, dorsifixed. Ovary sessile, subglobose, 1.5 mm in diameter, 3-celled. Capsule membranous, loculicidal, 3-valved. Seed 1–3 per locule, turgid, black.

Phenology: Flowering in October–November. Seed released towards end of November, early December.

Pollinators: Insects.

Habitat and aspect: *Schizobasis intricata* is grows on quartzitic sandstone cliffs (east- and south-facing). Along the lower Mzimnyati River (Buffalo River) it was collected at an altitude of about 500 m, near the confluence with the Thukela River. Plants are difficult to reach where they are firmly rooted in crevices large enough to support the roots and stem clusters

scattered in rock crevices. Average summer temperature is about 26°C and for winter 14°C. Rainfall is experienced mainly in summer, with averages of 800–1000 mm per annum.

Altitude: 250–2000 m.

Associated vegetation: Thukela Valley Bushveld of the Sub-Escarpment Savanna Bioregion of the Savanna Biome (Mucina *et al.* 2005).

Associated cremnophytes: *Schizobasis intricata* grows in association with *Aloe arborescens*, *Bulbine natalensis*, *Cotyledon orbiculata*, *Crassula orbicularis*, *Cyanotis speciosa* and *Plectranthus madagascariensis*.

Geology: Quartzitic sandstone of the Natal Group (Cape Supergroup).

DISTRIBUTION

Schizobasis intricata is widespread in the eastern parts of South Africa, occurring on cliff faces in dry savanna.

RELATED SPECIES

Differs from *Bowiea* by its firm, non-climbing inflorescence.

ADAPTATIONS TO THE CLIFF ENVIRONMENT

Habit: Plants solitary or in small groups, with epigeous, photosynthetically active bulbs and persistent, ascending-spreading inflorescence. Plants grow in nutrient-poor sandstone soil and have a slow metabolism. Long-lived perennials.

Size and weight: Heads small to medium-sized.

Bulb: Succulent, solitary or dividing to form epigeous clusters.

Leaves

Orientation: Rudimentary.

Colour: Green.

Age and persistence: Soon deciduous.

Armament: Soft edible bulb scales suggest a reduction in armament as a direct result of reduced herbivory.

Sexual reproduction

Inflorescence and flowers: Inflorescence ascending or drooping, persistent and photosynthetically active (having taken over the function of the leaves), even after flowering. This is a xeromorphic adaptation of reducing water loss through reduced leaf surface and a photosynthetically functional inflorescence.

Fruit/Seed

Size: Seed black, angular-rounded, ideal for establishment in crevices.

Dispersal: Light, angular seeds shaken from the capsules and dispersed by gravity to crevices below.

Time: Seed dispersal coincides with the rainy season.

Vegetative reproduction: Bulbs are often cluster-forming, filling crevices. Young bulbs root and increase their numbers further, thus an efficient vegetative expansion and a backup ensuring survival under the harsh conditions on the cliff.

CONSERVATION STATUS

A species seldom encountered, not threatened.

ADDITIONAL NOTES

Horticulture: *Schizobasis intricata* is easy to grow and makes an interesting specimen plant for the specialist plant lover. It is best grown in bushveld gardens, in containers and in a sandy, well-drained mixture. Keep dry during winter for its resting phase and place in a warm, partially shady situation.

VOUCHER

Van Jaarsveld 18213 (NBG).

ILLUSTRATIONS AND MAP

Figures 80a–80c, Map 80.

Dicotyledons

ASCLEPIADACEAE

Huernia R.Br.

81. *H. pendula* E.A.Bruce

Lavrania Plowes

82. *L. haagnerae* Plowes

Tromotriche Haw.

83. *T. baylissii* (L.C.Leach) Bruyns
84. *T. choanantha* (Lavranos & H.Hall) Bruyns

HUERNIA R.Br.

81. *Huernia pendula* E.A.Bruce in The Flowering Plants of Africa 28: t. 1108 (1951).

Cremonophyte growth form: Pendulous stem, cluster, succulent (of light to medium weight, cliff hanger).

Growth form formula: E:Ex:P:Ss (vb) (eg)

Etymology: Greek *pendula*, pendulum, pertaining to its hanging nature.

DESCRIPTION AND HABITAT

Plants sparsely branched, pendent from rock faces, often filling crevices and rooting where stems touch the ground. Branches initially erect or flat, becoming pendulous from ledges, up to 900 mm long. Stems very obscurely 4-angled, cylindrical, 5–8 mm in diameter, green sometimes purplish mottled, becoming greyish green, articulated at nodes. Inflorescence 3- or 4-flowered subsessile cymes towards base of stem and lateral branches. Flowers pendulous, opening successively; pedicels short, up to 8 mm long. Corolla bowl-shaped 10-15 x 8-10 mm, lobes ascending to spreading, up to 5-7 mm in diameter, 5-6 mm long, dark maroon on inside, densely papillate. Fruit paired fusiform follicles.

Phenology: Flowering from spring to midsummer. Flowers with scent of decaying meat. Seeds wind-dispersed.

Pollinators: Probably flies and bluebottles.

Habitat and aspect: Cliffs overlooking the Kei River where the plants grow on ledges, in crevices and fissures, sharing the habitat with other succulent cremonophytes. Summers are hot, winters cooler. The average daily maximum temperature is 28°C and average daily minimum 12°C. Rainfall occurs mainly in summer (thunder showers), 300–800 mm per annum.

Altitude: 400–800 m.

Associated vegetation: Eastern Valley Bushveld of the Savanna Biome (Mucina *et al.* 2005).

Associated cremnophytes: Other cremnophytes at Collywobbles: *Albuca batteniana*, *Aloe reynoldsii*, *Bulbine natalensis*, *Cotyledon orbiculata* and *Haworthia cymbiformis* var. *setulifera*.

Geology: Shale of the Emakwezini Formation (Beaufort Group, Karoo Supergroup).

DISTRIBUTION

Confined to cliffs of east-flowing river valleys between Kei and Bashee Rivers (Eastern Cape).

RELATED SPECIES

Distinguished from related (not cremnophilous) *Huernia* species by its long, subterete stems and pendulous nature. The other species are cluster-forming, usually square-stemmed and well-camouflaged, while the pendulous stems of *H. pendula* are exposed on the cliffs.

ADAPTATIONS TO THE CLIFF ENVIRONMENT

Habit: Pendulous, sparsely branched (leafless) but conspicuous succulent branches up to 900 mm long. Branches rooting on ledges.

Size and weight: Of light to medium weight.

Stem: Subterete to almost terete, succulent, obscurely 4-angled (5–8 mm in diameter), with obscure shallow grooves along the angles, leaf tubercles decussately arranged, 6–7 mm apart. Side branches articulated at the attachment or base and spreading at right angles, rooting where touching the ground; epidermis smooth. The subterete stems are an adaptation to the hot xeric conditions of the vertical habitat, the branch ramification pattern, rooting where it touches the soil, also ensuring optimum vegetative establishment.

Leaves

Orientation: Rudimentary, reduced to inconspicuous scales.

Colour: Green, occasionally purplish mottled, becoming grey-green, the latter an adaptation to the xeric habitat.

Age and persistence: Slow-growing, long-lived perennials.

Armament: Conspicuous armament lacking.

Sexual reproduction

Inflorescence and flowers: Subsessile cymes towards base of stem and lateral branches, with pendulous, bowl-shaped flowers. This arrangement suggests a specific pollinator. Flowers dark maroon, pendulous, the size in comparison to the small stems maximising visibility from the bottom of the cliff, an adaptation to the cliff environment.

Fruit/Seed

Size: Follicles paired, fusiform.

Dispersal: Flattened seeds dispersed by wind.

Time: Seeds released in summer and autumn, maximising establishment of seedlings during the rainy season.

Vegetative reproduction: Stems actively growing and lengthening and will occupy new crevices or fissures (when finding new ground), establishing new clusters—an efficient backup for survival in this dry, hostile environment.

CONSERVATION STATUS

Although *Huernia pendula* is not very common (classified as rare), it is not threatened owing to the sheer, safe habitat.

ADDITIONAL NOTES

Horticulture: Easily grown from cuttings, thriving in a sandy, humus-rich soil in cultivation. It is one of the easiest stapeliads to grow. This growth vigour maximises survival. Like other indigenous cremnophilous stapeliads, it has subterete stems as opposed to the cluster-forming and square-stemmed taxa normally growing on level ground. Best grown on steep embankments, in hanging baskets or on rockeries in thicket and bushveld gardens (Van Jaarsveld 2010).

VOUCHER

Van Jaarsveld 17861 (NBG).

ILLUSTRATIONS AND MAP

Figures 81a–81e, Map 81.

LAVRANIA Plowes

82. *Lavrania haagnerae* Plowes in *Cactus and Succulent Journal* (U.S.) 58: 123 (1986).

Cremonophyte growth form: Stem succulent, cluster (of medium weight to heavy, cliff hugger).

Growth form formula: E:Ex:De:St (vb)

Etymology: After Mrs C.H. Haagner who first collected this species.

DESCRIPTION AND HABITAT

Cluster-forming, up to 150 mm high, shallow-rooted, branched from base, bearing 20–100 grey-green stems; growth decumbent or semiplagiotropic, not pendulous. Stems cylindrical,

cactoid in appearance, 20–30 mm in diameter, with 10–12 regular rows of parallel, neatly arranged, flattened, polygonal tubercles each bearing a small, persistent, conical leaf. Inflorescence reduced on basal half of stem on secondary shoots; primary shoot sterile. Flowers in groups of 3–15 arising from peduncular patches near base, opening in succession. Corolla 13–16 mm in diameter, whitish green on outside, regularly red-mottled on inside; tube shallowly cup-shaped. Fruit a follicle, up to 70 × 3–4 mm, diverging 30–60°. Seed 7 mm long, flat, grey, circular, with pale cream border.

Phenology: Flowering in spring (October). Seeds wind-dispersed.

Pollinators: Probably flies. Bruyns (1993) reports ‘the flowers of *L. haagnerae* are notable for their intense and regular mottling with red spots and their unusually strong odour reminiscent of rock-rabbit dung and urine (*Procavia capensis*)’.

Habitat and aspect: Mainly south-facing cliffs and ledges, but also on other aspects. Temperature (within the subtropics), very hot in summer. The average daily maximum of about 30°C and average daily minimum temperature about 17°C. Winters are cooler but frost absent. Rainfall occurs in summer months, ranging from 50 and 150 mm per annum. Plants grow on medium to small inaccessible rocky ledges and can fill a horizontal crevice up to a meter long (Bruyns 1993).

Altitude: 700–900 m.

Associated vegetation: Mosaic of arid mopane savanna (*Colophospermum mopane* dominant) and Namib Desert vegetation.

Associated cremnophytes: About 12 km east of Sesfontein, *Lavrانيا haagnerae* shares its habitat with the following cliff dwellers: *Aloe dewinteri*, *Ceraria* sp., *Commiphora multijuga*, *Cyphostemma uter*, *Drimia* sp., *Ornithogalum* sp., *Oxalis* sp., *Petalidium* sp. and *Sterculia africana*.

Geology: Proterozoic dolomite cliffs (Damara Sequence).

DISTRIBUTION

East of Sesfontein, Kaokoveld (Namibia), growing on the western fringe of the dolomite escarpment and river valley cliff faces (Khowarib Poort). *Lavrانيا haagnerae* is known only from two sites (Bruyns 1993) about 40 km apart, always confined to inaccessible, vertical dolomite cliff faces on the escarpment edge of the Namib Desert.

RELATED SPECIES

Related to the other *Lavrانيا* species but at once distinguished by its dense clusters of decumbent to semiplagiotropic, succulent stems. The stems have regular rows (irregular in all other *Lavrانيا* species) of neatly arranged, parallel, flattened, polygonal tubercles, each with a small, conical, persistent leaf. There are also differences in the inflorescence, with markedly fewer inflorescences arising on secondary shoots in the basal parts of the stem. In the other four *Lavrانيا* species (non-cremnophytes) the inflorescences are apically produced. Although the inflorescences in *L. haagnerae* are initially produced on the apical part of the secondary stems, their growth is suppressed until the stems have lengthened and they subsequently then

occur on the basal portion of the stem. The flowers of *L. haagnerae* are larger (compared to those of the other *Lavrania* species) and more conspicuous. The seeds are the largest in the genus *Lavrania* (Bruyns 1993).

ADAPTATIONS TO THE CLIFF ENVIRONMENT

Habit: *Lavrania haagnerae* differs from the other four *Lavrania* species in its dense conspicuous clusters of up to 100 stems. The decumbent or semiplagiotropic growth is ideal for exploiting rocky ledges, with very little competition and in the absence of large herbivores. The regularly arranged tubercles make the plants conspicuous.

Size and weight: Clusters often large, of medium weight to heavy.

Stem: Stems with regularly arranged tubercles, rooting at nodes. The regularly arranged tubercles are more conspicuous, suggesting less investment in camouflage mechanisms.

Leaves

Orientation: Reduced and rudimentary (see above).

Colour: Glaucous.

Age and persistence: Slow-growing, long-lived perennial.

Armament and camouflage: Without conspicuous armament or camouflage properties.

Sexual reproduction

Inflorescence and flowers: With fewer, but larger and thus more conspicuous flowers, produced at the base of the stems, not apically as in the other species. This arrangement suggests a specific pollinator.

Fruit/Seed

Size: Seed about 7 mm in diameter, the largest in the genus.

Dispersal: The large, flat seeds suggest dispersal by wind on the cliffs.

Time: Seeds released during the rainy season in late spring and summer.

Vegetative reproduction: With an expanding habit, rooting where stems touch the ground, exploiting available space by active vegetative growth, very unlike its non-cremophilous relatives. Other *Lavrania* species grow on hilly to flat, rocky terrain with either solitary or fewer stems, less conspicuous owing to fewer, cryptic stems (irregularly arranged tubercles) and adapted to a habitat frequently disturbed by large herbivores and with competition from other plants. These other species grow cryptically and are never common.

CONSERVATION STATUS

Classified as rare (Loots 2005). Endemic to the dolomite region east of Sesfontein. Despite a restricted distribution, it is not threatened as it is well protected by the sheer cliff-face habitat.

ADDITIONAL NOTES

General: *Lavrania haagnerae* was first collected and recorded by Clem and Peggy Haagner in August 1969 (Plowes 1986).

Horticulture: Best for dry subtropical desert gardens. Plants can be grown in full sun or partial shade and are ideal for steep embankments or rockeries. Outside the native habitat it is best grown under controlled conditions in a greenhouse. Keep completely dry in winter. Feed in late spring and water sparingly in the summer. The soil should be sandy and preferably slightly alkaline. Add dolomitic lime when necessary. Plants easily grown from stem cuttings or division.

VOUCHER

Van Jaarsveld 19879 (NBG, WIND).

ILLUSTRATIONS AND MAP

Plate 82, Figures 82a–82c, Map 82.

TROMOTRICHE Haw.

83. *Tromotriche baylissii* (L.C.Leach) Bruyns in South African Journal of Botany 61,4: 206 (1995).

Cremonophyte growth form: Pendulous stem, cluster, succulent (of medium weight, cliff hanger).

Growth form formula: E:Ex:P:Ss (vb) (eg)

Etymology: After Mr Roy Bayliss (1909–1994), succulent plant enthusiast and the first collector of this species.

DESCRIPTION AND HABITAT

Plants sparsely branched from base, pendent from rock faces, often filling crevices and some stems becoming subterranean and rooting. Stems obtusely 4-angled, sulcate along sides, tubercle-toothed; older branches becoming smooth and rounded; arboreal stems hanging from ledges, up to 1.5 m long. Leaves rudimentary, inconspicuous. Inflorescence produced at tips of branches, shortly pedunculate, produced repeatedly from apices of growing stems. Flowers opening successively; pedicels short, up to 13 mm long. Corolla 5-angled, tubular-campanulate, up to 15 mm long, 13 mm wide, red-purple on inside; surface satin-like; lobe margins sometimes with vibratile clavate cilia. Fruit paired fusiform follicles up to 60 mm long.

Phenology: Flowering from spring to midsummer. Flowers with scent of decaying meat, thus attracting pollinators. Seeds wind-dispersed.

Pollinators: Probably flies and bluebottles.

Habitat and aspect: Southern and eastern aspects of sheer cliff faces, growing in ledges, fissures and crevices (300–600 m in altitude). Temperature in summer hot, cooler in winter with the occasional cold fronts. Average daily maximum temperature is about 26°C and average daily minimum about 10°C. Rainfall (cyclonic winter rainfall and summer thunder showers) is in summer and winter and range from 200–300 mm per annum.

Altitude: 400–600 m.

Associated vegetation: Gamka Thicket of the Albany Thicket Biome (Mucina *et al.* 2005). Thicket Biome with elements of the Succulent Karoo Biome.

Associated cremnophytes: At Geelhoutboskloof, the following species have been observed in association with our species: *Adromischus cristatus* var. *zeyheri*, *Albuca cremnophila*, *Cotyledon tomentosa* subsp. *tomentosa*, *Cyrtanthus labiatus*, *C. montanus*, *Delosperma elsiae*, *Gasteria rawlinsonii*, *Haworthia gracilis* var. *picturata*, *H. viscosa*, *Othonna lobata* and *Plectranthus verticillatus*.

Geology: Quartzitic sandstone of the Nardouw Subgroup (Table Mountain Formation, Cape Supergroup), on south-facing cliffs.

DISTRIBUTION

Confined to tributaries of the Gamtoos, Kouga and Baviaanskloof Rivers and Grootrivier where they flow through the Cape Fold Belt mountains (from east of Willowmore to just west of Hankey).

RELATED SPECIES

Distinguished from related level-ground *Tromotriche* species by its long subterete stems, pendulous nature and pendulous spreading campanulate flowers. The other species are cluster-forming and well camouflaged. Its closest relative is *T. choanantha*, another cremnophyte very similar in vegetative features, but with a slightly longer corolla and with flowers produced at the base of the long stems.

ADAPTATIONS TO THE CLIFF ENVIRONMENT

Habit: Pendulous, sparsely branched (leafless) but conspicuous succulent branches up to 1.5 m long. Branches on ledges rooting and often becoming subterranean.

Size and weight: Clusters of medium weight.

Stem: Stems obscurely 4-angled (7–12 mm in diameter) to almost terete, with shallow grooves along the angles, tessellate, tubercle-toothed, becoming rounded with age, rooting where touching the ground. These subterete, rope-like stems are a response to the very xeric and exposed cliff environment.

Leaves

Orientation: Reduced and rudimentary (see above).

Colour: Stems dark bluish green.

Age and persistence: Plants slow-growing, long-lived perennials.

Armament and camouflage: Plants without conspicuous armament or camouflage properties.

Sexual reproduction

Inflorescence and flowers: Inflorescences apically and successively produced along the sides of the young stems. This arrangement suggests a specific pollinator. Flowers campanulate, pendulous, spreading, thus maximising visibility from the bottom of the cliff.

Fruit/Seed

Dispersal: Flattened seeds released from the follicles and then dispersed by wind.

Time: Seeds released in summer and autumn, maximising establishment of seedlings during the rainy season.

Vegetative reproduction: Stems often negatively phototropic, growing into the soil or crevices and establishing new clusters. Stems lengthen and will root where they find new ledges or crevices, forming new colonies. This active vegetative growth and establishment of new colonies represent an efficient backup ensuring survival in this dry, hostile environment.

CONSERVATION STATUS

Little-known species, not threatened owing to the sheer cliff-face habitat.

ADDITIONAL NOTES

Horticulture: Plants of *Tromotriche baylissii* are easily propagated by division or from seed and are best grown as specimen pot plants. It is best suited to dry thicket and succulent karoo gardens, suitable for growing in dappled shade on steep embankments. Water sparingly throughout the year and renew soil every second year. Feed in spring. Outside its habitat, it is best suited to containers in a greenhouse where conditions can be controlled.

VOUCHER

Van Jaarsveld 17717 (NBG).

ILLUSTRATIONS AND MAP

Figures 83a–83e, Map 83.

84. *Tromotriche choanantha* (Lavranos & H.Hall) Bruyns in South African Journal of Botany 61,4: 204 (1995).

Cremnophyte growth form: Pendulous stem, cluster, succulent (of medium weight, cliff hanger).

Growth form formula: E:Ex:P:Ss (vb) (eg)

Etymology: Greek *choane*, funnel, and *anthos*, flower, pertaining to the funnel-shaped corolla.

DESCRIPTION AND HABITAT

Plants sparsely branched, pendent from rock faces, often filling crevices, some stems becoming subterranean and rooting. Stems obtusely 4-angled, sulcate along sides, tubercle-toothed; older branches becoming smooth and rounded; arboreal stems hanging from ledges, up to 2 m long. Leaves rudimentary, inconspicuous. Inflorescence shortly pedunculate, produced at base of stems. Flowers opening successively; pedicels short, up to 10 mm long. Corolla tubular-campanulate, up to 20 mm in diameter, red-purple on inside; surface satin-like; tube 16 mm long. Fruit paired fusiform follicles up to 100 mm long.

Phenology: Flowering from spring to midsummer. Flowers with scent of decaying meat, thus attracting pollinators. Seeds wind-dispersed.

Pollinators: Pollinated probably by flies and bluebottles.

Habitat and aspect: All aspects (more common on southern and eastern aspects) of sheer cliff faces, growing on suitable ledges, crevice and fissures. Plants often share their habitat with other cliff-dwelling succulent plants. Temperature hot in summer and with occasional cool cyclonic fronts in winter. Average daily maximum is about 25°C and average daily minimum 9°C. Rainfall (cyclonic winter rainfall and summer thunder showers) is experienced in winter and summer and ranges from 200 and 300 mm per annum.

Altitude: 250–900 m.

Associated vegetation: Gamka Thicket (Albany Thicket Biome) and Western Gwarrieveld of the Rainshadow Valley Karoo Bioregion of the Succulent Karoo Biome (Mucina *et al.* 2005).

Associated cremnohytes: Observations at ‘Die Hel’ north of Calitzdorp include *Bijlia dilatata*, *Cotyledon tomentosa* subsp. *tomentosa*, *Crassula perforata*, *C. rupestris* and *Senecio ficoides*.

Geology: Quartzitic sandstone of the Nardouw Subgroup (Table Mountain Formation, Cape Supergroup).

DISTRIBUTION

Confined to cliffs along the Gamka River from Die Hel to the Huis River Pass (Groot Swartberg Mountains) between Ladismith and Calitzdorp.

RELATED SPECIES

Distinguished from related (not cremnophilous) *Tromotriche* species by its long subterete stems, pendulous nature and pendulous, spreading, campanulate flowers. The other species are cluster-forming and usually well camouflaged, while *T. choanantha* has conspicuous

pendulous stems. *Tromotriche choanantha* is immediately distinguished from *T. baylissii* by its flowers produced at the base of the stems (apically produced in *T. baylissii*).

ADAPTATIONS TO THE CLIFF ENVIRONMENT

Habit: *Tromotriche choanantha* has pendulous, sparsely branched (leafless) but conspicuous succulent branches up to 2 m long. Branches on ledges rooting, often becoming subterranean.

Size and weight: Of medium weight.

Stem: Obscurely 4-angled (6–12 mm in diameter) to almost terete, with shallow grooves along the angles, tessellate, tubercle-toothed, becoming rounded with age, rooting where touching the ground; epidermis minutely pubescent (becoming glabrescent with age). These subterete, rope-like stems are thought to be a response to the very xeric and exposed cliff environment.

Leaves

Orientation: Reduced and rudimentary (see above).

Colour: Stems dark bluish green.

Age and persistence: Slow-growing, long-lived perennials.

Armament: Plants without conspicuous armament.

Sexual reproduction

Inflorescence and flowers: Inflorescences are basally produced in the stem grooves of young branches, shortly pedunculate. This arrangement suggests a specific pollinator. Although the stem remains functional and lengthening, no additional flowers develop. The flowers are campanulate, pendulous and spreading, maximising visibility from the bottom of the cliff.

Fruit/Seed

Dispersal: Flat seeds wind-dispersed.

Time: Seeds released from the splitting follicles in summer and autumn, maximising establishment of seedlings during the main rainy season.

Vegetative reproduction: Stems are often negatively phototropic, growing into the soil or crevices and thus establishing new clusters. Stems lengthen and will root where they find new ledges or crevices, forming new colonies. This active vegetative growth and establishment of new colonies represent an efficient backup ensuring survival in this dry, hostile environment.

CONSERVATION STATUS

Endemic, with a restricted distribution but not threatened owing to the undisturbed habitat.

ADDITIONAL NOTES

First record: First collected and recorded by Mr P.O. le Roux in 1937. Plants from this collection were grown at Kirstenbosch and flowered in September 1938 (Leach 1978).

Horticulture: Plants of *Tromotriche choanantha* are easily grown by division or from seed, as specimen pot plants. It is best suited to dry thicket and succulent karoo gardens, in dappled shade on steep embankments. Water sparingly throughout the year and renew soil every second year. Feed in spring. Outside the habitat it requires controlled conditions in a greenhouse.

VOUCHER

Van Jaarsveld 17161 (NBG).

ILLUSTRATIONS AND MAP

Figures 84a–84d, Map 84.

ASTERACEAE

Kleinia Mill.

85. *K. galpinii* Hook.f.

Othonna L.

86. *O. armiana* Van Jaarsv.
87. *O. capensis* L.H.Bailey
88. *O. cremnophila* B.Nord. & Van Jaarsv.
89. *O. triplinervia* DC.

Senecio L.

90. *S. medley-woodii* Hutch.
91. *S. muirii* L.Bolus
92. *S. pondoensis* Van Jaarsv. & A.E.van Wyk
93. *S. serpens* G.D.Rowley
94. *S. talinoides* Sch.Bip. subsp. *talinoides*

KLEINIA Mill.

85. *Kleinia galpinii* Hook.f. in Journal of Horticultural and Practical Gardening, Ser. 3: 3 (1892).

Crempnophyte growth form: Compact to short-stemmed shrublets (of medium weight, cliff hugger).

Growth form formula: A:S:Lper:R:C:Ca:La (vb) (r)

Etymology: After Ernest Edward Galpin (1858–1941) who first collected this species near Barberton in Mpumalanga.

DESCRIPTION AND HABITAT

Cluster-forming, erect to decumbent, sparsely branched (1–5 branches), whitish green, succulent suffrutex, up to 120 mm tall, all parts covered with a waxy bloom. Roots slightly succulent at base, up to 3 mm in diameter; plants often sprouting from just below ground. Branches terete, succulent, greyish green, up to 10 mm in diameter, becoming deciduous towards base; with pungent odour when damaged. Leaves alternate, crowded in central rosette, dorsiventrally flattened, ascending, oblanceolate to narrowly obovate; 40–80 × 15–22 mm; midrib prominent; surface whitish green; margin slightly revolute; base cuneate; apex acute; petiole indistinct. Inflorescence a loose terminal panicle, up to 300 mm long, bearing up to 8 terminal capitula, with gradual change from leaves to bracts, each capitulum clasped by 2–5 bracts. Capitulum 30 mm long, up to about 40 mm in diameter, nodding in bud stage; involucre with about 12 phyllaries up to 18 mm long; receptacle alveolate, flat. Florets numerous, orange. Style arms up to 5 mm long. Achene angular, glabrous, cylindrical, 6 mm long; pappus 10 mm long.

Phenology: Flowering in summer to early winter (January–August).

Pollinators: Insects.

Habitat and aspect: Quartzitic sandstone cliffs and steep slopes. Plants rooted in crevices and on rock ledges. Fog often occurs in summer. Winters are cool but frost is a rarity owing to the slope. The average daily maximum temperature is 22°C and the average daily minimum is 14°C. Rainfall mainly from spring to autumn but occasionally also in winter, ranging from 1250–2000 mm per annum.

Altitude: 600–1525 m.

Associated vegetation: Barberton Montane Grassland (Mucina *et al.* 2005) and elements of afro-montane forest.

Associated cremnophytes: *Albuca shawii*, *Crassula lanceolata*, *C. sarcocaulis*, *C. swaziensis*, and *Plectranthus verticillatus*.

Geology: Quartzitic sandstone of the Moodies Group (Barberton Supergroup, Keyser 1997).

DISTRIBUTION

Kleinia galpinii is known only from the Barberton region and adjacent area (Mpumalanga and northern Swaziland).

RELATED SPECIES

Kleinia galpinii is related to *K. fulgens*, which occurs widespread from KwaZulu-Natal to the Limpopo Province. Superficially they are close, but *K. fulgens* (a stoloniferous species) lacks the whitish green leaves, has much longer stems and the leaves usually have a toothed margin.

ADAPTATIONS TO THE CLIFF ENVIRONMENT

Habit: Compact, rosulate, sparsely branched succulent herb with perennial base.

Size and weight: Clusters small, of light weight.

Leaves

Orientation: Ascending, often pointing towards the light source, avoiding direct light (with tips pointed towards the sun, thus the least amount of direct exposure). Leaves are also crowded in dense rosettes, typical of dry habitats.

Colour: Whitish green (pruinose), protected by a waxy bloom protecting the plant from extreme exposure.

Age and persistence: Evergreen, with firm long-lived leaves, but plants simply resprouting from basal shoots after frost or fire. Older leaves withering from the base. The fleshy leaves becoming turgid after rain, but often in a semi-desiccated state during dry periods.

Armament: The soft, fragile plants are without obvious armament. The pungent leaf resin is deterrent to insects and other herbivores.

Sexual reproduction

Inflorescence and flowers: Inflorescence conspicuous, displaying its bright orange capitulum (rich flowering) and attracting butterflies.

Fruit/Seed

Size: Achene angular, glabrous, cylindrical, 6 mm long; pappus 10 mm long.

Dispersal: Achenes wind-dispersed.

Time: Achenes ripening in summer and autumn, coinciding with summer and autumn rain.

Vegetative reproduction: Plants have vegetative renewal shoots that sprout after fire or drought. The shoots root when the mother plant dies, establishing new populations. This is an efficient vegetative backup strategy for survival under the harsh, xeric cliff-face conditions.

CONSERVATION STATUS

Localised and confined to the gorges but not threatened owing to the inaccessible habitat.

ADDITIONAL NOTES

Horticulture: *Kleinia galpinii* is an ornamental species (leaves and flowers), especially when coming into flower. Best for highveld and moist bushveld gardens, grown in rockeries, on embankments or simply as a pot plant in full sun. Outside its habitat, it should be grown under controlled conditions in a greenhouse. Propagate by division, from stem cuttings or seed.

VOUCHER

Van Jaarsveld 19360 (NBG).

ILLUSTRATIONS AND MAP

Plate 85, Figures 85a–85d, Map 85.

OTHONNA L.

86. *Othonna armiana* Van Jaarsv. in South African Journal of Botany 52,6: 569–571 (1986).

Cremonophyte growth form: Dwarf-sized compact shrublet (of light to medium weight, cliff squatter).

Growth form formula: A:S:Lar:D:Ca:La (r)

Etymology: After Mr A.R. (Anthony) Mitchell of the Island of Wight, England, who discovered this species while researching the genus *Conophytum*.

DESCRIPTION AND HABITAT

Dwarf-sized, summer-deciduous, succulent herb with fibrous roots. Caudex 30–70 mm in diameter, napiform, flattened distally with age, tapering towards base, dark brown, longitudinally fissured. Branches short, compact, 3–20 mm long, 3–10 mm in diameter, with persistent cartilaginous phyllopodia 2–5 mm long, 3 mm in diameter, brownish purple and truncate at apex; young branches slightly woolly, becoming glabrous. Leaves 5–22 × 5–18 mm, succulent; blade orbicular to obovate, rarely ovate, dorsiventrally compressed, glabrous, apically rounded, basally cuneate or rarely truncate, with entire to serrate margins, abaxially tinged with purple; petiole 2–4 mm long, slightly woolly at base. Peduncle terminal, erect, 1 or 2, 60–90 mm long, 1–1.5 mm thick, terete, glabrous, with 2–5 radiate heads 4–5 mm in diameter. Involucre campanulate, 6 mm deep; involucre bracts 8, uniseriate, ovate-lanceolate, 5–7 mm long, acute; receptacle convex, shallowly alveolate. Ray florets 8, in a single row, fertile. Achene 1.5 mm long, 1 mm wide, oblong to obovoid, finally 3 mm long when ripe, dark brown, cano-pubescent, 10-ribbed; pappus consisting of many persistent bristles.

Phenology: Flowering summer to early winter (February–May). Seeds (achenes) wind-dispersed.

Habitat and aspect: South-facing diabase rock faces in the northeastern Richtersveld, Northern Cape (800–900 m in altitude). Rainfall is mainly in winter and ranges from 100 and 150 mm per annum. Plants grow on medium to small inaccessible rocky ledges.

Altitude: 800–900 m.

Associated vegetation: Kahams Mountain Desert (Mucina *et al.* 2005).

Associated cremnoophytes: Associated cremnoophytes on the Rooiberg (Eksteenfontein), Richtersveld, are *Conophytum gratum*, *Crassula macowanii* and *C. pseudohemisphaerica*.

Geology: Proterozoic diabase.

DISTRIBUTION

Othonna armiana is known only from the Rooiberg, a diabase mountain massif northeast of Eksteenfontein in the Richtersveld.

RELATED SPECIES

Othonna armiana is related to *O. herrei*, which is widespread in the central mountain range of the Richtersveld. It is a taller shrublet (without the compact nature of *O. armiana*).

ADAPTATIONS TO THE CLIFF ENVIRONMENT

Habit: Compact, dwarf-sized, caudiciform plants.

Size and weight: Clusters small, of light to medium weight.

Leaves

Orientation: Ascending, often pointing towards the light source (with tips pointing towards the sun, thus the least amount of direct exposure), crowded in rosettes.

Colour: Glaucous, protected by a waxy bloom, shielding the plant from extreme exposure.

Age and persistence: Plants deciduous during the long, dry summer when they aestivate, new leaves appearing in autumn.

Armament: The soft, fragile leaves are without obvious armament. The pungent leaf resin and firm, cartilaginous phyllopodia are deterrent to insects and other herbivores.

Sexual reproduction

Inflorescence and flowers: Conspicuous yellow ray florets, pollinated by insects. Another example of rich flowering (large inflorescence compared to the relatively small plant body).

Fruit/Seed

Size: Achene oblong to obovoid, 1.5 mm long, 1 mm in diameter, finally when ripe 3 mm long, dark brown, cano-pubescent, 10-ribbed; pappus consisting of numerous persistent bristles.

Dispersal: Achenes dispersed by wind.

Time: Achenes ripening in autumn and winter, coinciding with the winter rainfall.

Vegetative reproduction: Absent.

CONSERVATION STATUS

Although classified as critically endangered (Raimondo *et al.* 2009), it is not threatened owing to the inaccessible habitat.

ADDITIONAL NOTES

Horticulture: Best for succulent karoo gardens, grown in rockeries, miniature succulent gardens and containers. Outside the habitat, it is best grown under controlled conditions in a greenhouse. Plants easily grown from seed sown in autumn.

VOUCHER

Van Jaarsveld 8188 (NBG).

ILLUSTRATIONS AND MAP

Plate 86, Figures 86a & 86b, Map 86.

87. *Othonna capensis* L.H.Bailey in Encyclopedia of American Horticulture: 1180 (1901).

Cremonophyte growth form: Pendent, mat-forming (of light to medium weight, cliff hanger).

Growth form formula: E:F:P:Els:E (vb)

Etymology: The epithet *capensis* refers to the Cape of Good Hope, South Africa.

DESCRIPTION AND HABITAT

Spreading, procumbent and mat-forming to pendent, glabrous, branched shrublets, branches up to 400 mm long, rooting at nodes, very variable in size. Roots fibrous. Branches terete, succulent, greyish to purplish green, sometimes developing aerial roots, at first soft becoming firm and deciduous towards base, internodes 1–25 mm apart. Leaves alternate, often crowded, erect, softly succulent, bluish green to purplish or reddish green, pruinose, cylindrical, linear-obovate, club-shaped to linear-fusiform, 17–35 × 4–11 mm; adaxial surface flat but always grooved, groove sometimes very faint, abaxial surface rounded with few faint striations; apex mucronate, sometimes purplish. Inflorescence a loose, lax, terminal corymb up to 155 mm long with up to 4 capitula, often solitary; bracts short, succulent, triangular, rarely club-shaped, 2–5 × 0.75–2.00 mm. Capitulum top-shaped, 5–8 mm broad at tip, with up to 8 phyllaries; phyllaries free at tip, triangular to triangular-lanceolate, with broad maroon striations. Ray florets 12–15, yellow, limb linear-lanceolate, 9–11 × 2.5–3.5 mm. Disc florets bisexual. Achene glabrous, 1 × 0.3 mm, tapering.

Phenology: Flowering almost throughout the year but with a peak in spring (September–November).

Pollinators: Insects.

Habitat and aspect: Sandstone, quartz or shale cliffs. Plants rooted in crevices and on rock ledges, the long extended branches rooting where they touch the soil or reach a crevice. Extreme temperatures as high of 40°C have been recorded. Winters are cooler but frost is a rarity or absent owing to the sheer habitat. The average daily maximum temperature is about 23–25°C and the average daily minimum is 10–14°C. Rainfall in summer and winter but more in spring or autumn, ranging from 300–500 mm per annum.

Altitude: 20–1220 m.

Associated vegetation: Mainly Gamtoos Thicket (Albany Thicket Biome), Upper Karoo Hardeveld (Nama-Karoo Biome) and dry Eastern Coastal Shaleband Vegetation of the Fynbos Biome (Mucina *et al.* 2005).

Associated cremonophytes: At Hoeree, *Othonna capensis* shares its habitat with *Adromischus cristatus* var. *zeyheri*, *Aloe perfoliata*, *Bulbine retinens* and *Crassula perforata*.

Geology: Quartzitic sandstone of the Table Mountain Group and shales of the Beaufort Group (Cape Supergroup).

DISTRIBUTION

Othonna capensis occurs widespread in the Eastern Cape, from the inland Graaff-Reinet escarpment mountains to the Kouga River in the south and further east to the dry Bashee River, confined to sheer cliff faces.

RELATED SPECIES

Othonna capensis is related to *O. carnososa* of similar sites along dry river valleys but not confined to cliff faces and more woody, with decumbent growth.

ADAPTATIONS TO THE CLIFF ENVIRONMENT

Habit: The plants often hang like curtains from crevices on the cliffs. The leaves are highly and softly succulent and can withstand periods of drought by producing anthocyanins (purplish red colour pigment) which protect the plants from penetration of excessive sunlight, further aiding its survival.

Size and weight: Clusters small, of light to medium weight.

Leaves

Orientation: Ascending, crowded, often pointing towards the light source (with tips towards the sun, thus the least amount of direct exposure). Leaves very succulent, storing copious amounts of moisture.

Colour: Greyish green, pruinose (bluish green covered with a powdery bloom).

Age and persistence: Plants evergreen, but leaves withering from the base although tending to remain persistent. The fleshy leaves becoming turgid after rain, but often in a semi-desiccated state (and channelled) during drought, an adaptation to the extreme dry cliff habitat.

Armament: The plants are soft and fragile, without armament.

Sexual reproduction

Inflorescence and flowers: Inflorescence a loose, lax, terminal corymb up to 155 mm long, bearing up to 4 often solitary capitula. Capitulum top-shaped, 5–8 mm broad at the top with up to 8 phyllaries.

Fruit/Seed

Size: Achene 1×1.03 mm, tapering, pappus 2–3 mm long.

Dispersal: Achenes dispersed by wind.

Time: Achenes ripening throughout the year, also coinciding with the rainfall.

Vegetative reproduction: The procumbent stems (up to 400–600 mm long) are flaccid, rooting where they find crevices lower down and forming new colonies. Detached plants landing in crevices or on ledges will root, an extensive vegetative backup strategy aiding long-term survival.

CONSERVATION STATUS

Confined to cliffs and not threatened owing to the inaccessible habitat.

ADDITIONAL NOTES

Horticulture: Best for thicket gardens, grown on steep embankments, in hanging baskets, on window sills or as a pot plant, in full sun or dappled shade. *Othonna capensis* is an excellent groundcover, with soil-binding properties. Propagate from cuttings, rooting rapidly.

VOUCHER

Van Jaarsveld 16809 (NBG).

ILLUSTRATIONS AND MAP

Plate 87, Figures 87a–87d, Map 87.

88. *Othonna cremnophila* B.Nord. & Van Jaarsv. in *Aloe* 42,1 & 2: 4–7 (2005).

Crempnophyte growth form: Compact succulent-stemmed shrublet (of medium weight to heavy, cliff squatter).

Growth form formula: E:F:As:S/H:Ca:D

Etymology: Greek *kremnos*, cliff, and Greek *phileein*, to love, pertaining to its cliff habitat.

DESCRIPTION AND HABITAT

Erect, branching, succulent shrubs, 200–600 mm high. Roots dark-brown, fibrous, taproot up to 7 mm in diameter. Stem basally simple, cylindrical, 35–90 mm in diameter, branching upwards, with erect-patent to ascending branches, upper branches 20–35 mm in diameter, cylindrical, apically abruptly tapering or cone-shaped and covered with white-felted wool, initially with woolly, later faintly alveolate depressed leaf scars 2–3 × 1–2 mm; older branches brownish green, becoming glabrous and almost smooth. Leaves alternate, petiolate, crowded in apical rosette with 6–8 leaves from late summer to early autumn, then deciduous, erect to patent to spreading; blade obovate, subpalmate, 30–80 × 25–40 mm, many-veined, basally tapering into petiole, pale to glaucous green with a powdery bloom, leathery, somewhat fleshy; surface smooth; margin crispate-undulate-dentate, slightly thickened; apex rounded; petiole (3–)5–15 mm long, linear, flattened. Synflorescence bearing 6–15 flower heads, terminal, erect, laxly paniculate, 170–260 mm tall. Peduncle up to 80 mm long, 4 mm in diameter at base, glaucous owing to powdery bloom, with small bract; bract and leaf axils covered with white felt-like wool; pedicels 25–60 mm long. Capitula 25–40 mm in diameter (including ligules); involucre campanulate, 7–10 mm high, 7–10 mm wide; involucre bracts

5–8, uniseriate, triangular-ovate, 6–8 mm long, 2.5–5.0 mm wide, tinged purplish, acute-acuminate, basally connate (for about a third); receptacle convex, alveolate. Ray florets 8, female, fertile, yellow; lamina oblong, 10–15 × 6–8 mm, 4–7-veined, obtuse to truncate, becoming recurved; tube cylindrical, 5–6 mm long. Style branches yellow, 1.5–2 × 0.3 mm, spreading. Cypsela oblong, subterete or somewhat compressed, 4–5 mm long, 1.5–2.0 mm wide, 10-ribbed, white-villous especially basally and between ribs, hairs mucilaginous when soaked; pappus bristles numerous, pluriseriate, 5–6 mm long, minutely barbellate, white, persistent. Disc florets functionally male; corolla yellow, 4–5 mm long; tube cylindrical; limb campanulate, 5-lobed; corolla lobes deltoid-ovate, 0.7–1.0 mm long, erect, midlined, with lateral veins. Anthers 1.5 mm long including ovate-obtuse appendage; base obtuse, excaudate; filament collar balusterform. Ovary narrowly oblong, 2.5–3.0 mm long, 5-ribbed, glabrous or sparsely minutely pilose-setose; style simple, sterile, tipped by rounded to truncate cone surrounded by collar of short sweeping hairs. Pappus bristles several, 3–4 mm long, minutely barbellate, white, caducous.

Phenology: Flowers in late autumn and winter.

Habitat and aspect: Small shrubs on quartzitic sandstone cliff faces on southern and eastern aspects. The southern slopes are cooler, with shady conditions. Winters are cool and subject to occasional coastal fog from the west coast; frost absent. The average daily maximum temperature is about 26°C and average daily minimum about 14°C. Rainfall occurs mainly from autumn (thunder showers) to spring (cyclonic winter rain), ranging from 75–150 mm per annum.

Altitude: 600–1000 m.

Associated vegetation: Rosyntjieberg Succulent Shrubland (Mucina *et al.* 2005).

Associated cremnophytes: *Aloe meyeri*, *Bulbine pendens*, *Conophytum taylorianum* subsp. *rosynense*, *Crassula pseudohemisphaerica*, *C. sericea* var. *sericea*, *Cyrtanthus herrei*, *Pelargonium desertorum*, *Trachyandra aridimontana* and *Tylecodon ellaphieae*. Other non-succulent cremnophilous plants on these cliffs include the small trees *Ficus cordata* and *F. ilicina*.

Geology: Quartzite of the Rosyntjieberg Formation (Orange River Group).

DISTRIBUTION

Othonna cremnophila is known only from the Rosyntjieberg to the northeast of Eksteenfontein in the Richtersveld.

RELATED SPECIES

Othonna cremnophila is at once distinguished from *O. cyclophylla* by its thick and sparsely branched cylindrical stems with white-felted wool on apical branches, larger obovate undulate-dentate leaves, and the distinctly radiate capitula with bright yellow rays. *Othonna cyclophylla* is a taller, much-branched shrub with whitish grey cortex on the rather thin stems, orbicular leaves 10–20 mm in diameter, with denticulate margins, and with a few-flowered synflorescence of disciform capitula. Another shrubby species in the region, *O. graveolens*, is

more similar in leaf shape, but also has disciform capitula (like *O. cyclophylla* but smaller and more numerous) and stems with a peeling, papery, light brown cortex.

ADAPTATIONS TO THE CLIFF ENVIRONMENT

Habit: Compact, succulent shrublet with cylindrical stems. It is a slow grower; growth is erect from a young age and the plants become firmly wedged in crevices. They are locally abundant but are mostly restricted to inaccessible places.

Size and weight: Clusters of medium weight to heavy.

Leaves

Orientation: Ascending-spreading.

Colour: Glaucous, protected by a waxy bloom, shielding the plant from extreme exposure.

Age and persistence: Long-lived perennials, deciduous in the long, dry summer when the plants aestivate, new leaves appearing in autumn.

Armament: The soft, fragile plants are without obvious armament.

Sexual reproduction

Inflorescence and flowers: Inflorescence terminal, erect, laxly paniculate, 170–260 mm tall (with 6–15 flower heads). *Capitula* 25–40 mm in diameter (including ligules).

Fruit/Seed

Size: Achene about 3 mm long, ribbed.

Dispersal: Achenes dispersed by wind.

Time: Achenes ripening in autumn and winter, coinciding with the winter rainfall.

Vegetative reproduction: Absent.

CONSERVATION STATUS

Localised, but not threatened owing to the inaccessible habitat.

ADDITIONAL NOTES

General: In September 2004, few plants of *Othonna cremnophila* were noticed in accessible sites on the cliffs, stunted and malformed owing to heavy grazing.

Horticulture: Best for succulent karoo gardens, grown in rockeries or containers, in full sun (Van Jaarsveld 2000b). Outside its arid habitat, it should be grown under controlled conditions in a greenhouse. Introduced into cultivation in 1980. Plants easily grown from seed sown in autumn.

VOUCHER

Van Jaarsveld 19119 (NBG).

ILLUSTRATIONS AND MAP

Frontispiece on p. ii, Plate 88, Figures 88a–88c, Map 88.

89. *Othonna triplinervia* DC., Prodrômus 6: 478 (1838). (Cliff-face forms in tributaries of the Gamtoos River.)

Cremnophyte growth form: Squat thickset shrublet (of medium weight, cliff squatter).

Growth form formula: E:F:As:S/H:Ca:Ev (r)

Etymology: The epithet *triplinervia* refers to the leaves, which often have three main veins on the lower surface.

DESCRIPTION AND HABITAT

Plants caulescent, evergreen, sparsely branched, forming small glabrous shrubs 240 mm in diameter. Branches decumbent to erect, up to 220 mm long, tapering to about 5–8 mm in diameter; caudex up to 70 × 50 mm, with smooth grey-brown bark and small leaf scars (cicatricose). Leaves fleshy, spreading, ascending, 24–45 × 22–35 mm, crowded at apex of branches, obovate; surface glaucous, 3-nerved, lower surface with powdery bloom; margin entire or sometimes shallowly to deeply lobed or toothed (up to 4-toothed or -lobed); apex obtuse; petiole short, 3–5 mm long. Inflorescence 110–200 mm long, a loose terminal corymb bearing up to 7 heads; peduncles 60–130 mm long. Capitulum 10 × 6 mm. Ray florets 5, ligulate, 15–24 × 7–8 mm, conspicuous, bright yellow. Seed (achene) hairy (villous), with long bristle-like pappus.

Phenology: Flowering almost throughout the year but with a peak in winter and spring (June–November). Seed (achenes) wind-dispersed.

Pollinators: Insects such as butterflies and bees.

Habitat and aspect: Sandstone cliffs and mainly on shady southern slopes. Plants rooted in crevices and on rock ledges, the long extended branches rooting where they touch the soil or a crevice. Extreme temperatures as high of 40°C have been recorded. Winters are cooler but frost is a rarity or absent owing to the sheer habitat. The average daily maximum temperature is 25°C and the average daily minimum is about 12°C. Rainfall in summer and winter but more in spring or autumn, ranging from 300–500 mm per annum.

Altitude: 400–700 m.

Associated vegetation: Mainly Gamtoos Thicket (Albany Thicket Biome) (Mucina *et al.* 2005).

Associated cremnophytes: At the Kouga Dam, *Othonna triplinervia* grows with *Adromischus cristatus* var. *zeyheri*, *Aloe perfoliata*, *A. pictifolia*, *Crassula perforata*, *Gasteria glomerata* and *Lampranthus affinis*.

Geology: Mainly quartzitic sandstone of the Table Mountain Group (Cape Supergroup).

DISTRIBUTION

Othonna triplinervia tends to be confined to the cliffs of the Gamtoos River and its tributaries (Grootrivier, Baviaanskloof and Kouga River).

RELATED SPECIES

Othonna triplinervia belongs to section *Carnosa* (about 30 species) and is one of the few evergreen and easily grown species. It is one of four *Othonna* species confined to cliffs. The others are the two summer-deciduous species *O. cremnophila* (Rosyntjieberg, Richtersveld) and *O. armiana* (Eksteenfontein, Richtersveld) and the evergreen, pendent *O. capensis* (Eastern Cape). There are two distinct elements (forms) of *O. triplinervia*, the first a tall, erect shrub, usually locally common and occurring in hilly terrain. The second is an obligate cremnophyte, a small, thick-stemmed shrublet, discussed here (see Van Jaarsveld 2006c).

ADAPTATIONS TO THE CLIFF ENVIRONMENT

Habit: The plants have a squat, compact growth and the branches can become spreading and drooping. The succulent stem conserves water, which is then available during dry periods between rainfall events.

Size and weight: Clusters small.

Leaves

Orientation: Ascending, lobed, succulent, helping to store moisture.

Colour: Glaucous green, pruinose (bluish green covered with a powdery bloom), a character enabling the plant to conserve water.

Age and persistence: Plants evergreen, but leaves withering from the base, becoming turgid after rain.

Armament: The plants are soft and fragile, without armament.

Sexual reproduction

Inflorescence and flowers: The inflorescence is large in comparison to plant size, a condition that can be viewed as rich flowering.

Fruit/Seed

Size: Achene hairy (villous), with long, bristle-like pappus.

Dispersal: Achenes dispersed by wind.

Time: Achenes ripening throughout the year, and also coinciding with the rainfall.

Vegetative reproduction: When stems come into contact with the soil or find adjacent crevices, they root and form new colonies. Detached plants landing in crevices or on ledges will root, an extensive vegetative backup strategy aiding long-term survival.

CONSERVATION STATUS

Confined to cliffs and not threatened owing to the inaccessible habitat.

ADDITIONAL NOTES

Common name: Kouga cliff-daisy.

Horticulture: Plants easily grown from stem cuttings or seed and grown as a specimen pot collection. Best for thicket gardens, grown on balconies, steep embankments, in hanging baskets, on window sills or as a pot plant, in full sun or dappled shade.

VOUCHER

Van Jaarsveld 17122 (NBG).

ILLUSTRATIONS AND MAP

Plate 89, Figures 89a–89e, Map 89.

SENECIO L.

90. *Senecio medley-woodii* Hutch. in *The Flowering Plants of South Africa* 3: t. 83 (1923).

Cremnophyte growth form: Subpendent shrublet (of medium weight to heavy, cliff squatter).

Growth form formula: E:F:As:S/H:Els (vb) (r)

Etymology: After the botanist John Medley Wood (1827–1915) of present-day KwaZulu-Natal.

DESCRIPTION AND HABITAT

Spreading, decumbent, sparsely branched shrublets up to 800 mm in diameter, covered with dense felt-like hairs, becoming glabrescent in part. Roots fibrous. Branches terete, succulent, greyish to purplish green, succulent, tapering, up to 400 mm long, at first soft, becoming firm and deciduous towards base. Leaves dorsiventrally flattened, ascending, shortly petiolate, firm, succulent, obovate to rhombic, 35–60 × 15–40 mm; surface whitish green owing to dense mat of white woolly hairs, becoming glabrescent with age, exposing the green surface; margin reddish, entire or bearing up to 5 shallow to larger triangular teeth; base cuneate; apex acute, mucronate. Inflorescence up to 14-flowered, a terminal loose corymb up to 190 mm

long; peduncle 30–90 mm long with a few smaller leaf-like bracts. Capitulum 37–50 mm in diameter, honeycombed at base, with up to 15 phyllaries. Ray florets up to 13, bright yellow. Disc florets dirty yellow. Achene linear, up to 4 mm long; pappus 9–10 mm long.

Phenology: Flowering from summer to early winter (February–July).

Pollinators: Insects.

Habitat and aspect: Vertical quartzitic sandstone or shale cliffs. Plants rooted in crevices and on rock ledges. Extreme temperatures as high of 40°C have been recorded. Winters are cooler but frost is a rarity or absent. The average daily maximum temperature is 24°C and the average daily minimum is 16°C. Rainfall mainly from spring to autumn but occasionally also in winter, ranging from 1000–1250 mm per annum.

Altitude: 460–800 m.

Associated vegetation: Mainly Eastern Valley Bushveld of the Savanna Biome (Mucina *et al.* 2005).

Associated cremnophytes: *Adromischus cristatus* var. *zeyheri*, *Aloe arborescens*, *Cotyledon orbiculata* var. *oblonga*, *Crassula perfoliata* var. *perfoliata*, *C. perforata*, *C. sarmentosa* var. *integrifolia*, *Delosperma* sp. A, *D. tradescantioides*, *Petopentia natalensis* and *Plectranthus ernstii*.

Geology: Mainly quartzitic sandstone of the Natal Group (Cape Supergroup), also on Beaufort shale (Karoo Supergroup).

DISTRIBUTION

Senecio medley-woodii is distributed from the Mzimvubu River (Port St Johns) in the south (Eastern Cape) to northern KwaZulu-Natal and just reaching Mpumalanga (cliffs adjacent to the Pongola River at Klipwal Gold Mine).

RELATED SPECIES

Senecio medley-woodii is related to *S. pyramidatus*, *S. haworthii* and *S. scaposus* occurring further to the south in the Eastern Cape. *Senecio scaposus* sometimes grows on cliffs. It differs from *S. pyramidatus* (thicket vegetation on hilly terrain) in being more flaccid and spreading.

ADAPTATIONS TO THE CLIFF ENVIRONMENT

Habit: Spreading stems rooting where they find a crevice.

Size and weight: Clusters of medium weight to heavy in larger shrubs.

Leaves

Orientation: Ascending, often pointing towards the light source (tips towards the sun, thus the least amount of direct exposure), crowded, the dense mat of wool protecting the plants from excessive sunlight and heat.

Colour and texture: Green, but with a dense woolly surface.

Age and persistence: Plants evergreen, bearing firm, long-lived leaves, older leaves withering from the base. The fleshy leaves becoming turgid after rain, but often in a semi-desiccated state during dry periods.

Armament: The soft, fragile plants are without obvious armament. The leaf margin is entire (northern populations) or distinctly dentate (Mzimvubu River).

Sexual reproduction

Inflorescence and flowers: Inflorescence a loose, terminal 14-flowered corymb. Flowers conspicuous and large in comparison to plant size (rich flowering).

Fruit/Seed

Size: Achene 4 mm long (excluding pappus), acting like a parachute.

Dispersal: Achenes dispersed by wind.

Time: Achenes ripening in summer, autumn and late winter, coinciding with summer and autumn rainfall.

Vegetative reproduction: The spreading to subpendent stems are flaccid, rooting where they find adjacent ledges or crevices below, forming new colonies. Detached plants landing in crevices or on ledges will root, an extensive vegetative backup strategy aiding long-term survival.

CONSERVATION STATUS

Localised and confined to the gorges but not threatened owing to the inaccessible habitat.

ADDITIONAL NOTES

Horticulture: *Senecio medley-woodii* has ornamental properties and is widely cultivated in South Africa. It is best for subtropical coastal gardens, grown on steep embankments, window sills or balconies. Plants easily grown from stem cuttings and make attractive pot plants (full sun or partial shade). Grow in a well-drained soil mixture.

VOUCHER

Van Jaarsveld, Xaba & Harrower 20 (NBG).

ILLUSTRATIONS AND MAP

Plate 90, Figures 90a–90c, Map 90.

91. *Senecio muirii* L.Bolus in *Annals of the Bolus Herbarium* 1: 192–193 (1915).

Cremonophyte growth form: Pendent leafy stems (of medium weight, cliff hanger).

Growth form formula: E:F:P:Els (vb) (eg)

Etymology: After John Muir (1874–1947), Scottish physician and botanical explorer who settled in South Africa.

DESCRIPTION AND HABITAT

Spreading, decumbent to pendent, leafy, succulent herb up to 1 m in diameter, rooting where stems touch the ground, all parts glabrous. Branches 5–6 mm in diameter, terete, at first softly succulent (flaccid), becoming purplish grey and slightly woody, older leaves becoming deciduous from base; branch tips often with aerial roots, rooting in crevices. Leaves obovate to oblong-obovate, dorsiventrally flattened, always vertically produced in spite of stems being pendent or spreading, succulent, bluish green, pruinose, crowded towards branch tips; lower surface with 3 prominent translucent veins; margin entire or with 1–3 pairs of shallow teeth; apex rounded to subacute, mucronate; base cuneate; petiole short, up to 2 mm long. Inflorescence a spreading to drooping, terminal, sparsely branched, lax corymb, up to 150–250 mm long. Capitulum oblong, 10 × 5 mm, with up to 8 phyllaries. Achene 3 × 0.8 mm; pappus 5–6 mm long.

Phenology: Flowering in spring, summer and autumn, often depending on rainfall.

Pollinators: Insects.

Habitat and aspect: Quartzitic sandstone and shale cliffs overlooking the Gourits River (and eastern Olifants River tributaries, and as far east as Meiringspoort). Plants rooted in crevices and on ledges. On hot days (berg wind conditions), temperatures can go up to 40°C. The average daily maximum temperature is about 23°C and average daily minimum about 11°C. Rainfall mainly in winter and summer, ranging from 300–400 mm per annum (thunder showers and cyclonic winter rain).

Altitude: 300–800 m.

Associated vegetation: Southern Cape Valley Thicket (Mucina *et al.* 2005).

Associated cremonophytes: At Badspoort near Calitzdorp, it grows with *Albuca thermarum*, *Bulbine ramosa*, *Cotyledon tomentosa* var. *tomentosa*, *Crassula atropurpurea*, *C. badspoortense*, *C. lactea* and *Tromotriche choanantha*.

Geology: Quartzitic sandstone of the Peninsula Formation and Bokkeveld shale (Cape Supergroup).

DISTRIBUTION

Confined to the mountainous region of the Gourits River and its tributaries, mainly from Calitzdorp to the Gourits Bridge along the N2.

RELATED SPECIES

Senecio muiirii is a distinct species not closely related to any other *Senecio* species. In habit it is similar to *S. pondoensis* growing on similar cliff faces in the northeastern part of the Eastern Cape. The latter has subterete leaves with a distinctive window along the groove of the upper surface.

ADAPTATIONS TO THE CLIFF ENVIRONMENT

Habit: Spreading shrublet with drooping, elongated stems, often phototropically negative and growing into crevices, rooting and forming new plants.

Size and weight: Plants of medium weight, large plants of medium weight to heavy.

Leaves

Orientation: Ascending, pointing towards the light source (tips towards the sun, thus the least amount of direct exposure), often crowded at branch ends.

Colour: Pruinose (bluish green covered with a powdery bloom).

Age and persistence: Evergreen, but leaves withering from the base, resulting in crowded leaves at the apices. Leaves becoming turgid after rain, but often in a semi-desiccated state during dry periods, then channelled. The leaves have three distinct translucent veins running along the lower leaf surface, providing avenues of light entering the inner tissues (coming into contact with chlorophyll).

Armament: The soft, fragile plants are without armament.

Sexual reproduction

Inflorescence and flowers: Inflorescence a spreading to drooping, terminal, sparsely branched, lax inconspicuous corymb.

Fruit/Seed

Size: Achene 3×0.8 mm, pappus 5–6 mm long.

Dispersal: Achenes dispersed by wind.

Time: Achenes ripening in summer and autumn, coinciding with autumn rainfall.

Vegetative reproduction: The spreading, pendent stems will root where they find adjacent ledges or crevices, forming new colonies (stem apices often with adventitious roots). Detached plants landing in crevices or on ledges will root, an extensive vegetative backup strategy aiding long-term survival.

CONSERVATION STATUS

Localised and confined to gorges but not threatened owing to its inaccessible, undisturbed habitat.

ADDITIONAL NOTES

Horticulture: Best for thicket and subtropical coastal gardens (Van Jaarsveld 2010), grown on steep embankments, window sills or balconies, also thriving in containers, in full sun or partial shade. Propagate from cuttings from spring to autumn. Outside the native habitat, it should be grown under controlled conditions in a greenhouse.

VOUCHER

Van Jaarsveld 16106 (NBG).

ILLUSTRATIONS AND MAP

Figures 91a–91e, Map 91.

92. *Senecio pondoensis* Van Jaarsv. & A.E.van Wyk in *Aloe* 45,2: 28–29 (2008a).

Cremonophyte growth form: Subpendent spreading shrublet (of medium weight, cliff squatter).

Growth form formula: E:F:As:S/H:Els (vb)

Etymology: After Pondoland in the Eastern Cape where this species occurs.

DESCRIPTION AND HABITAT

Spreading, decumbent, sparsely branched, glabrous shrublets, stoloniferous, rooting at nodes. Roots fibrous. Branches terete, succulent, up to 400 mm long, greyish to purplish green, succulent, tapering, at first soft, becoming firm and deciduous towards base. Leaves ascending, softly succulent, bluish green, pruinose, linear-fusiform, often falcate, 45–60 × 5–7 mm, subterete; older leaves paler, becoming deciduous towards base of stem; adaxial surface flat to grooved, with translucent window over length of groove, abaxial surface rounded with few faint striations; apex mucronate, purplish. Inflorescence a spreading, lax corymb, terminal, branched, purplish green, 60–80 mm long; bracts slender, linear, up to 5–11 × 0.5 mm. Capitula 4–8, campanulate, 10 × 3.5 mm, with up to 8 phyllaries; involucre bracts 1 or 2, whitish green, terete, 4 × 0.5 mm, purple-tipped. Disc florets tubular, 6–7 × 0.5 mm, with pappus of white bristles 4–5 mm long; tube greenish white in basal part, expanding and white over the distal 2 mm; corolla lobes white, 5.1 × 0.75 mm, acute. Stigma bifid, white, becoming 6.5 mm long after expanding slightly (1 mm) above capitulum. Anthers 1 × 0.5 mm; filaments 0.5 mm long. Achene 1.5 × 0.3 mm; pappus 4–5 mm long.

Phenology: Flowering in spring (October–November), but also in spring. Seeds (achenes) with non-specialist dispersal strategy; dispersed in summer and autumn.

Pollinators: Insects.

Habitat and aspect: Quartzitic south-facing sandstone cliffs and on top of ledges. Plants rooted in crevices and on rock ledges. Extreme temperatures as high of 40°C have been

recorded. Winters are cooler but frost is a rarity or absent. The average daily maximum temperature is 24°C and the average daily minimum is 16°C. Rainfall mainly from spring to autumn but occasionally also in winter, ranging from 1000–1250 mm per annum.

Altitude: 200–250 m.

Associated vegetation: Eastern Valley Bushveld (Mucina *et al.* 2005).

Associated cremnophytes: At the Mzamba River, *Senecio pondoensis* shares its habitat with *Adromischus cristatus* var. *zeyheri*, *Aloe arborescens*, *Cotyledon orbiculata* var. *oblonga*, *Crassula perfoliata* var. *perfoliata*, *C. perforata*, *C. sarmentosa* var. *integrifolia*, *Delosperma* sp. A and *Petopentia natalensis*.

Geology: Quartzitic sandstone of the Natal Group (Cape Supergroup).

DISTRIBUTION

Senecio pondoensis is known only from the Mzamba River Gorge (Eastern Cape).

RELATED SPECIES

Senecio pondoensis is related to *S. talinoides* of similar sites along dry river valleys, but differs in its soft nature, flaccid stems that are stoloniferous from the base, and in its leaves with a distinct long, narrow window on the midrib (upper surface).

ADAPTATIONS TO THE CLIFF ENVIRONMENT

Habit: Spreading shrublet with decumbent stems rooting where they find a crevice, or producing stolons from the base. The leaves are crowded towards the ends of the branches.

Size and weight: Clusters small, of light to medium weight.

Leaves

Orientation: Ascending, often pointing towards the light source (tips towards the sun, thus the least amount of direct exposure), crowded, with longitudinal window allowing light to penetrate more efficiently on the shady south-facing cliffs, maximising absorption of light.

Colour: Pruinose (bluish green covered with a powdery bloom).

Age and persistence: Evergreen, but leaves withering from the base. The fleshy leaves becoming turgid after rain, but often in a semi-desiccated state during dry periods.

Armament: The soft, fragile plants lack conspicuous armament.

Sexual reproduction

Inflorescence and flowers: Capitula inconspicuous.

Fruit/Seed

Size: 1.5 × 0.3 mm pappus 4–5 mm long.

Dispersal: Achenes are wind-dispersed.

Time: Achenes ripen in summer and autumn and coinciding with autumn rainfall.

Vegetative reproduction: The spreading to subpendent stems will root where they find adjacent ledges or crevices below, forming new colonies. Detached plants landing in crevices or on ledges will root, an extensive vegetative backup strategy aiding long-term survival. The basal stoloniferous nature also ensures continued vegetative regeneration.

CONSERVATION STATUS

Localised and confined to the gorges but not threatened owing to the inaccessible habitat.

ADDITIONAL NOTES

Horticulture: Best for subtropical coastal gardens and steep embankments, window sills or balconies, also doing well in containers, in full sun or partial shade. Propagate from cuttings from spring to autumn. Outside the native habitat, it should be grown under controlled conditions in a greenhouse.

VOUCHER

Van Jaarsveld 19297 (NBG).

ILLUSTRATIONS AND MAP

Plate 92, Figures 92a–92c, Map 92.

93. *Senecio serpens* G.D.Rowley in National Cactus and Succulent Journal 10,2: 31 (1955).

Cremonophyte growth form: Cluster-forming to drooping shrublets (of medium weight to heavy, cliff hugger).

Growth form formula: E:F:As:S/H:Els (vb)

Etymology: The epithet *serpens*, creeping, pertains to the stems.

DESCRIPTION AND HABITAT

Sprawling, decumbent to subpendent, branched, glabrous shrublets, forming loose mats, rooting at nodes, stoloniferous from base. Roots fibrous. Branches terete, succulent, up to 200 mm long; young branches flaccid, tapering, pruinose, becoming green and eventually grey green in old stems, 5–9 mm in diameter, covered in old leaf scars. Leaves variable in shape and size, dorsiventrally flattened, adaxially concave, becoming subterete when turgid, elliptic to linear-elliptic, 20–35 × 9–10 mm in exposed habitats, 35–45 × 10 mm in

protected sites, often flattened fusiform; margin entire; surface densely pruinose, both surfaces with 8–19 translucent veins, adaxial surface flat to concave or grooved, abaxial surface rounded; apex obtuse to acute, mucronate, brownish to purplish. Inflorescence an erect, terminal, branched corymb, 200–300 mm high, with few linear bracts up to 5 mm long, discoid. Capitula few, with 10–14 phyllaries 12 mm long. Disc florets 15–30, white; corolla lobes recurved. Achene hispid.

Phenology: Flowering from spring to autumn (October–May).

Pollinators: Insects.

Habitat and aspect: Vertical quartzitic sandstone cliffs (all aspects). Plants rooted in crevices and on rock ledges. Extreme temperatures as high of 40°C have been recorded. Winters are cooler but frost is a rarity or absent. The average daily maximum temperature is 22°C and the average daily minimum is 12°C. Rainfall mainly in winter and occasionally in summer, about 500–700 mm per annum.

Altitude: 300–1000 m.

Associated vegetation: Peninsula Sandstone Fynbos of the Fynbos Biome (Mucina *et al.* 2005).

Associated cremnoophytes: At Chapman’s Peak cliffs, it grows with *Adromischus hemisphaericus*, *Aloe maculata*, *Cotyledon orbiculata* var. *orbiculata*, *Crassula nudicaulis*, *C. rupestris*, *Euphorbia caput-medusae*, *Lampranthus falciformis* and *Ruschia promontorii*.

Geology: Quartzitic sandstone, Peninsula Formation (Cape Supergroup).

DISTRIBUTION

Restricted mainly to the Cape Peninsula, but with outliers from Rooiels and Hangklip to near Hermanus.

RELATED SPECIES

Related to *Senecio crassulaefolius*, a common, widespread species with much larger, erect stems and sturdier, less flaccid leaves.

ADAPTATIONS TO THE CLIFF ENVIRONMENT

Habit: Spreading to sprawling stems rooting where they find a crevice. Compact, bluish green leaves in apical clusters. The vegetative reproductive mode is a natural backup system ensuring long-term survival on the cliff face.

Size and weight: Clusters small, of light weight.

Leaves

Orientation: Ascending, often pointing towards the light source (tips towards the sun, thus the least amount of direct exposure), crowded, with longitudinal translucent veins allowing

light to penetrate more efficiently, especially on shady south-facing cliffs. Leaves becoming channelled during the dry season.

Colour: Pruinose (bluish green, covered with a powdery bloom).

Age and persistence: Evergreen, but leaves withering from the base. The fleshy leaves becoming turgid after rain, but often in a semi-desiccated state during dry periods, also channelled during dry periods, an adaptation to the extreme, dry habitat.

Armament: The soft, fragile plants are without armament.

Sexual reproduction

Inflorescence and flowers: Inflorescence inconspicuous.

Fruit/Seed

Size: Not seen.

Dispersal: Achenes are dispersed by wind.

Time: Achenes ripening in winter, coinciding with autumn rainfall.

Vegetative reproduction: The spreading, decumbent to subpendent stems will root where they find adjacent ledges or crevices, forming new colonies. Detached plants landing in crevices or on ledges will root, an extensive vegetative backup strategy aiding long-term survival.

CONSERVATION STATUS

Localised, common in the habitat and not threatened.

ADDITIONAL NOTES

Horticulture: *Senecio serpens* is an ornamental species (striking with its bluish green leaves) best for fynbos gardens, grown on steep embankments, window sills or balconies, also thriving in containers, in full sun or partial shade (Van Jaarsveld 2000b). Propagate from cuttings from spring to autumn. Outside the native habitat, it should be grown under controlled greenhouse conditions.

VOUCHER

Van Jaarsveld 19955 (NBG).

ILLUSTRATIONS AND MAP

Figures 93a–93d, Map 93.

94. *Senecio talinoides* Sch.Bip. subsp. *talinoides*, Schultz in Flora 28: 499 (1845).

Cremonophyte growth form: Decumbent shrublet (of medium weight, cliff squatter).

Growth form formula: E:F:As:S/H:Els (vb)

Etymology: The epithet *talinoides* alludes to similarity to the genus *Talinum* in the family Portulacaceae.

DESCRIPTION AND HABITAT

Spreading, decumbent, sparsely branched, glabrous shrublets, rooting at nodes. Roots fibrous. Branches terete, succulent, up to 400 mm long, greyish to purplish green, often with remnants of old petioles, tapering, at first soft, becoming firm and deciduous towards base. Leaves ascending, firm, succulent, dull bluish green, pruinose, crowded towards branch tips, linear-fusiform, often falcate, 45–80 × 5–7 mm, subterete; adaxial surface flat to slightly grooved, abaxial surface rounded, with few faint striations; apex mucronate; older leaves paler, becoming deciduous towards base of stem. Inflorescence a spreading, terminal, branched, purplish green, lax corymb, 60–80 mm long, with small bracts and 4–8 campanulate capitula. Capitulum 10 × 3.5 mm, with up to 8 phyllaries; involucre bracts 1 or 2, whitish green, terete, 2 × 0.5 mm. Stigma bifid, white, becoming extended above capitulum. Achene oblong, 4 × 0.5 mm; pappus 7 mm long.

Phenology: Spring (October–November), but also after rain.

Pollinators: Insects.

Habitat and aspect: Quartzitic south-facing sandstone cliffs. Plants rooted in crevices and on rock ledges. Extreme temperatures as high of 40°C have been recorded. Winters are cooler but frost is a rarity or absent. The average daily maximum temperature is 24°C and the average daily minimum is 16°C. Rainfall mainly from spring to autumn but occasionally also in winter, ranging from 1000–1250 mm per annum.

Altitude: 400–1800 m.

Associated vegetation: Mainly Eastern Valley Bushveld of the Savanna Biome (Mucina *et al.* 2005).

Associated cremonophytes: At the Bashee River at Collywobbles, *Senecio talinoides* grows on south-facing cliffs together with *Adromischus cristatus* var. *zeyheri*, *Aloe reynoldsii*, *Bulbine thomasiae*, *Cotyledon orbiculata* var. *flanaganii*, *Crassula perfoliata* var. *perfoliata*, *C. perforata* and *Haworthia cymbiformis* var. *setulifera*.

Geology: Quartzitic sandstone of the Natal Group (Cape Supergroup) and Beaufort shale (Karoo Supergroup).

DISTRIBUTION

Senecio talinoides occurs widespread along the cliffs of the dry river valleys of the Eastern Cape, from the Mzimvubu River in the north to East London in the south.

RELATED SPECIES

Senecio talinoides is related to *S. pondoensis* growing on similar cliff faces of the Eastern Cape. It is at once distinguished by its firmer leaves lacking the window on the adaxial surface. It is also related to the robust *S. ficoides* commonly found in thickets of the Eastern Cape growing on various formations and often also on cliff faces. The latter has much larger leaves and inflorescence.

ADAPTATIONS TO THE CLIFF ENVIRONMENT

Habit: Spreading stems rooting where they find a crevice. Compact, bluish green leaves are cluster-forming, providing some shade.

Size and weight: Clusters small to medium-sized, large specimens of medium weight to heavy.

Leaves

Orientation: Ascending, often pointing towards the light source (tips towards the sun, thus the least amount of direct exposure), crowded.

Colour: Dull green, pruinose (covered with a powdery bloom).

Age and persistence: Evergreen, but leaves withering from the base, resulting in crowded leaves at the apices. Leaves becoming turgid after rain, but often in a semi-desiccated state during dry periods and then also channelled, an adaptation to the extreme, dry habitat.

Armament: The aromatic resinous sap is a deterrent to many insect species.

Sexual reproduction

Inflorescence and flowers: Inflorescence inconspicuous.

Fruit/Seed

Size: Achene oblong, grooved, 4×0.5 mm, pappus 7 mm long.

Dispersal: Achenes dispersed by wind.

Time: Achenes ripening in summer and autumn, coinciding with autumn rainfall.

Vegetative reproduction: The spreading, decumbent to subpendent stems will root where they find adjacent ledges or crevices, forming new colonies. Detached plants landing in crevices or on ledges will root, an extensive vegetative backup strategy aiding long-term survival.

CONSERVATION STATUS

Localised and confined to steep gorges and river valleys, but not threatened owing to the inaccessible habitat.

ADDITIONAL NOTES

Horticulture: Best for thicket and subtropical coastal gardens (Van Jaarsveld 2000b), grown on steep embankments, window sills or balconies, also doing well in containers, in full sun or partial shade. Propagate from cuttings from spring to autumn. Outside its native habitat, it should be grown under controlled conditions in a greenhouse.

VOUCHERS

Van Jaarsveld 17804, 17873 (NBG).

ILLUSTRATIONS AND MAP

Figures 94a–94c, Map 94.

CACTACEAE

Rhipsalis Gaertn.

95. *R. baccifera* (J.Mill.) Stearn subsp. *mauritiana* (DC.) Barthlott

RHIPSALIS Gaertn.

95. *Rhipsalis baccifera* (J.Mill.) Stearn subsp. *mauritiana* (DC.) Barthlott in *Bradleya* 5: 100 (1987).

Cremnophyte growth form: Drooping terete stems (of medium weight, cliff hanger).

Growth form formula: E:Ex:P:St (vb) (eg)

Etymology: The epithet *baccifera*, bearing berries, pertains to the fruit.

DESCRIPTION AND HABITAT

Spreading, much branched, cluster-forming stem succulent, with drooping branches up to 600 mm long. Roots fibrous. Stems articulated, terete, soft green to reddish green, 3–6 mm in diameter, with scattered areoles with soft bristles (up to 4 mm long), especially in young plants. Flowers 1 or 2 per areole, green, small, inconspicuous, self-fertile; hypanthium bulbous, with few sepaloid segments and reduced areoles; petaloid segments oblong, 4–6, up to 3 mm long. Stamens 5–10. Ovary embedded in hypanthium; style short. Berry sessile, globose to oblong-globose, up to 10 mm in diameter. Seed oblong, irregular, 1 mm long, black to dark brown, shiny, reticulate.

Phenology: Flowering in spring and summer. Berries dispersed by frugatory birds.

Pollinators: Insects.

Habitat and aspect: Quartzitic sandstone or shale cliffs. Plants rooted in crevices and on rock ledges but also epiphytic in trees. Winters are cool but frost is a rarity or absent. The average daily maximum temperature is about 24°C and the average daily minimum about 16°C. Rainfall mainly from spring to autumn but occasionally also in winter, ranging from 1000–1250 mm per annum.

Altitude: 1000–1750 m.

Associated vegetation: Mainly KwaZulu-Natal Coastal Belt of the Indian Ocean Coastal Belt and Eastern Valley Bushveld of the Savanna Biome (Mucina *et al.* 2005).

Associated cremnophytes: At Oribi Gorge, *Rhipsalis baccifera* grows together with *Aloe arborescens*, *Crassula perforata*, *C. perfoliata* var. *perfoliata*, *Delosperma* sp. A, *D. tradescantioides*, *Gasteria croucheri*, *Petopentia natalensis*, *Plectranthus ernstii* and *Senecio medleyi-woodii*.

Geology: Mainly sandstone of the Natal Group (Cape Supergroup), also on shale.

DISTRIBUTION

Rhipsalis baccifera subsp. *mauritiana* occurs widespread in southeastern Africa and central Africa, Madagascar and most of the Indian Ocean islands.

RELATED SPECIES

Rhipsalis baccifera subsp. *mauritiana* has no relatives in South Africa, in fact it is the only member of the Cactaceae in South Africa.

ADAPTATIONS TO THE CLIFF ENVIRONMENT

Habit: Spreading, leafless stems, often with aerial roots where they find a crevice.

Size and weight: Clusters small to medium-sized, of light to medium weight.

Stems: Stems terete, pendent from a clustered growth, taking over the photosynthesis process, becoming purplish green to reddish green during stress owing to the production of anthocyanins.

Leaves

Orientation: Leaves absent.

Armament: The soft, fragile plants are without obvious armament.

Sexual reproduction

Inflorescence and flowers: Flowers 1 or 2 per areole, green, small, inconspicuous, self-fertile.

Fruit/Seed

Size: Seed 1 mm long, irregular.

Dispersal: Seed embedded in a fleshy white berry and dispersed by birds.

Time: Seeds ripening in summer and autumn, coinciding with summer and autumn rainfall.

Vegetative reproduction: The drooping to subpendent stems will root where they find adjacent ledges or crevices, forming new colonies. Detached plants landing in crevices or on ledges will root, an extensive vegetative backup strategy aiding long-term survival.

CONSERVATION STATUS

Rhipsalis baccifera subsp. *mauritiana* is localised and confined to cliffs or grows as an epiphyte on trees, but it is not threatened owing to the inaccessible habitat. In spite of its traditional medicinal use, it is still common (Smith *et al.* 1999).

ADDITIONAL NOTES

Cultural use: Smith *et al.* (1999) reported the sale of *Rhipsalis baccifera* on the medicinal plant (muti) market in Durban. It is locally known by its Zulu name *ugebeleweni*, which means ‘hanging from the cliffs’. It is mixed with other plant ingredients and used for magical purposes. Its Afrikaans name, *bostou*, means ‘rope from the forest’.

Horticulture: *Rhipsalis baccifera* is a collector’s item, best for subtropical coastal gardens. It can be grown on steep embankments, window sills or balconies, and also thrives in containers or hanging baskets, in full sun or partial shade. Propagate from cuttings from spring to autumn. Outside the native habitat, it should be grown under controlled conditions in a greenhouse.

VOUCHER

Van Jaarsveld 22399 (NBG).

ILLUSTRATIONS AND MAP

Figures 95a & 95b, Map 95.

CRASSULACEAE

Adromischus Lem.

96. *A. cristatus* (Haw.) Lem. var. *mzimvubuensis* Van Jaarsv.
97. *A. cristatus* (Haw.) Lem. var. *schonlandii* (E.Phillips) Toelken
98. *A. cristatus* (Haw.) Lem. var. *zeyheri* (Harv.) Toelken
99. *A. diabolicus* Toelken
100. *A. fallax* Toelken
101. *A. leucophyllus* Uitewaal
102. *A. liebenbergii* Hutchison subsp. *orientalis* Van Jaarsv.
103. *A. schuldtianus* (Poelln.) Poelln. subsp. *brandbergensis* B.Nord. & Van Jaarsv.
104. *A. subdistichus* Makin ex Bruyns
105. *A. umbraticola* C.A.Sm. subsp. *ramosus* Toelken

Cotyledon L.

106. *C. barbeyi* Schweinf. var. A
107. *C. eliseae* Van Jaarsv.
108. *C. pendens* Van Jaarsv.
109. *C. tomentosa* Harv. subsp. *tomentosa*

Crassula L.

110. *C. alba* Forssk. var. *pallida* Toelken
111. *C. atropurpurea* (Harv.) D.Dietr. var. *anomala* (Schönland & Baker f.) Toelken
112. *C. aurusbergensis* G.Will.
113. *C. badspoortense* Van Jaarsv.
114. *C. brachystachya* Toelken
115. *C. capitella* Thunb. subsp. *thyrsiflora* (Thunb.) Toelken (*C. turrita*)
116. *C. cremnophila* Van Jaarsv. & A.E.van Wyk
117. *C. cymbiformis* Toelken
118. *C. exilis* Harv. subsp. *cooperi* (Regel) Toelken
119. *C. exilis* Harv. subsp. *exilis*
120. *C. exilis* Harv. subsp. *sedifolia* (N.E.Br.) Toelken
121. *C. expansa* Dryand. subsp. *fragilis* (Baker) Toelken
122. *C. foveata* Van Jaarsv.
123. *C. intermedia* Schönland
124. *C. lanuginosa* Harv. var. *lanuginosa*
125. *C. montana* Thunb. subsp. *montana*
126. *C. montana* Thunb. subsp. *quadrangularis* (Schönland) Toelken
127. *C. nemorosa* (Eckl. & Zeyh.) Endl. ex Walp.
128. *C. orbicularis* L.
129. *C. peculiaris* (Toelken) Toelken & Wickens
130. *C. pellucida* L. subsp. *spongiosa* Toelken
131. *C. perforata* Thunb. subsp. *kougaensis* Van Jaarsv. & A.E.van Wyk
132. *C. perforata* Thunb. subsp. *perforata*
133. *C. pseudohemisphaerica* Friedrich
134. *C. pubescens* Thunb. subsp. *rattrayi* (Schönland & Baker f.) Toelken
135. *C. rupestris* Thunb. subsp. *marnieriana* (H.E.Huber & H.Jacobsen) Toelken
136. *C. rupestris* Thunb. subsp. *rupestris* (cliff form)
137. *C. sediflora* (Eckl. & Zeyh.) Endl. & Walp. var. *sediflora*

138. *C. sericea* Schönland var. *sericea*
139. *C. setulosa* Harv. var. *jenkinsii* Schönland
140. *C. setulosa* Harv. var. *longiciliata* Toelken
141. *C. setulosa* Harv. var. *setulosa*
142. *C. sladenii* Schönland
143. *C. smithii* Van Jaarsv., D.G.A.Styles & G.McDonald
144. *C. socialis* Schönland
145. *C. streyi* Toelken
146. *C. tabularis* Dinter
147. *C. tomentosa* Thunb. var. *glabrifolia* (Harv.) Toelken

Tylecodon Toelken

148. *T. aurusbergensis* G.Will. & Van Jaarsv.
149. *T. bleckiae* G.Will.
150. *T. bodleyae* Van Jaarsv.
151. *T. bruynsii* Van Jaarsv. & S.A.Hammer
152. *T. buchholzianus* (Schuldt & P.Stephan) Toelken var. *fasciculatus* G.Will.
153. *T. cordiformis* G.Will.
154. *T. decipiens* Toelken
155. *T. ellaphieae* Van Jaarsv.
156. *T. longipes* Van Jaarsv. & G.Will.
157. *T. petrophilus* Van Jaarsv. & A.E.van Wyk
158. *T. singularis* (R.A.Dyer) Toelken
159. *T. sulphureus* (Toelken) Toelken var. *armianus* Van Jaarsv.
160. *T. torulosus* Toelken
161. *T. viridiflorus* (Toelken) Toelken

ADROMISCHUS Lem.

96. *Adromischus cristatus* (Haw.) Lem. var. *mzimvubuensis* Van Jaarsv., in Van Jaarsveld & Van Wyk in Aloe 40,2: 40 (2003f).

Cremnophyte growth form: Cluster-forming (of light weight, cliff hugger).

Growth form formula: A:S:Lper:Lc:Ts (vb)

Etymology: After its cliff-face habitat along the Mzimvubu River.

DESCRIPTION AND HABITAT

Plants sparsely branched, almost acaulescent, up to 60 mm high (without inflorescence), 60–110 mm in diameter. Roots fibrous. Branches erect to decumbent, very short, up to 10 mm, green, usually not visible owing to reddish brown aerial roots. Leaves crowded, in lax to dense rosette up to 110 mm in diameter, lorate-obovate to broadly obovate, 40–80 × 20–30 mm, biconvex when turgid, dorsiventrally compressed, ascending, distal third or apex incurved and flat to slightly concave; apex truncate to rounded; base cuneate, decurrent on stem; surface immaculate, slightly hairy, becoming glabrescent, pale green to olive-green; margin horny, straight to undulating, continuous on to stem. Inflorescence a simple or

branched, brownish green, spike-like thyrse up to 230 mm high, bearing 2- or 3-flowered cymes; surface covered with club-shaped trichomes; bracts triangular, adpressed, 3×1 mm; buds ascending, spreading, slightly tapering; pedicels 1.0–1.5 mm long. Calyx tubular, 3.5 mm long; lobes triangular, $1.5\text{--}2.0 \times 1$ mm. Corolla tubular, 12×4 mm; tube cylindrical, grooved, pale green, dotted with maroon; lobes broadly triangular-ovate, 5×3 mm, white-pink, maroon-red at throat, cuspidate, at first spreading, becoming recurved against tube with bases of lobes fused for 1.5 mm; apex purplish mottled; throat rough owing to club-shaped trichomes. Stamens 10 mm long, shortly included, fused to lobes in basal half; anthers yellowish, 7×4 mm. Squamae translucent, rectangular, 8×8 mm; apex slightly emarginate. Carpels 8 mm long tapering into long, erect styles.

Phenology: Flowering in summer and autumn (November–January).

Pollinators: The tubular flowers are pollinated by insects.

Habitat and aspect: *Adromischus cristatus* var. *mzimvubuensis* was observed only on Ecca Shale cliffs (Karoo Supergroup), on all aspects. Temperatures vary and may reach 40°C in summer. Winters are cooler but frost is a rarity or absent. The average daily maximum temperature is about 22°C and the average daily minimum about 12°C . Rainfall occurs mainly in summer and ranges from 400–700 mm per annum.

Altitude: 460–800 m.

Associated vegetation: Eastern Valley Bushveld of the Savanna Biome (Mucina *et al.* 2005).

Associated cremnophytes: *Cotyledon orbiculata* var. *flanaganii* (easternmost record), *Crassula cultrata* (easternmost record), *C. intermedia*, *C. multicava* subsp. *floribunda*, *C. perforata*, *Cyanotis speciosus*, *Delosperma tradescantioides*, *Gasteria croucheri* (southernmost record), *Ornithogalum longibracteatum*, *Senecio medley-woodii* and *Senecio* sp.

Geology: It was observed only on sheer Ecca shale cliffs (Karoo Supergroup), on all aspects.

DISTRIBUTION

Adromischus cristatus var. *mzimvubuensis* is confined to the Mzimvubu River in the Eastern Cape. The plants vary considerably in size and leaf shape, some forms with almost obovate leaves (more exposed north- and west-facing) and undulating margins, whereas others have mostly oblong leaves without the undulations. They are locally quite common.

RELATED SPECIES

Adromischus cristatus var. *mzimvubuensis* vary considerably in size and leaf shape, some forms with almost obovate leaves (more exposed north- and west-facing sites) and undulating margins, whereas others have mostly oblong leaves without the undulations. They are locally quite common. It is distinguished from the other varieties by its acaulescent rosettes of dorsiventrally flattened leaves which are often incurved, with a continuous horny margin to the base of the petioles. It has ginger-brown aerial roots and 2- or 3-flowered cymes. All the other varieties (var. *cristatus*, var. *clavifolius*, var. *schonlandii* and var. *zeyheri*) have stems that are 20–50 mm long and leaves with distinct petioles. The horny margin in the other varieties does not extend right around the leaf, and is confined to the distal part of the leaf. In

var. *zeyheri* (its closest relative) the margin sometimes extends to about a third from the base. The latter, however, lacks aerial roots and always develops stems up to 50 mm long. In both var. *mzimvubuensis* and var. *zeyheri* the leaves are dorsiventrally flattened. Another difference is the 3-flowered cymes found on the inflorescence, compared to the usually 1-flowered (rarely 2-) cymes in the other varieties. Var. *cristatus*, var. *clavifolius* and var. *schonlandii* are all confined to the Eastern Cape region west of the Kei River. Var. *zeyheri* is confined to quartzitic sandstone cliff faces in the Kouga Mountains and appears again in Oribi Gorge in southern KwaZulu-Natal, and remains remarkably constant, taking into consideration that var. *mzimvubuensis* occurs in between these two localities.

ADAPTATIONS TO THE CLIFF ENVIRONMENT

Habit: The plants form loose, much-branched clusters with leaves crowded at the apices. Conspicuous, often sprawling from the cliff face, well adapted to its well-drained, vertical habitat.

Size and weight: Clusters small, of light weight.

Stem: Branches erect to decumbent, very short (up to 10 mm), green and usually not visible owing to reddish brown aerial roots.

Leaves

Orientation: The relatively large leaves maximising absorption of light on the shady cliffs. Leaves firm, becoming easily detached by slight disturbances.

Age and persistence: Functional for more than a year.

Armament and camouflage: Soft-leaved plant bodies without conspicuous armament or camouflage properties, adapted to the undisturbed cliff face.

Sexual reproduction

Flowers: Flowering in summer (November–January).

Fruit/Seed

Size: Seed minute and ideal for establishment in crevices.

Dispersal: Fruiting capsule dehiscent, with seeds spontaneously released and dispersed by wind.

Time: Autumn, coinciding with autumn rain and thus maximising establishment.

Vegetative reproduction: Like other *Adromischus* species, this plant proliferates from leaves that have become detached, a vegetative reproductive backup system ensuring long-term survival.

CONSERVATION STATUS

Classified as rare (Raimondo *et al.* 2009). Locally common and well protected in the cliff habitat.

ADDITIONAL NOTES

Horticulture: *Adromischus cristatus* var. *mzimvubuensis* is most suitable for thicket and subtropical coastal gardens, best grown in partial shade in containers. The soil should be sandy and well drained. Keep dry during the winter months. Easily cultivated and propagated from leaf cuttings.

VOUCHER

Van Jaarsveld, Xaba & Harrower 101 (NBG).

ILLUSTRATIONS AND MAP

Figures 96a–96d, Map 96.

97. *Adromischus cristatus* (Haw.) Lem. var. *schonlandii* (E.Phillips) Toelken in *Bothalia* 12: 390 (1978).

Cremnophyte growth form: Small, cluster-forming (of light weight, cliff hugger).

Growth form formula: A:S:Lper:Lc:Ts (vb)

Etymology: In honour of Selmar Schönland (1860–1940), German botanist who worked in South Africa.

DESCRIPTION AND HABITAT

Small, compact, little-branched (2–5-branched) succulents, up to 60 mm in diameter. Stems up to 30 mm long, succulent, densely covered with aerial roots, 5–70 mm in diameter. Leaves densely crowded, narrowly obtriangular to club-shaped, 15–30 × 10–15 mm; surface green to yellowish green, glandular hairy; margin acute, undulating, horny, purplish brown; apex obtuse, rounded or sometimes truncate; base cuneate; petiole terete, decurrent on blade. Inflorescence a spike-like thyrses, 120–170 mm high, bearing 1-flowered cymes; pedicel 1 mm long; buds spreading, terete, tapering, purplish tipped. Calyx 2–3 mm long. Corolla 11–13 mm long; tube green, up to 3 mm in diameter when fully opened; lobes ovate-triangular, up to 4 mm, white to pinkish, with club-shaped trichomes in throat; apices acute. Anthers included.

Phenology: Flowering in summer and autumn (January–May).

Pollinators: The tubular flowers are pollinated by insects.

Habitat and aspect: Shady quartzitic sandstone cliff faces in deep kloofs and river gorges, on all aspects but more common on the southern faces. Temperatures vary and may reach 40°C in summer. Winters are cooler but frost is a rarity or absent. The average daily maximum temperature is about 22°C and the average daily minimum 11°C. Rainfall occurs mainly in summer but also in winter, ranging from 300–400 mm per annum.

Altitude: 100–1500 m.

Associated vegetation: Gamtoos Thicket of the Albany Thicket Biome (Mucina *et al.* 2005).

Associated cremnophytes: Plants in the Baviaanskloof grow together with *Adromischus cristatus* var. *zeyheri*, *Aloe pictifolia*, *Bulbine natalensis*, *Crassula rupestris* and *Cyrтанthus montanus*.

Geology: Quartzitic sandstone of the Peninsula Formation and Natal Group (Cape Supergroup).

DISTRIBUTION

Adromischus cristatus var. *schonlandii* is known only from the tributaries of the Gamtoos River (Baviaanskloof, Kouga River and Grootrivier) near Patensie in the east (Eastern Cape).

RELATED SPECIES

Distinguished from the other varieties by its almost obtriangular, club-shaped, very brittle leaves and herb-like aroma.

ADAPTATIONS TO THE CLIFF ENVIRONMENT

Habit: Plants form small globose clusters (leaves crowded at the apex).

Size and weight: Clusters of light weight.

Stem: Succulent and up to 7 mm in diameter, covered with the dense aerial roots.

Leaves

Orientation: Narrow, obtriangular to club-shaped leaves maximising water storage in the well-drained cliff environment. In older specimens the blade is sometimes almost terete and sticky.

Age and persistence: Functional for more than a year.

Armament and camouflage: Soft-leaved plant bodies without conspicuous armament or camouflage properties, adapted to the undisturbed cliff face. The herb-like smell perhaps a chemical defence against phytophagous insects.

Sexual reproduction

Flowers: Flowering from summer to autumn (November–May), but sporadically at other times.

Fruit/Seed

Size: Seed minute and ideal for establishment in crevices.

Dispersal: Fruiting capsule dehiscent, with seeds spontaneously released and dispersed by wind.

Time: Autumn and winter, coinciding with the cooler rainy season and thus maximising establishment.

Vegetative reproduction: The leaves become detached very easily and will root, proliferate and establish new colonies if they fall into a new crevice, an efficient vegetative backup or adaptation to the xeric cliff-face environment.

CONSERVATION STATUS

Classified as rare (Raimondo *et al.* 2009). Locally common and well protected in the cliff habitat.

ADDITIONAL NOTES

Variability: Local variation within a short range (fragility, shape and size of leaves) shows genetic plasticity and adaptability to the cliff face.

Horticulture: Easily cultivated from leaf cuttings or division; its vigour can be viewed as maximising survival. Does well in containers, in partial shade. Best for thicket gardens. Grow where frost is not severe.

VOUCHERS

Van Jaarsveld 15348, 17102 (NBG).

ILLUSTRATIONS AND MAP

Plate 97, Figures 97a–97d, Map 97.

98. *Adromischus cristatus* (Haw.) Lem. var. *zeyheri* (Harv.) Toelken in *Bothalia* 12: 390 (1978).

Cremonophyte growth form: Small, subpendent, cluster-forming (of light to medium weight, cliff hugger).

Growth form formula: E:F:P:Els (vb)

Etymology: In honour of Karl Zeyher (1799–1858), well known German botanical explorer in South Africa.

DESCRIPTION AND HABITAT

Small, compact to lax, little-branched, succulent shrublets. Stems succulent, green, 5–10 mm in diameter, sometimes drooping from cliff faces. Roots fibrous; aerial roots absent or rarely produced. Leaves variable in size and shape, broadly obtriangular, dorsiventrally flattened, 20–60 × 15–45 mm; surface green to yellowish green, glandular hairy; margin acute, undulating, horny, green to purplish brown; apex obtuse, rounded or truncate; base cuneate; petiole terete, decurrent on blade. Inflorescence a spike-like thyrses 140–380 mm high, bearing 1-flowered cymes; pedicel 1 mm long; buds spreading, terete, tapering, purplish tipped. Calyx

2–3 mm long. Corolla 10–12 mm long; tube green, up to 8 mm in diameter when fully opened; lobes ovate-triangular, up to 4 mm, white to pinkish, with club-shaped trichomes in throat; apices acute. Anthers included.

Phenology: Flowering in summer and autumn (January–May).

Pollinators: The tubular flowers are pollinated by insects.

Habitat and aspect: Quartzitic sandstone cliff faces, in deep, sheltered, shady kloofs and river gorges, on all aspects but more on the south-facing ones. Temperatures vary and may reach 40°C in summer. Winters are cooler but frost is a rarity or absent. Average daily maximum temperature is 20–23°C and average daily minimum 10–14°C. Rainfall occurs mainly in summer, but in the southern parts in winter as well, ranging from 300–700 mm per annum.

Altitude: 50–800 m.

Associated vegetation: Mainly Gamtoos Thicket and KwaZulu-Natal Coastal Belt of the Indian Ocean Coastal Belt (Mucina *et al.* 2005).

Associated cremnophytes: On south-facing cliffs at Oribi Gorge, plants of *Adromischus cristatus* var. *zeyheri* grow in association with *Aloe arborescens*, *Bulbine natalensis*, *Delosperma ecklonis*, *Gasteria croucheri* and *Plectranthus ernstii*.

Geology: Quartzitic sandstone of the Peninsula Formation and Natal Group (Cape Supergroup).

DISTRIBUTION

Adromischus cristatus var. *zeyheri* has a disjunct distribution. Known from the tributaries of the Gamtoos River (Baviaanskloof, Kouga River and Grootrivier) near Patensie in the east (Eastern Cape) and then again from Oribi Gorge and Umtamvuna River Valley (KwaZulu-Natal) and the adjacent Mzamba River (Eastern Cape).

RELATED SPECIES

Differs from var. *cristatus* by its longer, green, hairless branches up to 100 mm long (little or unbranched) and leaves of which the upper margin is broad and undulating. Distinguished from the ordinary level-ground forms of *Adromischus cristatus* by its longer stems, which are less compact, and by a lack of the conspicuous aerial roots of the latter. The var. *zeyheri* has larger, broader, flattened leaves that are not brittle when handled.

ADAPTATIONS TO THE CLIFF ENVIRONMENT

Habit: Plants form loose, little-branched subpendent clusters with leaves crowded at the apices. Stems becoming subpendent to pendent, up to 200 mm long, an adaptation to its xeric but shady conditions.

Size and weight: Clusters of small to medium weight.

Stem: Succulent, green, and up to 10 mm in diameter, not covered with the dense aerial roots as in level-ground species, a character that can be related to its shady, south-facing habitat and

optimising absorption of light through the branches. The longer stems (and sometimes subpendulous nature) can be viewed as adaptation to the cliff environment.

Leaves

Orientation: The relatively large, dorsiventrally flattened leaves maximising absorption of light on the shady cliffs. The leaves are firm, not becoming detached by slight disturbances like those of related level-ground species (detached leaves rooting and proliferating, forming new plants).

Age and persistence: Functional for more than a year.

Armament and camouflage: Soft-leaved plant bodies without conspicuous armament or camouflage properties, adapted to the undisturbed cliff face.

Sexual reproduction

Flowers: Flowering from summer to autumn (November–May) but sporadically at other times.

Fruit/Seed

Size: Seed minute and ideal for establishment in crevices.

Dispersal: Fruiting capsules dehiscent, with seeds spontaneously released and dispersed by wind.

Time: Autumn and winter, coinciding with the cooler rainy season and thus maximising establishment.

Vegetative reproduction: Detached leaves and pendent stems finding new crevices will root spontaneously, an efficient backup strategy for survival in this xeric cliff-face environment.

CONSERVATION STATUS

Locally common and well protected in the cliff habitat.

ADDITIONAL NOTES

Horticulture: Easily cultivated and best suited to containers in thicket gardens. Outside its native habitat, it should be grown under controlled conditions in a green house. It is best grown in dappled shade, in a sandy, slightly acid mixture. Its vigour can be viewed as maximising survival. Easily grown from leaf or stem cuttings.

VOUCHERS

Van Jaarsveld 11295, 15990, 16054, 16656 (NBG).

ILLUSTRATIONS AND MAP

Figures 98a–98c, Map 98.

99. *Adromischus diabolicus* Toelken in Bothalia 12: 633 (1979).

Cremonophyte growth form: Small, mat-forming (of light to medium weight, cliff hugger).

Growth form formula: A:S:Lper:Lc:Ts (vb)

Etymology: The epithet *diabolicus* perhaps pertaining to the hot, dry habitat where the plant grows on life-threatening, sheer cliff face.

DESCRIPTION AND HABITAT

Dwarf-sized, densely branched, compact plant, up to 50 mm high, 80 mm in diameter, from tuberous rootstock. Branches green at first, becoming grey, up to 3 mm in diameter. Leaves 15–20 × 7–17 mm, brittle, obovate to broadly obovate or rarely orbicular, grey-green to green, immaculate, biconvex, or flat on adaxial surface during drought; margin horny in distal part; apex obtuse, rounded to truncate; base cuneate. Inflorescence a spike-like monochasium up to 150 mm long, bearing 1–3 flowers; pedicel(s) 5–10 mm long. Calyx up to 3.5 mm long. Corolla 12.5–14.0 mm long; tube funnel-shaped, yellowish green; lobes ovate-triangular, 2.5–3.5 mm long, with club-shaped trichomes in throat; apices acute. Anthers included.

Phenology: Flowering in midsummer (November–December).

Pollinators: The tubular flowers are pollinated by insects.

Habitat and aspect: Shady quartz cliff faces on southern aspects of mountains. Temperatures vary and may reach 45°C in summer. Winters are cooler but frost is absent. The average daily maximum temperature is 26–28°C and the average daily minimum 13–15°C. Rainfall occurs mainly in spring, autumn and winter (cyclonic cold fronts and thunder showers in late summer and autumn), ranging from 50–100 mm per annum.

Altitude: 300–800 m.

Associated vegetation: Eastern Gariiep Rocky Desert of the Desert Biome (Mucina *et al.* 2005).

Associated cremonophytes: Plants on south-facing cliffs at Pellaberg grow in association with *Adromischus trigynus*, *Aloe dabenorisana*, *Conophytum fulleri*, *Crassula exilis* subsp. *exilis*, *C. garibina* and *Tylecodon sulphureus* var. *armianus*.

Geology: Metaquartzitic gneiss of the Hom Formation (Bushmanland Group).

DISTRIBUTION

Northern Bushmanland, Pellaberg, Dabenorisberg, Blesberg Mine in eastern Richtersveld.

RELATED SPECIES

Closely related to *Adromischus nanus*, but differs in its dense mat-forming habit. This vigorous vegetative output that fills crevices is probably an adaptation to the cliff environment, maximising on its long-term survival. Most species of non-cliff habitats have mottled leaves.

ADAPTATIONS TO THE CLIFF ENVIRONMENT

Habit: The plants are slow-growing, forming tight, dense, much-branched mats with leaves crowded at the apices. The plants are conspicuous on the cliff face, often filling an entire crevice. There is a reduction in size (compared to level-ground species), which can be viewed as an adaptation to the well-drained, vertical, small crevice habitat.

Size and weight: Clusters small, of light to medium weight.

Stem: Succulent, grey, up to 10 mm in diameter, forming dense mats, rooting at the nodes, thus ensuring a successful vegetative strategy and reducing competition from other cliff dwellers.

Leaves

Orientation: Texture firm, leaves not becoming detached by slight disturbances like those of related level-ground species, not readily forming plantlets when they do become detached like those of so many other *Adromischus* species. This reduction in vegetative output can be viewed as a different mechanism of vegetative increase and as an adaptation to the undisturbed cliff face.

Colour: Light green.

Age and persistence: Perennial, thus functional for more than a year.

Armament and camouflage: Soft-leaved plant bodies without conspicuous armament or camouflage properties, adapted to the undisturbed cliff face. Mottled leaves prominent on most of the level-ground species.

Sexual reproduction

Flowers: Flowering from summer to autumn (November–December).

Fruit/Seed

Size: Seed minute and ideal for establishment in crevices.

Dispersal: Fruiting capsules dehiscent, with seeds spontaneously released and dispersed by the wind.

Time: Summer and autumn, in time for autumn rains and thus maximising establishment.

Vegetative reproduction: Forming dense vegetative mats, rooting at the nodes. This ensures long-term survival on the cliff (vegetative backup) and also excludes competition from other succulent plants.

CONSERVATION STATUS

Rare (Raimondo *et al.* 2009), but well protected in the cliff habitat.

ADDITIONAL NOTES

Horticulture: Easily cultivated, its vigour viewed as maximising survival. Best for dry desert gardens, grown in small containers and on rockeries. Grow in sandy soil, in dappled shade. Easily propagated from cuttings or dividing mats. Very slow-growing (compared to species in fertile soil such as another cremnophyte, *Adromischus fallax* from shale soils), a strategy adapting to the low nutritional value of the quartzitic cliff habitat and the very xeric conditions.

VOUCHER

Van Jaarsveld 19155 (NBG).

ILLUSTRATIONS AND MAP

Figures 99a–99c, Map 99.

100. *Adromischus fallax* Toelken in *Bothalia* 12: 387 (1978).

Creemnophyte growth form: Mat-forming (of light to medium weight, cliff hugger).

Growth form formula: E:F:As:S/H:Es (vb)

Etymology: Latin *fallax*, deceptive, perhaps pertaining to its status.

DESCRIPTION AND HABITAT

Plants low, forming loose clusters or mats. Roots fibrous. Branches decumbent, flaccid, up to 200 mm long, 4–8 mm in diameter, sometimes drooping. Leaves sometimes arranged in a apical rosette, 20–50 × 8–20 mm, oblanceolate to elliptic, spreading, soft, grey-green, immaculate; adaxial surface concave; abaxial surface convex; apex obtuse to acute; base cuneate. Inflorescence a thyrse, 100–300 mm high, bearing 1–5 flowers; pedicel(s) 5–15 mm long. Calyx up to 4–5 mm long. Corolla 10–13 mm long; tube funnel-shaped; lobes triangular-ovate, up to 3.0–4.5 mm long, pink, with club-shaped trichomes in throat; apices acute. Anthers included.

Phenology: Flowering in midsummer (January–February).

Pollinators: The tubular flowers are pollinated by insects.

Habitat and aspect: South-facing cliffs more than a 1000 m above sea level. Plants firmly rooted in crevices, and size often depends on the growing space allowed by the crevice. The average daily maximum temperature is about 23°C and the average daily minimum about 8°C. Temperature high in summer (30°C). Winters are cooler but with occasional frost or snow. Rainfall occurs mainly in summer (also occasional cold fronts in winter), with a peak in spring and autumn, ranging from 300–400 mm per annum (thunder showers or cyclonic winter rain).

Altitude: 800–1500 m.

Associated vegetation: Camdeboo Escarpment Thicket of the Albany Thicket Biome (Mucina *et al.* 2005).

Associated cremnophytes: On the Tandjiesberg near Graaff-Reinet, the following species have been recorded: *Cotyledon orbiculata* var. *orbiculata*, *Crassula exilis* subsp. *cooperi*, *C. lanceolata* subsp. *lanceolata*, *C. nemorosa*, *C. perforata*, *Delosperma* spp., *Drimia uniflora* and *Haemanthus humilis* subsp. *hirsutus*.

Geology: Beaufort shales (Adelaide Subgroup, Karoo Supergroup).

DISTRIBUTION

Confined to the southern great escarpment margin from Graaff-Reinet to Beaufort West in the west.

RELATED SPECIES

Distinguished from non-cremnophilous *Adromischus* species by its leaves, which are persistent. *Adromischus fallax* does not readily root from cuttings like most other level-ground *Adromischus* species. The leaves are a uniform grey-green and not mottled as found in many level-ground species. The section *Brevipedunculata* consists of six species of which most are associated with steep slopes and cliffs. Plants in this section generally occur under somewhat shady conditions and have softer leaves that do not have the horny margin and do not proliferate readily when detached. *Adromischus caryophyllaceus* is the only member of section *Brevipedunculata* that occurs on level ground and has mottled leaves.

ADAPTATIONS TO THE CLIFF ENVIRONMENT

Habit: Plants relatively fast growing and forming loose clusters with leaves crowded at the apices. Branches rooting where they touch ground. The plants are conspicuous on the cliff face, often filling an entire crevice.

Size and weight: Clusters small, of light to medium weight.

Stem: Succulent, grey-green, up to 10 mm in diameter and 200 mm long, sometimes drooping from the cliff face. The long stems can be viewed as an adaptation to its undisturbed cliff-face habitat.

Leaves

Orientation: Leaves are larger and more flattened compared to those of non-cremnophilous *Adromischus* species, maximising absorption of light on the shady cliffs. Detached leaves furthermore do not readily proliferate to form plantlets as in the other *Adromischus* species. This difference in vegetative output can be viewed as an alternative mechanism of vegetative increase and as an adaptation to the undisturbed cliff face.

Colour: Grey green, immaculate.

Age and persistence: Functional for more than a year.

Armament and camouflage: Soft, flaccid plant bodies without conspicuous armament or camouflage properties, adapted to the undisturbed cliff face.

Sexual reproduction

Flowers: Tubular, with pink lobes, pollinated by insects. Flowering from summer to autumn (December–February).

Fruit/Seed

Size: Minute and ideal for establishment in crevices.

Dispersal: Fruiting capsules dehiscent, with seeds spontaneously released and dispersed by wind.

Time: Summer and autumn, in time for autumn rains and thus maximising establishment.

Vegetative reproduction: Plants increase by vegetative growth and stems will root when they touch the ground or become detached and fall on a ledge or in a crevice.

CONSERVATION STATUS

Classified as rare (Raimondo *et al.* 2009). Locally common and well protected in the cliff habitat.

ADDITIONAL NOTES

Horticulture: Best for dry karoo and thicket gardens. It is easily cultivated, its vigour viewed as maximising survival. Easily propagated by cuttings or division and grown in sandy soil. Thrives in containers, in partial shade. Keep dry in winter.

VOUCHER

Van Jaarsveld 16690 (NBG).

ILLUSTRATIONS AND MAP

Plate 100, Figures 100a–100c, Map 100.

101. *Adromischus leucophyllus* Uitewaal in National Cactus and Succulent Journal 9: 58 (1954).

Cremonophyte growth form: Small mats and drooping clusters (of light to medium weight, cliff hugger).

Growth form formula: E:F:P:Els (vb)

Etymology: Greek *leukos*, white, and *phyllon* leaf, alluding to the pale-coloured (pruinose) leaves.

DESCRIPTION AND HABITAT

Dwarf-sized, sparsely branched, spreading, succulent herb, up to 55 × 130 mm. Roots fibrous, often stilted. Stems 2–6 mm in diameter, succulent, at first grey-green with powdery bloom, becoming brownish, up to 6 mm in diameter at base. Leaves 10–30 × 8–25 mm, dorsiventrally compressed, obovate to suborbicular, very brittle, grey to whitish green, with powdery bloom, occasionally with few purplish spots, usually immaculate, young leaves green, shiny; margin horny, acute, decurrent on petiole; adaxial surface flat to convex; abaxial surface convex; apex rounded, mucronate; base cuneate. Inflorescence an erect spike-like thyse up to 150 mm high, bearing 1–4-flowered cymes; buds ascending, terete, tapering. Calyx 2.0–2.5 mm long. Corolla cylindrical, 11–13 × 3 mm, slightly widening to throat; lobes triangular-lanceolate, white with pink median stripes, with club-shaped trichomes at throat. Anthers not protruding.

Phenology: Flowering in midsummer (January–February).

Pollinators: The tubular flowers are pollinated by insects.

Habitat and aspect: Quartzitic sandstone cliffs of kloofs and mountain slopes. *Adromischus leucophyllus* grows on all aspects but more on southern ones. In summer the temperature may reach 40°C. Winters are cooler but frost is absent. The average daily maximum temperature is about 25°C and the average daily minimum about 10°C. Rainfall in summer and winter, ranging from 300–400 mm per annum.

Altitude: 500–1000 m.

Associated vegetation: Mosaic of South Sonderend Sandstone Fynbos and Robertson Karoo (Mucina *et al.* 2005).

Associated cremnophytes: At Waterkloof, near De Doorns, it has been recorded in association with the following cliff dwellers: *Adromischus filicaulis* subsp. *marlothii*, *Aloe perfoliata*, *Crassula badspoortense*, *C. muscosa* var. *muscosa*, *C. perforata*, *Haemanthus coccineus*, *Nerine ridleyi* and *Senecio crassulaefolius*.

Geology: Mainly quartzitic sandstone of the Table Mountain Group (Cape Supergroup).

DISTRIBUTION

Adromischus leucophyllus is confined to the western Little Karoo, from De Doorns (Worcester) in the west to near Ladismith in the east.

RELATED SPECIES

Adromischus leucophyllus is related to *A. subdistichus*, another cremnophyte from the eastern Little Karoo and western extreme of the Baviaanskloof, but without the pale white leaves. *Adromischus leucophyllus* varies considerably in size, with a dwarf-sized form on the Warmwaterberg (near Barrydale). At Waterkloof near De Doorns, plants are robust and larger than average.

ADAPTATIONS TO THE CLIFF ENVIRONMENT

Habit: Plants form loose, sparsely branched clusters, often becoming drooping and well-adapted to its well-drained, vertical habitat.

Size and weight: Clusters small, of light to medium weight.

Stem: Branches spreading to decumbent, up to 200 mm long.

Leaves

Orientation: The pale, orbicular leaves covered in a powdery waxy bloom, protecting the plants from excessive sunlight and preventing too much transpiration in the xeric cliff-face environment. Leaves brittle, easily becoming detached by slight disturbances.

Colour: Whitish green, covered with a powdery bloom, well-adapted to the dry cliff habitat.

Age and persistence: Functional for more than a year.

Armament and camouflage: Plants with brittle leaves without armament or camouflage properties, adapted to the undisturbed cliff face.

Sexual reproduction

Flowers: Flowering in summer (November–January).

Fruit/Seed

Size: Seed minute and ideal for establishment in crevices.

Dispersal: Fruiting capsules dehiscent, with seeds spontaneously released and dispersed by wind.

Time: Autumn, coinciding with autumn rain and thus maximising establishment.

Vegetative reproduction. *Adromischus* species generally regenerate rapidly from detached leaves and the same is true for *A. leucophyllus*. This behaviour is an effective vegetative reproductive backup system ensuring long-term survival.

CONSERVATION STATUS

Locally common and well protected in the cliff habitat.

ADDITIONAL NOTES

Horticulture: *Adromischus leucophyllus* with its pale, white leaves is an ornamental species, popular in cultivation and most suitable for rockeries and containers in succulent karoo

gardens. It is easily cultivated and propagated by leaves, this vigour viewed as maximising survival. Grow in sandy soil, in partial shade.

VOUCHERS

Van Jaarsveld 17429, 19556, 19634 (NBG).

ILLUSTRATIONS AND MAP

Plate 101, Figures 101a–101d, Map 101.

102. *Adromischus liebenbergii* Hutchison subsp. *orientalis* Van Jaarsv., in Van Jaarsveld & Van Wyk in Aloe 40,2: 39–40 (2003f).

Cremonophyte growth form: Small, cluster-forming (of medium weight, cliff hugger).

Growth form formula: E:F:S/H:As:Es (vb)

Etymology: The epithet *orientalis*, eastern, pertains to its distribution towards the east.

DESCRIPTION AND HABITAT

Small, sparsely branched shrublets, up to 200 mm high, about 120 mm in diameter. Roots fibrous. Branches erect to decumbent, 170 mm long, grey to grey-green, up to 20 mm in diameter. Leaves obtriangular to narrowly obtriangular, 40–55 × 30–40 mm, dorsiventrally compressed, ascending, biconvex when turgid; apex truncate to rounded; base cuneate, with indistinct, short, subterete petiole; surface waxy, flaking, dull green to grey-green, immaculate; margin entire, horny at truncate apex, without a mucro. Inflorescence a green, spike-like thyrse, up to 200 mm high, bearing 1-flowered cymes, with suppressed buds; bracts triangular, adpressed, 2 × 1.3 mm; pedicel 1.5 × 1 mm; buds ascending-spreading to spreading, slightly tapering. Calyx tubular, 3.5 mm long; lobes triangular, 1 × 1 mm. Corolla 10–11 × 2.5–2.8 mm, tubular; tube cylindrical, not grooved, pale green; lobes white, broadly triangular, up to 2 mm long, cuspidate, reflexed against tube; apex purplish mottled; margin undulate, frilled; throat rough, pale green, not grooved. Stamens 10 mm long, shortly exerted, fused to lobes in basal half; anthers yellowish, 7 × 4 mm. Squamae translucent, rectangular, 8 × 8 mm; apex slightly emarginate. Carpels 8 mm long, tapering into erect styles.

Phenology: Flowering in summer (November–January).

Pollinators: The tubular flowers are pollinated by insects.

Habitat and aspect: *Adromischus liebenbergii* subsp. *orientalis* occurs on north-facing, exposed cliff faces of the lower Mbashe River in the Eastern Cape. Winters are cool but frost is absent. The average daily maximum temperature is about 22°C and the average minimum temperature about 14°C. Rainfall occurs mainly in spring and summer and ranges from 600–1000 mm per annum.

Altitude: 300–800 m.

Associated vegetation: Eastern Valley Bushveld (Sub-Escarpment Savanna Bioregion) of the Savanna Biome (Mucina *et al.* 2005).

Associated cremnophytes: At the Mbashe River near Ludonga, it has been observed rooted firmly in rock crevices and on ledges, sharing its habitat with other drought-adapted cliff dwellers such as *Aloe reynoldsii*, *Crassula lactea*, *C. perfoliata* var. *minor*, *C. perforata*, *Kalanchoe rotundifolia*, *Ornithogalum longibracteatum*, *Plectranthus madagascariensis* and *Portulacaria afra*. Larger non-succulent plants in its habitat include *Commiphora harveyi* and *Ficus ingens*.

Geology: Ecca shale cliffs (Cape Supergroup).

DISTRIBUTION

Known only from the Kei and Mbashe Rivers in the Eastern Cape, growing on sheer cliff faces. They are locally abundant.

RELATED SPECIES

Adromischus liebenbergii subsp. *orientalis* is at once distinguished from the typical subspecies by its much larger, robust stature, larger obtriangular leaves of 40–55 × 30–40 mm without distinct petioles and lacking a mucro at the leaf apex. The truncate to rounded apices are not flattened towards the leaf tips. Subsp. *liebenbergii* differs in its rhombic-spathulate leaves, 12–25 × 12–20 mm, which are distinctly flattened towards the apex, with a distinct petiole up to 10 mm long and a mucro at the apex. In subsp. *orientalis* the petiole is short and indistinct. In both taxa the leaf surface is grey-green, lacking spots. Subsp. *liebenbergii* occurs in the southern Great Karoo in the Whitehill and Laingsburg region. It occurs in a mosaic of Succulent Karoo and Nama-Karoo on exposed rocky ridges and outcrops.

ADAPTATIONS TO THE CLIFF ENVIRONMENT

Habit: Small, stout clusters.

Size and weight: Clusters of medium weight.

Stem: Branches erect to decumbent, 170 mm long, grey to grey-green, up to 20 mm in diameter.

Leaves

Orientation: Ascending, obtriangular to narrowly obtriangular.

Colour: Dull green to grey green, without spots.

Age and persistence: Functional for more than a year.

Armament and camouflage: Soft-leaved plant bodies without conspicuous armament or camouflage properties, adapted to the undisturbed cliff face.

Sexual reproduction

Flowers: Flowers tubular, with pink lobes, pollinated by insects. Flowering in summer (November).

Fruit/Seed

Size: Seed minute and ideal for establishment in crevices.

Dispersal: Fruiting capsules dehiscent, with seeds spontaneously released and dispersed by wind.

Time: Summer, in time for the autumn rains and thus maximising establishment.

Vegetative reproduction: Leaves rooting when they become detached.

CONSERVATION STATUS

Classified as rare (Raimondo *et al.* 2009). Locally common, well protected and not threatened owing to the undisturbed cliff habitat.

ADDITIONAL NOTES

Horticulture: Best for bushveld and thicket gardens. Plants do well in cultivation and are easily grown from leaf cuttings. They thrive in containers. Water sparingly throughout the year.

VOUCHER

Van Jaarsveld 16908 (NBG).

ILLUSTRATIONS AND MAP

Figure 102a, Map 102.

103. *Adromischus schuldianus* (Poelln.) Poelln. subsp. *brandbergensis* B.Nord. & Van Jaarsv., in Van Jaarsveld *et al.* in *Bothalia* 34,1: 35–38 (2004b).

Cremonophyte growth form: Small, cluster-forming (of light weight, cliff hugger).

Growth form formula: A:S:Lper:Lc (vb)

Etymology: After its habitat on the Brandberg in central Namibia.

DESCRIPTION AND HABITAT

Dwarf-sized, mat-forming, branched succulent, up to 70 mm high, filling crevices in granite rock fissures. Roots fibrous. Branches short, succulent, in cultivation up to 70 × 10 mm. Leaves alternate, spreading, subfusiform-ellipsoid to semiterete, 20–70 × 10–15 mm, without distinct margin, flattened to shallowly concave above, tapering to base and to acute-obtuse, often

somewhat recurved tip, dark green, marbled with white or dull red areas. Peduncle 150–500 mm long (in cultivation), 1.2–1.5 mm thick, simple or branching above middle, terete, glabrous, greenish brown or reddish, with 2–15 almost patent flowers in a one-sided raceme; bracts 1.5 mm long, acute, succulent; bracteoles 2, basal, subulate, 1 mm long, acute; pedicels 5–17 mm long, somewhat thickened towards apex. Calyx lobes narrowly triangular, 1.8–2.0 mm long, 0.6–1 mm wide, acute. Corolla 12–15 mm long, pinkish white or wax-coloured; tube cylindrical, 2.5–3.0 mm wide; lobes patent, deltoid, acute, with somewhat wavy margins; throat bright purple inside. Squamae oblong, bifid, 1 mm long, 0.8 mm wide, white. Filaments white or pinkish; 5 longer ones adnate for 5 mm, 12 mm long; 5 shorter ones adnate for 3 mm, 10 mm long; anthers 0.4 mm long. Styles subulate-filiform, 5–8 mm long, apically white, basally light green.

Phenology: Flowering in early summer (November).

Pollinators: The tubular flowers are pollinated by insects.

Habitat and aspect: Granite cliffs and steep south- and east-facing slopes of the Brandberg. It is nowhere common, but occurs scattered in protected fissures and crevices in small to dense groups owing to vegetative proliferation. The Brandberg is an isolated granite inselberg of about 21 × 25 km in diameter and Königstein (2573 m) represents the highest peak in Namibia. It is surrounded by the Namib Desert, with typical species such as *Welwitschia mirabilis*, annual herbs and grasses, and foothills with woody species including *Acacia montis-usti*, *Adenolobus garipensis*, *Commiphora saxicola*, *C. virgata*, *C. wildii* and *Moringa ovalifolia*. Rainfall in the habitat is about 200–400 mm per annum (on the foothills less than 100 mm).

Altitude: 500–2200 m.

Associated vegetation: Mosaic of Arid Savanna and Desert.

Associated cremnophytes: Associated plants in the same habitat include *Aloe dichotoma*, *A. hereroensis*, *A. littoralis*, *Cyphostemma currorii* and *Kalanchoe lanceolata*, also *Diospyros acocksii*, *Euphorbia mauritanica*, *Ficus ilicina*, *Obetia carruthersiana*, *Salvia garipensis* and *Tetradenia riparia*.

Geology: Granite.

DISTRIBUTION

Known only from the Brandberg massif in northern central Namibia.

RELATED SPECIES

Adromischus schuldtianus subsp. *brandbergensis* belongs to section *Boreali* (Toelken 1978), which includes a few other *Adromischus* taxa confined to northern parts of South Africa and Namibia, for example *A. trigynus*, *A. umbraticola* and *A. schuldtianus* subsp. *schuldtianus*. The subsp. *brandbergensis* is at once distinguished from them by its subfusiform (to almost terete) leaves which are distinctly concave on the upper side. It is found the furthest north in Africa of any other *Adromischus* taxon. Of all the members of section *Boreali*, *A. trigynus* has the most southern distribution. It is confined to dolerite outcrops, growing in shallow soil at altitudes above 1000 m in the Nama-Karoo Biome, in an area that receives predominantly summer and autumn rainfall. *Adromischus trigynus* ranges from southern Namibia and

Pofadder in the west to Aliwal North and the southern Free State in the east. *Adromischus umbraticola* occurs mainly on south-facing cliffs and in shallow soil associated with sandstone and quartzite outcrops on the Highveld of Gauteng, mountains of the North West Province and further north to the Blouberg and Chuniespoort (Limpopo Province). It is common on rocky ridges of the Witwatersrand and the Magaliesberg range. The vegetation of its habitat consists mainly of short, dry savanna. It has very brittle leaves and plants often colonise shallow pockets of soil, with little competition from mesophytic taxa. *Adromischus schuldtianus* subsp. *schuldtianus* is characterised by oblanceolate to obovate leaves. Toelken (1985) recognises two subspecies mainly differentiated by their stem and branch length, 40–80 mm tall and little branched, with branches 10–30 mm long in subsp. *schuldtianus*, which occurs in arid savanna in central Namibia, from the Erongo and Awas Mountains in the north to near Aus and the Karas Mountains in the south. It grows on rock outcrops, usually with a southern aspect. The second subspecies, *A. schuldtianus* subsp. *juttae*, is confined to the Karasberg in southern Namibia and is differentiated by its longer branches; the plants occur in Nama-Karoo. Bruyns (1990) observed variability in the leaf shape of subsp. *brandbergensis* on the Brandberg. He found flat- and subfusiform-leaved plants occurring together. However, in spite of some local variation, most specimens encountered on the Brandberg are represented by the subterete-leaved plants.

ADAPTATIONS TO THE CLIFF ENVIRONMENT

Habit: Plants forming dense clusters and filling up crevices. Branches and leaves rooting where they touch ground. The plants are conspicuous on the cliff face, often filling an entire crevice.

Size and weight: Clusters of light to medium weight.

Stem: Branches short and succulent, in cultivation up to 70 × 10 mm.

Leaves

Orientation: Alternate, subfusiform-ellipsoid, the flattened adaxial side with a faint window, which can be viewed as an adaptation allowing and spreading light to the abaxial surface in the often shady cliff environment. The subfusiform leaves are typical of many cremophilous succulent plant species, an adaptation to the harsh cliff habitat.

Colour: Dark green and marbled with white or dull red areas.

Age and persistence: Functional for more than a year.

Armament and camouflage: Soft-leaved plant bodies without conspicuous armament or camouflage properties, adapted to the undisturbed cliff face.

Sexual reproduction

Flowers: Flowers tubular, with pink lobes, pollinated by insects.

Fruit/Seed

Size: Seed minute and ideal for establishment in crevices.

Dispersal: Wind-dispersed.

Time: Summer, in time for the autumn rains and thus maximising establishment.

Vegetative reproduction: Like other *Adromischus* species, this plant proliferates from detached leaves (caused by heavy wind or other disturbances), a vegetative reproductive backup system ensuring long-term survival. *Adromischus schuldtianus* subsp. *brandbergensis* often fills entire crevices.

CONSERVATION STATUS

Locally common and well protected in the undisturbed cliff habitat, not threatened.

ADDITIONAL NOTES

Horticulture: Easily cultivated but should be kept dry in winter. Best for Namib and Karoo gardens. Thrives in small containers (well-drained, sandy medium), under controlled conditions. Easily grown from cuttings or division. Does well in partial shade.

VOUCHER

Van Jaarsveld 17969 (NBG).

ILLUSTRATIONS AND MAP

Figures 103a–103c, Map 103.

104. *Adromischus subdistichus* Makin ex Bruyns in South African Journal of Botany 58,1: 50–51 (1992).

Cremonophyte growth form: Small, cluster-forming and drooping stems (of light weight, cliff hugger).

Growth form formula: E:F:P:Els:E (vb)

Etymology: Latin *sub*, almost, Greek *dis*, twice, and *stichous*, a line, referring to the leaves which are almost in two opposite rows.

DESCRIPTION AND HABITAT

Little-branched, small, decumbent to erect plant, up to 70 mm high, 150 mm in diameter. Roots fibrous. Branches green at first and up to 3 mm in diameter, becoming grey-green and 4–5 mm in diameter. Leaves 15–20 × 10–17 mm, spreading to ascending, brittle, obovate, grey-green, shiny, sometimes purplish but not spotted; adaxial surface flat to convex; abaxial surface convex; margin white, acute, horny for most of the length, shortly decurrent on stem; apex obtuse or rounded, mucronate; base auriculate. Inflorescence a spike-like thyrses up to 180 mm high, bearing 1- or 2-flowered cymes; pedicel 4–8 mm long; buds spreading, terete, tapering. Calyx up to 2 mm long. Corolla 11–12 mm long; tube greenish yellow; lobes

lanceolate-triangular, 3–4 mm, pink, with club-shaped trichomes in throat; apices acute. Anthers shortly exerted.

Phenology: Flowering in midsummer (January–February).

Pollinators: The tubular flowers are pollinated by insects.

Habitat and aspect: *Adromischus subdistichus* grows on quartzitic sandstone (southern aspects). The average daily maximum temperature is 26°C and the average daily minimum 11°C. Temperatures vary and may reach 40°C in summer. Winters are cooler but frost is a rarity or absent. Although the rainfall occurs in summer and winter (from 300–400 mm per annum), it is more in the summer months.

Altitude: 500–2000 m.

Associated vegetation: Groot Thicket (Mucina *et al.* 2005).

Associated cremnophytes: At Toorwaterspoort southwest of Willowmore, *Adromischus subdistichus* grows on south-facing cliffs together with cliff dwellers such as *Albuca tortuosa*, *Bulbine* sp., *Cotyledon woodii*, *Crassula capitella* subsp. *thyrsiflora*, *C. cotyledonis*, *C. muscosa* var. *muscosa*, *C. pellucida* subsp. *marginalis*, *C. perfoliata* var. *minor*, *C. pubescens* var. *radicans*, *C. rupestris*, *Cyrtanthus montanus*, *Drimia uniflora* (*Litanthus pusillus*), *Haemanthus albiflos*, *Haworthia decipiens* var. *decipiens*, *H. viscosa*, *Lampranthus affinis*, and *Senecio talinoides*.

Geology: Mainly quartzitic sandstone of the Table Mountain Group (Cape Supergroup).

DISTRIBUTION

Adromischus subdistichus is confined to the eastern Little Karoo, from Toorwaterspoort west of Willowmore to the Nuwekloof Pass at the western end of Baviaanskloof.

RELATED SPECIES

Adromischus subdistichus is related to *A. leucophyllus*, another cremnophyte from the western Little Karoo. Differences are discussed under the latter.

ADAPTATIONS TO THE CLIFF ENVIRONMENT

Habit: Plants form loose, sparsely branched clusters, often with drooping stems and well-adapted to its well-drained, vertical habitat.

Size and weight: Clusters small, of light weight.

Stem: Branches spreading to decumbent, up to 200 mm long.

Leaves

Orientation: Orbicular, brittle, easily becoming detached by slight disturbances.

Colour: Glaucous green, turning reddish during periods of drought and thus protecting the plants from excessive sunlight and preventing unnecessary transpiration.

Age and persistence: Functional for more than a year.

Armament and camouflage: Soft-leaved plant bodies without conspicuous armament or camouflage properties, adapted to the undisturbed cliff face.

Sexual reproduction

Flowers: Flowering in summer (November–January).

Fruit/Seed

Size: Seed minute and ideal for establishment in crevices.

Dispersal: Fruiting capsules dehiscent, with seeds spontaneously released and dispersed by wind.

Time: Autumn, coinciding with autumn rain and maximising establishment.

Vegetative reproduction: Like other *Adromischus* species, this plant proliferates from detached leaves (caused by heavy wind or other disturbances), a vegetative reproductive backup system ensuring long-term survival.

CONSERVATION STATUS

Locally common and not threatened owing to the undisturbed cliff habitat.

ADDITIONAL NOTES

Horticulture: *Adromischus subdistichus* is popular in cultivation, best suited to rockeries and containers in thicket, succulent karoo and dry fynbos gardens. It is easily cultivated and propagated by leaves, this vigour viewed as maximising survival. Grow in sandy soil, in partial shade. Thrives in containers.

VOUCHER

Van Jaarsveld 17408 (NBG).

ILLUSTRATIONS AND MAP

Plate 104, Figures 104a–104d, Map 104.

105. *Adromischus umbraticola* C.A.Sm. subsp. *ramosus* Toelken in *Bothalia* 12: 386 (1978).

Cremonophyte growth form: Small, cluster-forming (of light weight, cliff hugger).

Growth form formula: A:S:Lper:Lc (vb)

Etymology: Latin, *ramus*, a branch, pertaining to its branching habit.

DESCRIPTION AND HABITAT

Dwarf-sized, compact, little-branched plant, up to 120 mm in diameter, with tuberous base. Branches decumbent, up to 120 mm long, grey to grey-green. Roots fibrous. Leaves 15–65 × 5–21 mm, dorsiventrally compressed, compact, brittle, ascending, oblanceolate, green tinged brown, rarely grey-green. Inflorescence a spike-like thyrses, up to 350 mm high, bearing 1-flowered cymes 1.5–3.5 mm long; pedicel 2–10 mm long; buds erect, 5-angled, gradually tapering. Calyx lobes up to 3 mm long. Corolla 10–13 long, tubular; tube 2 mm in diameter, dull green, grooved lengthwise; lobes triangular-ovate, up to 2.5 mm long, white or tinged pink, acute. Anthers shortly exserted.

Phenology: Flowering in early summer (November).

Pollinators: The tubular flowers are pollinated by insects.

Habitat and aspect: Mainly cliffs (all aspects), sometimes in the shade. Plants firmly rooted in crevices. Temperature high in summer (30°C and more). The average daily maximum temperature is about 22–24°C and the average daily minimum 8–10°C. Rainfall occurs mainly in summer, ranging from 600–800 mm (thunder showers).

Altitude: 1500–1700 m.

Associated vegetation: Gold Reef Mountain Bushveld and Waterberg Mountain Bushveld of the Central Bushveld Bioregion, Savanna Biome (Mucina *et al.* 2005).

Associated cremnoophytes: On sheer cliffs in the Blouberg (Limpopo Province), plants grow with *Aeollanthus canescens*, *Aloe arborescens*, *A. vogtsii*, *Cotyledon barbeyi*, *Crassula setulosa* var. *setulosa*, *C. swaziensis*, *Plectranthus mutabilis* and *Sarcostemma viminalis*.

Geology: Quartzitic sandstone (Setlaole Formation, Waterberg Group and Wylties Poort Formation, Soutpansberg Group).

DISTRIBUTION

Known only from isolated collections near Middelburg (Mpumalanga), Chuniespoort, the Soutpansberg and the Blouberg (Limpopo Province).

RELATED SPECIES

Distinguished from the var. *umbraticola* mainly by its longer stems. The var. *umbraticola* also often occurs on cliff faces, its leaves usually grey-green and only rarely mottled. The plant belongs to section *Boreali* consisting of three species of which *A. trigynus* and *A. schuldtianus* occur on level ground. *Adromischus trigynus* has distinctly mottled leaves and *A. schuldtianus* somewhat mottled leaves.

ADAPTATIONS TO THE CLIFF ENVIRONMENT

Habit: Plants forming loose clusters and stems sometimes becoming drooping. Branches and leaves rooting where they touch ground. The plants are conspicuous on the cliff face, often filling an entire crevice.

Size and weight: Clusters small, of light weight.

Stem: Succulent, grey to grey-green, up to 120 mm long. This length is much longer than in related species, suggesting an adaptation in becoming pendent from the cliff face.

Leaves

Orientation: Brittle when becoming detached, suggesting a vegetative reproductive strategy so as to fully occupy the crevice.

Colour: Uniform dull green, not mottled and tinged brownish.

Age and persistence: Functional for more than a year.

Armament and camouflage: Soft-leaved plant bodies without conspicuous armament or camouflage properties, adapted to the undisturbed cliff face.

Sexual reproduction

Flowers: Flowers tubular, with pink lobes, pollinated by insects. Flowering in summer (November).

Fruit/Seed

Size: Seed minute and ideal for establishment in crevices.

Dispersal: Fruiting capsules dehiscent, with seeds spontaneously released and dispersed by wind.

Time: Summer, in time for the autumn rains and thus maximising establishment.

Vegetative reproduction: Like other *Adromischus* species, this plant proliferates from detached leaves (caused by heavy wind or other disturbances), a vegetative reproductive backup system ensuring long-term survival.

CONSERVATION STATUS

Locally common and well protected in the cliff habitat.

ADDITIONAL NOTES

Horticulture: Easily cultivated, its vigour viewed as maximising survival. Easily grown from cuttings or division. Thrives in containers, in partial shade. Best for bushveld gardens, grown on rockeries or in containers.

VOUCHER

Van Jaarsveld 19794 (NBG).

ILLUSTRATIONS AND MAP

Figures 105a–105c, Map 105.

COTYLEDON L.

106. *Cotyledon barbeyi* Schweinf. var. A, Schweinfurth in The Gardeners' Chronicle, Ser. 3, 13: 624 (1893). (Wyllies Poort form.)

Cremonophyte growth form: Small rounded shrublets (of medium weight, cliff squatter).

Growth form formula: E:F:As:S/H:Es (vb)

Etymology: The specific epithet honours William Barbey (1842–1914), Swiss philanthropist and botanist.

DESCRIPTION AND HABITAT

Erect, branched, dwarf-sized, compact shrublet, up to 100 mm tall. Branches ascending, 5–7 mm in diameter at base; bark brownish grey. Leaves glabrous, 25–40 × 17–25 mm, oblanceolate; adaxial surface flat; surface glabrous, pale white-green, with powdery bloom; margin reddish; apex mucronate, reddish; base cuneate; petiole short. Inflorescence an erect thyrse of 3–5 dichasia, up to 100 mm high; peduncle with 1 or 2 pairs of bracts. Calyx lobes green, 6 × 4 mm. Corolla tubular, orange-red, 20 mm long; tube 14–18 mm long; base inflated with 5 bulges in between calyx lobes, each bulge 5 mm long; lobes free for 15 mm at apex, recurved. Stamens exserted for 5–14 mm, fused to base of corolla, in 2 whorls, free for 22 mm; anthers yellow, spherical. Squamae spreading, oblong, 4–5 × 1.5 mm, yellow-green. Carpels tapering, decurrent on styles, 28 mm long.

Phenology: Flowering in midwinter (June–August).

Pollinators: The conspicuous tubular flowers are pollinated by sunbirds.

Habitat and aspect: West-facing sandstone cliffs on the lower northern slopes of the Soutpansberg. Plants rooted in crevices and on ledges. Temperature can often go up to 40°C. Average daily maximum temperature about 29°C and average daily minimum 17°C. Rainfall occurs mainly in summer, ranging from 350–400 mm per annum (mainly thunder showers).

Altitude: 400–600 m.

Associated vegetation: Soutpansberg Mountain Bushveld of the Savanna Biome (Mucina *et al.* 2005).

Associated cremnophytes: *Adromischus umbraticola*, *Albuca fastigiata*, *Aloe petrophila*, and *Crassula swaziensis*.

Geology: Sandstone of the Wyllies Poort Formation (Soutpansberg Group).

DISTRIBUTION

Known only from Wyllies Poort on the northern foothills of the Soutpansberg.

RELATED SPECIES

Cotyledon barbeyi is distinctive and easily distinguished by the ampulaceous corolla with a distinctive bulge between the calyx lobes. It is very variable in size, habit and leaf shape, with many local forms. This cremnophilous form can be distinguished by its smaller stature and small, white leaves and slightly smaller flowers.

ADAPTATIONS TO THE CLIFF ENVIRONMENT

Habit: The small shrublets, 100 mm high, and reduction in size can be viewed as an adaptation to the well-drained, vertical habitat.

Size and weight: Clusters small, of medium weight.

Stem: Woody but more flexible than the shrubby forms of *Cotyledon barbeyi*.

Leaves

Orientation: Ascending, smaller than in the normal non-cremnophilous forms.

Colour: Pale whitish green, surface covered with a powdery bloom (both sides), with a reddish purple margin in distal third. The pruinose nature and production of anthocyanins (reddish colour under dry conditions) suggest a response to the xeric, hot, cliff-face habitat, reducing penetration of excessive light.

Age and persistence: Plants long-lived perennials. Leaves also persistent and long-lived.

Armament and camouflage: Soft-leaved plant bodies without conspicuous armament or camouflage properties.

Sexual reproduction

Flowers: Flowering in winter and early spring.

Fruit/Seed

Size: Seed minute and ideal for establishment in crevices.

Dispersal: Seeds spontaneously released upon dehiscence of the capsules and dispersed by wind.

Time: Spring, just in time for the spring rains and thus maximising establishment.

Vegetative reproduction: Stems root when they find a new crevice. Fallen stems will root when landing on a suitable ledge, an efficient backup strategy for survival in this xeric cliff-face environment.

CONSERVATION STATUS

Locally common and well protected in the cliff habitat.

ADDITIONAL NOTES

Variability: *Cotyledon barbeyi* is very variable, with many forms. The Wyllies Poort form appears to be a small obligate cremnohyte.

Horticulture: It has ornamental value and is most suitable for dry bushveld gardens, on steep embankments in full sun. It also does well in containers, in well-drained, slightly acidic soils. Keep dry in summer. It is easily propagated from stem cuttings. This growing vigour can be viewed as maximising its survival under the xeric cliff conditions.

VOUCHER

Van Jaarsveld 18035 (NBG).

ILLUSTRATIONS AND MAP

Plate 106, Figures 106a & 106b, Map 106.

107. *Cotyledon eliseae* Van Jaarsv. in *Bradleya* 15: 65–66 (1997a).

Cremonohyte growth form: Small shrublet (of medium weight, cliff squatter).

Growth form formula: E:F:As:S/H:Es (vb) (r)

Etymology: After Elise Bodley (1922–1998), botanical artist who painted the type plant and artist of *Cotyledon* and *Tylecodon* species in Van Jaarsveld & Koutnik (2004).

DESCRIPTION AND HABITAT

Rounded, dwarf-sized, branched shrublet, up to 200 mm high (without inflorescence). Branches up to 5 mm in diameter; older branches woody, with peeling bark. Leaves glandular hairy, green, obovate, 15 × 34–10–14 mm; both surfaces convex; margin reddish purple in distal third. Inflorescence a thyrse with 1–3 dichasia, up to 90 mm long; peduncle brownish purple, 2 mm in diameter; pedicels up to 18 mm long. Calyx lobes 2.5 × 3 mm, with green purplish markings. Corolla tube deep red, 12 mm long, 5–6 mm wide; lobes 15 mm long, lanceolate, spreading, glabrous on inside (except tuft of hairs where stamens fused). Stamens 12 mm long, white, flattened; anthers flattened, 1 mm in diameter. Squamae square, 1 × 1 mm, yellow, fleshy, spreading ascending.

Phenology: Flowering in late spring and early summer (October–January).

Pollinators: The conspicuous tubular flowers are pollinated by sunbirds.

Habitat and aspect: Southeast-facing cliffs overlooking the Gourits River. Plants rooted in crevices and on ledges. On hot days with berg wind conditions the temperature can go up to 40°C. The average daily maximum temperature is about 23°C and average daily minimum 11°C. Rainfall in winter and in summer, ranging from 300–400 mm per annum (thunder showers and cyclonic winter rain).

Altitude: 200–300 m.

Associated vegetation: Southern Cape Valley Thicket of the Thicket Biome (Mucina *et al.* 2005).

Associated cremnohytes: At the Gourits Bridge near Albertinia, it grows with *Albucca kirstenii*, *Aloe arborescens*, *Crassula atropurpurea*, *C. lactea* and *Haworthia turgida*.

Geology: Quartzitic sandstone of the Peninsula Formation (Cape Supergroup).

DISTRIBUTION

Confined to the mountainous region of the lower Gourits River Valley between the national road and Schoemanshoek farm.

RELATED SPECIES

Distinguished from *Cotyledon woodii*, the common level-ground Little Karoo species, by its smaller, compact growth (200 mm high), hairy leaves and tall erect peduncles (rich-flowering inflorescence) bearing 3 or more flowers. *Cotyledon woodii* is a much-branched, stiff, erect shrub up to 1 m high, usually with glabrous leaves and not densely flowering, the inflorescence often reduced to a single flower. Branches often droop from cliff faces and plants are less woody. *Cotyledon eliseae* can also be confused with *C. tomentosa* subsp. *tomentosa*, the latter with distinctly apically toothed, broader leaves and a short inflorescence. Its corolla has a shorter tube, narrowing towards the throat (parallel-sided and longer in *C. eliseae*).

ADAPTATIONS TO THE CLIFF ENVIRONMENT

Habit: The small clusters of up to 20 cm high and reduction in size can be viewed as an adaptation to the well-drained, vertical habitat.

Size and weight: Clusters of medium weight.

Stem: Woody, but more flexible than in *Cotyledon woodii* and occasionally subpendulous; can be viewed as an adaptation to the cliff environment.

Leaves

Orientation: Ascending, obovate, convex on both surfaces, with reddish purple margin in distal third.

Colour and texture: Epidermis green, covered with glandular hairs (sticky). The reddish colour (production of anthocyanins) under dry conditions reduces penetration of excessive light, an adaptation to the xeric cliff conditions. Plants adapted to grow in partial shade, explaining the green leaf colour.

Age and persistence: Plants long-lived perennials. Leaves also persistent and long-lived.

Armament and camouflage: Plants without any conspicuous armament or camouflage properties as opposed to the level-ground species, which have firm leaves and more woody branches.

Sexual reproduction

Flowers and fruit: Flowers pendent, in late spring and summer (November–January), the capsules becoming erect after fertilisation.

Fruit/Seed

Size: Seed minute and ideal for establishment in crevices.

Dispersal: Seeds spontaneously released by the dehiscent erect capsules and dispersed by wind.

Time: Summer and autumn, just in time for the winter rains and thus maximising establishment.

Vegetative reproduction: Stems root when they find new crevices. Fallen stems will root when landing on a suitable ledge, an efficient backup strategy for continued existence in this xeric cliff-face environment.

CONSERVATION STATUS

Classified as rare (Raimondo *et al.* 2009). Locally common, well protected in the cliff habitat.

ADDITIONAL NOTES

Horticulture: *Cotyledon eliseae* is best grown in thicket gardens. It is ideal for steep embankments (dappled shade or full sun) and also thrives in containers and hanging baskets, preferably in partial shade. Easily cultivated, displaying vigorous growth. Propagation is from seed or cuttings.

VOUCHER

Van Jaarsveld 14629 (NBG).

ILLUSTRATIONS AND MAP

Figures 107a & 107b, Map 107.

108. *Cotyledon pendens* Van Jaarsv., in Van Jaarsveld & Van Wyk in Aloe 40,2: 36–37 (2003f).

Cremonophyte growth form: Drooping mats (of medium weight, cliff hanger).

Growth form formula: E:F:P:Els (eg) (vb) (r)

Etymology: Latin *pendens*, hanging, after its pendent growth.

DESCRIPTION AND HABITAT

Much-branched, rapid-growing shrublets. Roots fibrous. Stems flaccid, dense, curtain-forming, pendent, up to 600 mm long (without inflorescence), about 2 mm in diameter, whitish green owing to a powdery bloom, sparsely glandular-hairy, becoming glabrescent, continuously branching from nodes, lower branches up to 5 mm in diameter, with brownish peeling bark, becoming more woody with age; nodes 7–15 mm apart. Leaves crowded, highly succulent, decussate, spreading, pendent; lamina ellipsoidal to elliptic-ovoid, 18–25 × 10–15 mm, 7–10 mm thick; apex mucronate; base cuneate; surface sparsely whitish grey-green owing to a powdery bloom, glandular-hairy becoming glabrescent; margin rounded, obscurely maroon-spotted and more so towards apex; petiole 1.5–2.0 mm long. Inflorescence a terminal, pendent thyrse, 50–90 mm long, ending in a simple dichasium bearing 2–4 flowers, rarely with a solitary flower, but then also with distinct peduncle 25–30 mm long, a pair of smaller opposite bracts and 2 or 3 very small bracts alternately arranged; peduncle glandular-hairy, 30–40 mm long, 2 mm in diameter, with a leaf-like pair of linear-elliptic bracts 5–10 × 2.5 mm; pedicels 8–12(–18) mm long, glandular-hairy; receptacle funnel-shaped, 12 mm long, glandular-hairy. Calyx lobes green, triangular, 5 × 5 mm, adpressed to flower. Corolla orange-red, 40–45 × 12–13 mm; tube cylindrical, up to 20 mm long, slightly bulging in middle; lobes linear-lanceolate, 25 × 8 mm long, slightly longer than tube, spreading, but not recoiling. Stamens 10, in 2 whorls, erect, yellowish green, 18 and 20 mm long respectively, fused to tube in basal third, with a dense tuft of hairs at point of attachment; anthers spheroid, yellow, 1.5–2.2 mm long. Squamae transversely oblong, sides rounded, 2 × 3 mm, erect, yellowish green; apices sometimes slightly emarginate. Carpels 5, tapering to slender styles 20 mm long. Capsule pendent or becoming spreading, but always pointed away from cliff face.

Phenology: Flowering in summer (end of November–January).

Pollinators: The conspicuous tubular flowers are pollinated by sunbirds.

Habitat and aspect: *Cotyledon pendens* grows on south-facing cliffs, the plants firmly rooted in crevices and forming drooping mats. The average daily maximum temperature is about 24°C, and average daily minimum about 14°C. Rainfall occurs mainly in summer and ranges from 1000–1250 mm per annum (mainly thunder showers, October–May).

Altitude: 300–400 m.

Associated vegetation: Eastern Valley Bushveld (Sub-Escarpment Savanna Bioregion) of the Savanna Biome (Mucina *et al.* 2005).

Associated cremonophytes: *Cotyledon pendens* shares its habitat with other succulent plants such as *Albuca batteniana*, *Bulbine thomasiae*, *Ceropegia sandersonii* (southernmost record),

Crassula cordata, *C. intermedia*, *C. perforata*, *Drimia anomala*, *D. loedolffiae*, *Haemanthus albiflos*, *Haworthia cymbiformis* var. *setulifera*, *Ledebouria* sp., *Ornithogalum longibracteatum*, *Pelargonium acraeum*, *Peperomia blanda*, *Plectranthus hadiensis* var. *hadiensis* and *Rhipsalis baccifera*. Other non-succulent plants sharing the habitat include *Bauhinia bowkeri*, *Ficus burkei*, *F. burtt-davyi* and *Schotia latifolia*.

Geology: Ecce sandstone and mudstone (Adelaide Subgroup, Karoo Supergroup).

DISTRIBUTION

Cotyledon pendens is endemic to the dry Bashee River Valley, from Collywobbles in the west to near the river mouth in the east.

RELATED SPECIES

Distinguished from *Cotyledon woodii* by its flaccid stems, rapid pendent growth and pendent terminal thyse. Like *C. woodii*, it often produces solitary flowers. *Cotyledon woodii* is a sturdy, erect, woody shrub up to 1 m high from the southern parts of the Eastern Cape; it grows in a variety of habitats, occasionally also on cliffs.

ADAPTATIONS TO THE CLIFF ENVIRONMENT

Habit: Pendent mats, branched from the base but less so towards the apex. The plants form conspicuous silvery mats with stems up to 600 mm long, a character that can be viewed as an adaptation to its sheer habitat.

Size and weight: Clusters small, of medium weight.

Stem: The soft, flaccid, pendent growth can be viewed as adaptation to the cliff environment.

Leaves

Orientation: Pendent and, compared to other *Cotyledon* species, there is a reduction in size.

Colour: Glaucous colour due to the powdery bloom can be viewed as an adaptation to the very xeric conditions of the cliff face.

Age and persistence: Plants long-lived perennials. Leaves also persistent and long-lived.

Armament and camouflage: Soft-leaved plant bodies without conspicuous armament or camouflage properties, as opposed to the level-ground species with firm leaves and more woody branches.

Sexual reproduction

Flowers: Flowering in summer (end November–January).

Fruit/Seed

Size: Seed minute and ideal for establishment in crevices.

Dispersal: After fertilisation the fruiting capsule becomes erect, the seeds spontaneously released by the dehiscent capsule and dispersed by wind.

Time: Autumn and coincides with rain experienced in autumn.

Vegetative reproduction: The stems of *Cotyledon pendens* will root where they come into contact with the soil or find cracks in the adjacent rock. It will also grow from detached leaves (like *Adromischus* and *Crassula*), which can root and proliferate, a unique adaptation in the genus *Cotyledon*. This vegetative proliferation represents a reproductive backup strategy for so many cremnophytes and reflects the harsh, difficult terrain.

CONSERVATION STATUS

Locally common and well protected in the cliff habitat.

ADDITIONAL NOTES

Horticulture: *Cotyledon pendens* is best grown in dry bushveld or thicket gardens and is suitable for steep embankments, rockeries and containers. Plants are mat-forming and this growth habit should prevent soil erosion. It would be ideal for dry, south-facing window sills and should preferably be grown in partial shade. A suitable subject for a hanging basket. Easily propagated from stem or leaf cuttings. Outside its habitat, it is best grown under controlled conditions in a greenhouse. Easily cultivated, its vigour viewed as maximising its survival.

VOUCHER

Van Jaarsveld 16889 (NBG).

ILLUSTRATIONS AND MAP

Plate 108, Figures 108a–108c, Map 108.

109. *Cotyledon tomentosa* Harv. subsp. *tomentosa*, Harvey, Flora capensis 2: 373 (1862).

Cremonophyte growth form: Small shrublet to rounded clusters, sometimes with drooping branches (of medium weight, cliff squatter).

Growth form formula: E:F:As:S/H:Es (vb) (r)

Etymology: Latin *tomentosa*, hairy, referring to the hairy leaves.

DESCRIPTION AND HABITAT

Dwarf-sized freely branched, compact, rounded, succulent shrublet, up to 110 mm high. Branches green, with long hairs. Leaves variable in hairiness, shape and teeth, oblanceolate to oblong oblanceolate, 23–65 × 15–32 mm, flattened, green, tomentose, with 3–8 reddish teeth in distal third. Inflorescence a thyrses of 1–3 dichasia, up to 160 mm high; peduncle reddish, 4 mm in diameter at base; pedicels 7–8 mm long. Calyx lobes green, 6 × 5 mm. Corolla orange-

red, 12–16 mm long; tube 15 × 9 mm, tapering; lobes recurved, free for 10 mm. Stamens exerted for 3 and 5 mm respectively; anthers yellow, 1.5 mm long, flattened. Squamae transversely oblong, 2 × 1 mm, green.

Phenology: Flowering in midwinter to spring (June–September).

Pollinators: The conspicuous tubular flowers are pollinated by sunbirds.

Habitat and aspect: Quartzitic sandstone cliff faces in kloofs and river valleys, on all aspects but more on the south-facing ones. Temperatures vary and may reach 40°C in summer. Winters are cooler but frost is a rarity or absent. The average daily maximum temperature is about 25–27°C and the average daily minimum 9–10°C. Rainfall occurs in winter and summer and ranges from 300–400 mm per annum.

Altitude: 300–700 m.

Associated vegetation: Gamka and Gamtoos Thicket of the Albany Thicket Biome (Mucina *et al.* 2005).

Associated cremnophytes: At Gert Smitskloof in the Baviaanskloof, it grows with *Adromischus cristatus* var. *zeyheri*, *Albuca cremnophila*, *Cyrtanthus montanus*, *C. labiatus*, *Delosperma elsieae*, *Gasteria rawlinsonii*, *Haworthia gracilis* var. *picturata*, *H. viscosa*, *Othonna triplinervia* and *Plectranthus verticillatus*.

Geology: Quartzitic sandstone, Peninsula Formation (Cape Supergroup).

DISTRIBUTION

Cotyledon tomentosa subsp. *tomentosa* is distributed from the Baviaanskloof and Kouga Mountains in the east to the mountains near Calitzdorp (Gourits River), but is confined to cliffs in often shady kloofs.

RELATED SPECIES

Distinguished from *Cotyledon tomentosa* subsp. *ladismithiensis*, a level-ground Little Karoo species, by its smaller, compact growth (110 mm high) and smaller hairy leaves. The subsp. *ladismithiensis* is a much-branched, stiff, erect shrub up to 400 mm high, usually with terete leaves. Also related to *C. eliseae*; for differences see under that species.

ADAPTATIONS TO THE CLIFF ENVIRONMENT

Habit: The small clusters of up to 110 mm high and reduction in size can be viewed as an adaptation to the well-drained, vertical habitat.

Size and weight: Clusters small, of medium weight.

Stem: Woody but more flexible than in *Cotyledon woodii* and occasionally subpendulous, a character that can be viewed as adaptation to the cliff environment. Unlike in level-ground *Cotyledon* species and most other Crassulaceae, the branches are strong and difficult to detach without pulling up whole plant.

Leaves

Orientation: Ascending, very hairy, oblanceolate to oblong oblanceolate, flattened, the large leaves in relation to plant size an adaptation maximising absorption of light. The function of the large, firm, reddish teeth on the leaf apices is unknown.

Colour and texture: Green, with 3–8 reddish teeth in distal third. The hairy nature is probably an adaptation reducing transpiration, compensating for the large leaf size and an adaptation resulting from the extreme run-off in the sheer habitat.

Age and persistence: Plants long-lived perennials. Leaves also persistent and long-lived.

Armament and camouflage: Soft-leaved plant bodies, no conspicuous armament or camouflage properties as in the level-ground species, which have firm leaves and more woody branches.

Sexual reproduction

Flowers: Flowering from midwinter to spring (July–September).

Fruit/Seed

Size: Seed minute and ideal for establishment in crevices.

Dispersal: After fertilisation the fruiting capsule becomes erect, the seeds spontaneously released by the dehiscent capsule and dispersed by wind.

Time: Spring and summer, coinciding with summer rainfall and maximising establishment.

Vegetative reproduction. Stems root where they find new crevices. Fallen stems will root on a suitable ledge, an efficient backup strategy for survival in this xeric cliff-face environment.

CONSERVATION STATUS

Although classified as vulnerable (VU C1, Raimondo *et al.* 2009), it is locally common, widespread and well protected in the cliff-face habitat.

ADDITIONAL NOTES

Horticulture: *Cotyledon tomentosa* subsp. *tomentosa* is best grown in thicket gardens and is suitable for rockeries and containers. It makes a worthwhile pot plant. It should preferably be grown in partial shade. Easily propagated from cuttings and easily grown. Outside the habitat, it is best grown under controlled greenhouse conditions (Van Jaarsveld 1988b).

VOUCHERS

Van Jaarsveld 17180, 17772 (NBG).

ILLUSTRATIONS AND MAP

Plate 109, Figures 109a–109c, Map 109.

CRASSULA L.

110. *Crassula alba* Forssk. var. *pallida* Toelken in Bothalia 12: 634 (1979).

Cremonophyte growth form: Small cluster (of medium weight, cliff squatter).

Growth form formula: A:S:Lper:R:C:La (vb)

Etymology: Latin *pallida*, pale, pertaining to the pale-coloured flowers.

DESCRIPTION AND HABITAT

Plants rosulate, proliferating from base to form small groups. Roots slightly fleshy. Leaves spirally arranged, dorsiventrally flattened, lanceolate to linear-lanceolate, 60–170 × 5–15 mm; upper surface folded to channelled, glabrous, green to yellowish green, sometimes with purple spots, lower surface purplish; margin ciliate; apex acute. Inflorescence an erect terminal flat-topped thyrse, up to 250 mm long, bearing many dichasia; bracts leaf-like, becoming shorter distally. Flowers pedicellate. Calyx lobes up to 2 mm long, acute, with marginal cilia. Corolla white, tubular, up to 4 mm long, erect; lobes oblong-obovate, up to 5.5 mm long, fused shortly at base, with acute, slightly hooded apices, spreading to recurved. Anthers dark brown.

Pollinators: The conspicuous diurnal white flowers suggest a day-flying insect.

Habitat and aspect: *Crassula alba* var. *pallida* occurs mainly on sandstone cliffs where the plants grow in shallow soil on sunny rocky ledges. Temperature moderate in summer and mild to cold in winter. Average daily maximum temperature is 24–26°C and daily minimum ranges from 12–14°C. Rainfall occurs mainly in summer (mainly thunder showers) and ranges from 1000–1500 mm per annum.

Altitude: 400–2000 m.

Associated vegetation: Lydenburg Montane Grassland of the Grassland Biome (Mucina *et al.* 2005).

Associated cremonophytes: At the Abel Erasmus Pass, *Aloe spicata*, *Crassula swaziensis* and *Tetradenia riparia* grow together with *C. alba* var. *pallida*.

Geology: Mainly quartzitic sandstone on various formations.

DISTRIBUTION

Crassula alba var. *pallida* is distributed from the northern Drakensberg in KwaZulu-Natal to Mount Anderson in Mpumalanga.

RELATED SPECIES

Differs from *Crassula alba* var. *alba*, a grassland species, by its cluster-forming habit and usually red to pinkish flowers. The var. *parvisepala* also has red flowers.

ADAPTATIONS TO THE CLIFF ENVIRONMENT

Habit: Cluster-forming, plants becoming conspicuous and not camouflaged.

Size and weight: Clusters small, of medium weight.

Stem: Erect, short, woody.

Leaves

Orientation: Compact, in ascending rosettes, becoming reddish during dry periods. This compact, rosulate nature can be viewed as an adaptation to the dry conditions on the cliff face. The soft texture and fragile nature suggest adaptation to the sheltered, undisturbed cliff face.

Colour: Epidermis green to yellowish green, becoming reddish. The reddish colour (production of anthocyanins) under dry conditions reduces penetration of excessive light, an adaptation resulting from the well-drained habitat.

Age and persistence: The plants are relatively slow-growing, long-lived perennials.

Armament: Soft-leaved plant bodies without conspicuous armament.

Sexual reproduction

Flowers: Flowers in late summer and autumn (March–April), pollinated by insects.

Fruit/Seed

Size: Seed minute and ideal for establishment in crevices.

Dispersal: Follicles dehiscent, with seeds spontaneously released and dispersed by the wind.

Time: Seeds released in late autumn or winter.

Vegetative reproduction: Plants proliferating and cluster-forming, filling up crevices. This differs from *Crassula alba* var. *alba* (solitary rosettes) on level ground and can be viewed as an adaptation to the cliff habitat.

CONSERVATION STATUS

Locally common and well protected in the cliff habitat.

ADDITIONAL NOTES

Horticulture: Best for highveld gardens, grown in rockeries and containers. Easily cultivated, its vigour viewed as maximising survival. Propagate from cuttings or division.

VOUCHER

Toelken 5694 (PRE).

ILLUSTRATIONS AND MAP

Figure 110a, Map 110.

111. *Crassula atropurpurea* (Harv.) D.Dietr. var. *anomala* (Schönland & Baker f.) Toelken in Journal of South African Botany 41: 96 (1975).

Cremonophyte growth form: Spreading, mat-forming (of medium weight, cliff hugger).

Growth form formula: E:F:As:S/H:Es (vb)

Etymology: Latin *anomala*, diverging from the normal.

DESCRIPTION AND HABITAT

Plants sparsely branched, forming loose, decumbent clusters up to 200 mm in diameter. Roots fibrous. Branches up to 10 mm in diameter, covered with short erect hairs, green, becoming yellowish. Leaves spreading, narrowly to broadly oblanceolate, dorsiventrally flattened, 10–25 × 5–13 mm; apex obtuse; base cuneate; margin horny; surface densely covered with short erect hairs, lower surface convex; younger leaves ascending; older leaves becoming deciduous. Inflorescence an erect, elongated thyse with several glomerate dichasia at the 3–5 nodes of peduncle; peduncle up to 200 mm long. Calyx lobes triangular-lanceolate, up to 3 mm long; margin ciliate. Corolla tubular; lobes fused at base, cream or white, panduriform to 2.0–4.5 mm long, ending in a beak-like structure. Squamae oblong-cuneate, pale yellow.

Phenology: Flowering from spring to early summer (October–December).

Pollinators: The white to cream corolla suggests a flying insect.

Habitat and aspect: Cliffs (mainly south-facing), in shade or partly exposed, in shallow soil on rocky ledges. It is hot in summer and cool in winter. Average daily maximum temperature is 18–20°C and daily minimum ranges from 7–10°C. Rainfall occurs mainly in winter (cyclonic winter rain) but with a portion of summer rain towards the east (thunder showers), ranging from 450–800 mm per annum.

Altitude: 800–2000 m.

Associated vegetation: Peninsula Sandstone Fynbos (Mucina *et al.* 2005).

Associated cremonophytes: On Table Mountain (Cape Town, Western Cape), the following plants occur on a cliff face: *Bulbine lagopus*, *Crassula lanceolata* var. *lanceolata*, *C. rupestris* subsp. *rupestris*, *Haemanthus coccineus* and *Scopelogenia verruculata*.

Geology: Mainly quartzitic sandstone of the Table Mountain Group (Cape Supergroup).

DISTRIBUTION

Crassula atropurpurea var. *anomala* occurs on the northern face of Table Mountain and from Worcester to Montagu, on sheer south-facing slopes.

RELATED SPECIES

Differs from other members in section *Globulea* immediately in its thicker branches (10 mm) and prominent dorsal appendage of the petals. Differs from var. *atropurpurea* in its decumbent branches and parts covered with erect hairs. Leaves are reddish, linear to broadly obovate, with obtuse apices. Inflorescence with basal 1 or 2 bracts without dichasia. Dichasia of densely clustered flowers. Corolla lobes with canaliculate dorsal appendage.

ADAPTATIONS TO THE CLIFF ENVIRONMENT

Habit: Sparsely branched, loose clusters, sometimes subpendulous.

Size and weight: Clusters small, of light to medium weight.

Stem: Decumbent, up to 10 mm in diameter, flaccid.

Leaves

Orientation: Spreading, younger leaves ascending, narrowly to broadly oblanceolate, dorsiventrally flattened.

Colour and texture: Dull green, surface densely covered with short erect hairs; older leaves becoming deciduous. The dense hairs can be viewed as an adaptation to the xeric cliff-face habitat.

Age and persistence: Plants are relatively rapid-growing but long-lived perennials.

Armament: Plants with soft, fragile, flaccid branches without conspicuous armament, an adaptation to the cliff habitat.

Sexual reproduction

Flowers: Inflorescence an erect, elongated thyse bearing cream to white flowers in spring.

Fruit/Seed

Size: Seed minute, ideal for establishment in crevices.

Dispersal: Follicles dehiscent, with seeds spontaneously released and dispersed by wind.

Time: Seeds released in summer and late summer.

Vegetative reproduction: Stems of *Crassula atropurpurea* var. *anomala* root where they come into contact with the soil, filling crevices—an ideal long-term survival backup on the sheer cliff face. Detached branches will root on other ledges or in new crevices.

CONSERVATION STATUS

Locally common and well protected in the cliff habitat.

ADDITIONAL NOTES

Horticulture: Best for dry fynbos gardens, grown in rockeries or small containers. Easily cultivated, its vigour viewed as maximising survival. Easily grown from seed or division.

VOUCHERS

Van Jaarsveld 16943, 17442 (NBG).

ILLUSTRATIONS AND MAP

Figures 111a–111d, Map 111.

112. *Crassula aurusbergensis* G.Will. in *Cactus and Succulent Journal* (U.S.) 64: 288–289 (1992).

Cremonophyte growth form: Dwarf-sized, compact cluster (of light weight, cliff hugger).

Growth form formula: A:S:Lper:R:C:Ts:La (vb)

Etymology: After the Aurusberg in southern Namibia.

DESCRIPTION AND HABITAT

Plants dwarf-sized, branched, compact succulents forming rounded tufts up to 95 mm in diameter. Roots fibrous. Branches short, internodes not visible. Leaves in rosettes, ascending-spreading, becoming spreading, oblanceolate to oblong-oblanceolate, 10–25 × 7–14 mm; lamina dorsiventrally compressed; upper surface flat to slightly convex, with off-centre groove, lower surface convex; epidermis glabrous, grey-green; margin ciliate; apex acute to round; older leaves persistent. Inflorescence a rounded thyrse with a peduncle up to 25 mm high, with few spherical dichasia. Calyx lobes narrow-triangular, papillate, up to 3 mm long, apices obtuse. Corolla up to 3 mm long, cup-shaped; lobes fused at base, white, apices obtuse, without dorsal appendage. Anthers yellow. Squamae fleshy, transversely oblong, yellow.

Phenology: Flowering in summer.

Pollinators: The small white flowers suggest a flying insect.

Habitat and aspect: *Crassula aurusbergensis* grows on south-facing cliffs. Plants are firmly rooted in crevices and size often depends on the growing space allowed by the crevice. It is locally abundant. Temperatures are moderate to high in summer but frequently drop owing to cold winds and fog from the Atlantic Ocean. Winters are cooler but frost is absent. Average daily maximum temperature about 16–18°C and average daily minimum for the region is 7–8°C. Rainfall is mainly in winter (cyclonic), ranging from 50–75 mm per annum.

Altitude: 900–1050 m.

Associated vegetation: Mainly Succulent Karoo.

Associated cremnophytes: Associated cremnophytes include *Conophytum ernianum*, *Holothrix filicornis* and *Tylecodon aurusbergensis*.

Geology: Quartzitic sandstone of the Namaqua Metamorphic Complex.

DISTRIBUTION

Endemic to Aurusberg, southern Namibia.

RELATED SPECIES

Crassula aurusbergensis belongs to section *Argyrophylla*. It differs from other members of the section in its small rosettes of smooth (margin crenulate, hyaline), unequally bilobed leaves with acute apices.

ADAPTATIONS TO THE CLIFF ENVIRONMENT

Habit: Conspicuous clusters, an adaptation to the undisturbed cliffs.

Size and weight: Clusters small, of light weight, up to about 100 mm in diameter.

Stem: Short, not visible.

Leaves

Orientation: Ascending-spreading, becoming spreading, open rosettes maximising penetration of light on the shady, south-facing cliffs.

Colour: Epidermis grey-green, glabrous, margin crenulate.

Age and persistence: Plants long-lived perennials. Leaves also persistent and long-lived, suggesting adaptation to the xeric cliff conditions and mineral-poor soil.

Armament and camouflage: Plants with soft leaves and plant bodies without conspicuous armament or camouflage properties, as opposed to the level-ground species such as *Crassula namaquensis*, *C. sericea* and *C. alstonii*, which are well camouflaged, with a different firmer leaf texture.

Sexual reproduction

Flowers: Corolla white.

Fruit/Seed

Size: Seed minute and ideal for establishment in crevices.

Dispersal: Follicles dehiscent, with seeds spontaneously released and dispersed by wind.

Time: Seeds dispersed during autumn rains, maximising establishment.

Vegetative reproduction: Plants proliferate from the base, forming small mats, rooting and spreading by vegetative means, filling crevices. This differs from the solitary rosulate forms on level ground and represents an adaptation to the cliff habitat.

CONSERVATION STATUS

Classified as rare (Loots 2005). Locally common and well protected in the cliff habitat.

ADDITIONAL NOTES

Horticulture: Best for containers in dappled shade. Keep dry during the summer months. Outside its desert habitat, it is best grown under controlled conditions in a greenhouse. Easily cultivated, its vigour viewed as maximising survival. Propagate by division.

VOUCHER

Williamson 4416 (NBG).

ILLUSTRATIONS AND MAP

Map 112.

113. *Crassula badspoortense* Van Jaarsv., in Van Jaarsveld & Van Wyk in *Aloe* 38,1 & 2: 29–30 (2001a).

Cremonophyte growth form: Loose clusters with spreading to drooping stems (of medium weight, cliff hanger).

Growth form formula: E:F:P:Els (vb)

Etymology: After its native habitat at Badspoort in the Little Karoo.

DESCRIPTION AND HABITAT

Spreading, sparsely branched (3–8 branches) shrublets, up to 100 mm high, up to 400 mm in diameter. Stems 3–4 mm in diameter, spreading, becoming pendulous; internodes 6–10 mm long. Leaves sessile, broadly ovate, 20–35 × 20–35 mm, flat to slightly biconvex, spreading at right angles but slightly ascending and forwardly curved; apex subacute; bases fused, amplexicaul, forming a sheath; surface smooth, glaucous to whitish green; margins entire; hydathodes concentrated towards margins. Inflorescence a short, rounded thyrse, up to 40 mm long, up to 65 mm in diameter, with many 5-merous, pedicellate flowers in dichasia; peduncle indistinct owing to gradual transition to bracts; basal bracts 8 × 5 mm, becoming smaller (2 × 1 mm) on inflorescence, triangular ovate. Flowers star-shaped, up to 4.5 mm in diameter, white; pedicels 2–5 mm long. Calyx lobes triangular, 1.3 × 0.8 mm, apices acute. Corolla

lobes lorate-lanceolate, 3.5×1.0 mm, recurved, apices obtuse to subacute. Stamens: filaments 2 mm long; anthers 0.2 mm long, dark maroon; pollen yellow. Squamae truncate, 0.3 mm in diameter, 0.2 mm high, thick, fleshy, yellowish orange. Carpels 2 mm long; ovary bottle-shaped, tapering into short, outward pointing style, inner side of ovary asperulous.

Phenology: Flowering in summer and autumn (January–March).

Pollinators: The small white flowers suggest a flying insect.

Habitat and aspect: *Crassula badspoortense* grows on south-facing quartzitic sandstone cliffs. Plants are firmly rooted in crevices and size often depends on the growing space allowed by the crevice. It is locally abundant to less prominent. Temperature moderate to high in summer and can reach 40°C. Winters are cooler but frost is absent. The average daily maximum temperature is 25–26°C and the average daily minimum for the region 9–10°C. Rainfall in winter (cyclonic) and summer (thunder showers), ranging from 250–350 mm per annum.

Altitude: 500–800 m.

Associated vegetation: Western Gwarrieveld, Succulent Karoo Biome (Mucina *et al.* 2005).

Associated cremnophytes: Associated cremnophytes observed at the type locality at Badspoort near Calitzdorp: *Aloe comptonii*, *Crassula cotyledonis*, *C. muscosa*, *C. perforata*, *Haemanthus coccineus*, *Lampranthus affinis*, *Litanthus pusillus* and *Tylecodon leucothrix*.

Geology: Quartzitic sandstone of the Peninsula Formation, Table Mountain Group (Cape Supergroup).

DISTRIBUTION

Western Little Karoo, from Badspoort on the Olifants River (west of Oudtshoorn) in the east to Waterkloof near De Doorns (Hex River Valley, Western Cape) in the west.

RELATED SPECIES

Distinguished from the related *Crassula rupestris* by its larger, almost whitish green leaves and larger, rounded inflorescence. The plants are sympatric. The young inflorescence is recurved at first, a diagnostic feature that separates *C. badspoortense* from *C. rupestris*.

ADAPTATIONS TO THE CLIFF ENVIRONMENT

Habit: Conspicuous, branches spreading to drooping from cliff face.

Size and weight: Clusters of medium weight, about 400 mm in diameter.

Stem: Flexible, shorter and pendulous or subpendulous. The softer, less woody and pendulous nature of the stems can be viewed as an adaptation to the cliff environment.

Leaves

Orientation: Fused into opposite discs, an adaptation to xeric conditions of the cliff face.

Colour: Epidermis white, grey-green to glaucous (covered with powdery bloom), an adaptation resulting from the extreme run-off in the sheer habitat.

Age and persistence: Plants long-lived perennials. Leaves also persistent and long-lived, an adaptation to the xeric cliff conditions.

Armament and camouflage: Soft-leaved plant bodies without conspicuous armament or camouflage properties, as opposed to the level-ground species, which are more woody.

Sexual reproduction

Flowers: In a large round-topped thyrses, conspicuous, from midsummer to autumn (November–April), diurnal.

Fruit/Seed

Size: Seed minute and ideal for establishment in crevices.

Dispersal: Follicles dehiscent, with seeds spontaneously released and dispersed by wind.

Time: Seeds dispersed during autumn rains, maximising establishment.

Vegetative reproduction: The vigorous, spreading growth ensures vegetative increase and branches will occupy new crevices by active growth. A branch blown from a cliff face and landing in a crevice, will root. This vegetative increase is an effective backup growth strategy ensuring long-term survival on the cliff.

CONSERVATION STATUS

Classified as rare (Raimondo *et al.* 2009). Locally common and well protected in the cliff habitat.

ADDITIONAL NOTES

Horticulture: Best for thicket and succulent karoo gardens, grown in rockeries, on embankments or as a pot plant. Outside its native habitat, it is best grown under controlled conditions in a greenhouse. Easily cultivated, its vigour viewed as maximising survival. Propagate from cuttings or seed.

VOUCHER

Van Jaarsveld 17169 (NBG).

ILLUSTRATIONS AND MAP

Figures 113a–113d, Map 113.

114. *Crassula brachystachya* Toelken in Journal of South African Botany 41: 97 (1975).

Cremonophyte growth form: Cluster-forming (of light weight, cliff hugger).

Growth form formula: A:S:Lper:R:C:Ts:La (vb)

Etymology: Greek *brachys*, short, and *stachus*, an ear of corn (a spike), pertaining to the sessile dichasia.

DESCRIPTION AND HABITAT

Plants rosulate, solitary or proliferating from base to form small, dense clusters, all parts fragile, brittle. Roots fleshy, up to 3 mm in diameter. Branches short but sometimes up to 100 mm long. Leaves in basal rosettes up to 150(–240) mm in diameter, spirally arranged, oblanceolate-oblong, (20–)30–80(–120) × 4–15(–20) mm; surface glabrous, dotted with crateriform hydathodes, spotted purplish towards apex; margin ciliate; apex acute. Inflorescence a spike-like thyrses (rarely up to 3), 110–230 mm high, bearing sessile dichasia on a distinct peduncle; bracts triangular-ovate, 12 × 9 mm, ciliate. Calyx lobes oblong-elliptic, 3.5–4.5 mm, ciliate. Corolla tubular, 6 mm long; lobes oblong, 4–5 mm long, fused shortly at base, apices spreading, white.

Phenology: Flowering in summer (November–January).

Pollinators: The conspicuous diurnal flowers suggest day-flying insects.

Habitat and aspect: Sheltered to exposed cliffs. Plants grow in shallow soil among leaf litter on shady rocky ledges and often in the shade of cliffs. Temperature is moderate in summer and mild in winter. Average daily maximum temperature is 20–23°C and daily minimum 5–8°C. Rainfall in winter (cyclonic) and summer, ranging from 200–400 mm per annum.

Altitude: 1300–2000 m.

Associated vegetation: Western Little Karoo of the Succulent Karoo Biome (Mucina *et al.* 2005).

Associated cremonophytes: At Besemfontein kloof, plants grow with *Aloe perfoliata*, *Drimia uniflora*, *Crassula rupestris* subsp. *rupestris* and *Euphorbia multifolia*.

Geology: Quartzitic sandstone of the Table Mountain and Witpoort Formation (Cape Supergroup).

DISTRIBUTION

Crassula brachystachya is confined to the Klein Swartberg foothills and adjacent regions of the Laingsburg district.

RELATED SPECIES

Crassula brachystachya belongs to section *Rosulares* which includes 22 species (Toelken 1985). It is related to *C. capitella* subsp. *thyrsiflora*, but is at once distinguished from this taxon by its distinct peduncle and abruptly shortened bracts.

ADAPTATIONS TO THE CLIFF ENVIRONMENT

Habit: Loose clusters, plants conspicuous and not camouflaged. The succulent roots and leaves in a rosette can be seen as an adaptation to the xeric cliff face.

Size and weight: Clusters small, of light weight.

Stem: Short (up to 100 mm), usually unexposed.

Leaves

Orientation: Rosulate, spreading and compact, an adaptation to the dry conditions on the cliff face.

Colour: Epidermis light green, becoming reddish during dry periods. The reddish colour (production of anthocyanins) reduces penetration of light and can be viewed as an adaptation to the xeric cliff conditions.

Age and persistence: Plants long-lived perennials.

Armament: With soft, flaccid leaves and brittle plant bodies without conspicuous armament, suggesting adaptation to the cliff environment.

Sexual reproduction

Flowers: Flowering from November–January, conspicuous, white, pollinated by insects.

Fruit/Seed

Size: Seed minute and ideal for establishment in crevices.

Dispersal: Follicles dehiscent, with seeds spontaneously released and dispersed by wind.

Time: Seeds released in summer, thus ready for the onset of autumn showers, maximising establishment.

Vegetative reproduction: *Crassula brachystachya* proliferates, forming small mats and cushions, an efficient vegetative backup strategy for surviving the harsh conditions on the cliff face. When an offshoot (or leaf) becomes detached (by heavy wind or some other disturbance), it will root if it falls into a new crevice, ensuring long-term survival.

CONSERVATION STATUS

Classified as rare (Raimondo *et al.* 2009). Although *Crassula brachystachya* is not common locally, it is well protected by the inaccessible cliff habitat.

ADDITIONAL NOTES

Horticulture: Best for succulent karoo gardens, in rockeries or containers. Outside its habitat, it should be grown under controlled conditions in a greenhouse, in a sandy well-drained soil.

Grow in dappled shade. Easily cultivated, and its vigour can be viewed as maximising survival. Propagate from seed or division. Leaves succumb to rust in moist coastal climates.

VOUCHER

Van Jaarsveld 19504 (NBG).

ILLUSTRATIONS AND MAP

Figures 114a–114d, Map 114.

115. *Crassula capitella* Thunb. subsp. *thyrsiflora* (Thunb.) Toelken in Journal of South African Botany 41: 100 (1975). (Baviaanskloof, Kougadam, Gourits form.)

Cremonophyte growth form: Mat-forming cluster (of light weight, cliff hugger).

Growth form formula: A:S:Lper:R:C:Ts:La (vb)

Etymology: Latin *thyrsus*, a thyrsus, and *flos*, a flower, pertaining to the inflorescence.

DESCRIPTION AND HABITAT

Plants proliferating from base, forming small, dense mats to clusters 80 mm in diameter. Roots fibrous. Branches short, herbaceous, 20–40 mm long, terete, sparsely to densely strigose, 1.5–3.0 mm in diameter, green, reddish when exposed. Leaves sessile, crowded, compact, 4-ranked, becoming smaller distally forming a pyramidal shape, ovate-triangular, 6–13 × 3–7 mm; surface glabrous, green to reddish; margin with translucent cilia. Inflorescence a conspicuous elongated, loose, spike-like thyrsus, often with stalked dichasia, 20–90 mm long; peduncle conspicuously reddish; bracts ovate, leaf-like, becoming smaller distally. Flowers 2 mm long, 3.0–3.5 mm in diameter, diurnal, sweetly scented. Corolla lobes oblong-ovate, white to pink, apices recurved.

Phenology: Flowering in summer (December–March) and early autumn. Flowers diurnal, strongly scented (unpleasant indoors).

Pollinators: The conspicuous diurnal flowers suggest a day-flying insect.

Habitat and aspect: Sheltered cliffs, often confined to dry river valleys and narrow shady kloofs (mainly on southern and eastern aspects). Plants are firmly rooted in crevices and size often depends on the growing space allowed by the crevice. Temperature high in summer, sometimes reaching 40°C. Winters are cooler but frost is absent. The average daily maximum temperature is about 26–27°C and the average daily minimum temperature about 10–11°C. Rainfall throughout the year but with a peak in spring and summer, ranging from 200–300 mm per annum (thunder showers or cyclonic winter rain).

Altitude: 300–1000 m.

Associated vegetation: Mainly thicket (Southern Cape, Gamtoos, Groot and Gamka Thicket) and Grootrivier Quartzitic Fynbos (Mucina *et al.* 2005).

Associated cremnophytes: At the Kouga Dam, it grows with *Albuca cremnophila*, *Aloe pictifolia*, *Cotyledon tomentosa*, *Crassula perfoliata* var. *minor*, *C. perforata*, *Cyrtanthus flammus* and *Gasteria glomerata*.

Geology: Quartzitic sandstone of the Peninsula Formation (Cape Supergroup) and shale cliffs (Gourits River).

DISTRIBUTION

Baviaanskloof and Kouga Mountains in the Eastern Cape and the lower Gourits River at the eastern end of the river.

RELATED SPECIES

Distinguished from the level-ground populations by its strictly 4-ranked leaves, smaller size and sometimes drooping branches and inflorescences. The related level-ground forms are much larger, more robust, with leaves and flowers more laxly and untidily arranged.

ADAPTATIONS TO THE CLIFF ENVIRONMENT

Habit: Conspicuous reduction in size and compact mats compared to the typical non-cremnophilous form of *Crassula capitella* subsp. *thyrsoflora*.

Size and weight: Clusters small, of light weight, forming mats up to 80 mm in diameter.

Stem: Short, usually unexposed owing to arrangement of leaves.

Leaves

Orientation: Leaves 4-ranked, forming compact pyramidal bodies. This reduction in size and compact growth can be viewed as an adaptation to the extreme xeric conditions of the cliff face.

Colour: Epidermis yellowish green, becoming reddish during dry periods. The stems have translucent white cilia. The reddish colour (due to anthocyanins) under dry conditions reduces penetration of light and is typical of many succulent plants in xeric habitats.

Age and persistence: Plants long-lived perennials.

Armament and camouflage: Soft-leaved plant bodies without conspicuous armament or camouflage properties, as opposed to the level-ground species of which some, such as *Crassula capitella* subsp. *capitella* and subsp. *nodulosa*, have a solitary habit or a few branches, the compact clusters suggesting adaptation to the largely undisturbed cliff-face habitat.

Sexual reproduction

Flowers: Flowering in late summer or early autumn, the strong scent suggesting a day-flying specialist pollinating agent (insect).

Fruit/Seed

Size: Seed minute and ideal for establishment in crevices.

Dispersal: Follicles dehiscent, with seeds spontaneously released and dispersed by wind.

Time: Seeds released in autumn at the onset of the rainy season, maximising establishment.

Vegetative reproduction: *Crassula capitella* subsp. *thyrsoiflora* is prolific from the base, forming dense vegetative clusters. As in most other *Crassula* taxa, these offshoots will root if they become detached and fall into a new crevice (as a result of heavy wind or other disturbances), a vegetative reproductive backup system ensuring long-term survival.

CONSERVATION STATUS

Locally common and well protected in the cliff habitat.

ADDITIONAL NOTES

Horticulture: Ideal for thicket and dry fynbos gardens, grown in miniature rockeries. It thrives in containers and the reddish colour of the leaves is appealing. Its vigour can be viewed as maximising survival. Dividing annually and rapidly, forming dense clusters. Easily grown from cuttings. Best grown in full sun or dappled shade, in sandy soil. Feed in spring.

VOUCHER

Van Jaarsveld 7234, 17115 (NBG).

ILLUSTRATIONS AND MAP

Plate 115, Figures 115a–115h, Map 115.

116. *Crassula cremnophila* Van Jaarsv. & A.E.van Wyk in *Aloe* 36,4: 71–72 (1999).

Cremnophyte growth form: Mat-forming cluster (of light weight, cliff hugger).

Growth form formula: A:S:Lper:R:C:Ts:La (vb)

Etymology: Greek *kremnos*, cliff, and Greek *phileein*, to love, pertaining to its cliff habitat.

DESCRIPTION AND HABITAT

Dwarf-sized, perennial, sparsely to moderately branched, forming clusters or small mats 12–25 mm high (up to 70 mm high with inflorescence). Leaves rosulate, alternately arranged, spreading, imbricate, recurved, forming a hemispherical body 20–70 mm in diameter; blade broadly obovate, 15–35 × 10–32 mm; surface glabrous, glaucous green; margin ciliate; apex rounded to subacute, mucronate. Inflorescence a terminal, erect, round-topped thyrse up to 30 mm in diameter, bearing numerous clustered dichasia; peduncle up to 35 mm long; bracts

lanceolate, 7×2 mm; flowers sessile to shortly pedicellate (up to 1 mm). Calyx lobes oblong-lanceolate, 3×1 mm long; margin ciliate; apex acute, ending in translucent bristle. Corolla scented, up to 7 mm long; lobes not fused at base, ascending-spreading, pink, oblong-ob lanceolate, up 7×1.5 mm; apices obtuse to subacute. Filaments 4 mm long, not broadening towards base; anthers yellow, 0.5 mm long. Squamae narrow-oblong, broadening towards apex, $5-7 \times 2$ mm translucent, slightly yellowish. Carpels 2.5 mm long; ovaries reniform, abruptly constricted into outward pointing, short, reflexed styles.

Phenology: Flowering from spring to midsummer (September–January).

Pollinators: The conspicuous diurnal flowers suggest a day-flying insect.

Habitat and aspect: Mainly sheltered south-facing cliffs (all aspects, more on southern ones). Plants grow in shallow soil among leaf litter on shady rocky ledges and often in the shade of cliff-dwelling shrubs or trees. Temperature is high in summer and mild in winter. The average daily maximum temperature is about 27°C and daily minimum about 12°C . Rainfall in winter (cyclonic winter rain) and summer (thunder showers), ranging from 200–300 mm per annum.

Altitude: 500–800 m.

Associated vegetation: Gamtoos Thicket of the Albany Thicket Biome (Mucina *et al.* 2005).

Associated cremnophytes: *Cotyledon orbiculata*, *Crassula lactea*, *C. perfoliata* var. *minor*, *C. perforata*, *Drimia anomala* and *Ornithogalum longibracteatum*.

Geology: Quartzitic sandstone (Table Mountain Formation, Cape Supergroup).

DISTRIBUTION

Crassula cremnophila is confined to the Baviaanskloof and Kouga Rivers.

RELATED SPECIES

Crassula cremnophila belongs to section *Rosulares*, which includes 22 species (Toelken 1985). It is related to both *C. montana* subsp. *quadrangularis* and *C. hemisphaerica* (section *Rosulares*). It is at once distinguished from these species by its glaucous leaves, hemispherical bodies and pink corolla 7 mm long. The flowers of *C. hemisphaerica* are 2–2.8 mm long. The stamens of *C. cremnophila* are also without black anthers. *Crassula montana* subsp. *quadrangularis* is a smaller mat-forming species (square bodies) with white flowers.

ADAPTATIONS TO THE CLIFF ENVIRONMENT

Habit: Sparsely clustered, plants conspicuous and not camouflaged. The tight, imbricate leaves and glaucous colouring can be seen as an adaptation to the xeric cliff face.

Size and weight: Clusters small, of light weight.

Stem: Short, usually unexposed.

Leaves

Orientation: Compact, rosulate, alternately arranged, becoming reddish during dry periods. The compact nature can be viewed as an adaptation to the dry conditions on the cliff face.

Colour: Glaucous, becoming reddish. The reddish colour (production of anthocyanins) under dry conditions reduces penetration of excessive light, an adaptation to the dry, well-drained habitat.

Age and persistence: Plants long-lived perennials.

Armament: Soft-leaved plant bodies without conspicuous armament.

Sexual reproduction

Flowers: Flowering from spring to midsummer, pollinated by insects.

Fruit/Seed

Size: Seed minute and ideal for establishment in crevices.

Dispersal: Follicles dehiscent, with seeds spontaneously released and dispersed by wind.

Time: Seeds released in summer and autumn, coinciding with rainy conditions and maximising establishment.

Vegetative reproduction: *Crassula cremnophila* proliferates, forming small mats and cushions, an efficient vegetative backup strategy helping the plants to survive the harsh conditions on the cliff face. When an offshoot becomes detached and falls into another crevice (as a result of heavy wind or other disturbance), it will root, ensuring long-term survival.

CONSERVATION STATUS

Classified as rare (Raimondo *et al.* 2009). Although *Crassula cremnophila* is not common locally, it is well protected by the inaccessible cliff habitat.

ADDITIONAL NOTES

Horticulture: Best for thicket gardens, grown in rockeries, miniature succulent gardens and containers. Easily cultivated, its vigour viewed as maximising survival. Propagate by division. Water sparingly throughout the year and it is best kept in dappled shade. Outside the cliff habitat, it is best grown under controlled conditions in a greenhouse.

VOUCHER

Van Jaarsveld 17368 (NBG).

ILLUSTRATIONS AND MAP

Plates 116 & 116a, Figures 116a–116d, Map 116.

117. *Crassula cymbiformis* Toelken in Flora of southern Africa 14: 163 (1985).

Cremonophyte growth form: Mat-forming cluster (of light weight, cliff hugger).

Growth form formula: A:S:Lper:R:C:Ts:La (vb)

Etymology: The epithet *cymbiformis*, boat-shaped, pertains to the leaves.

DESCRIPTION AND HABITAT

Sparsely branched, decumbent to erect, tufted, succulents, up to 120 mm high (in flower). Roots fibrous. Branches firm, decumbent. Leaves sessile, 4-ranked; lamina 15–95 × 15–32 mm, green to reddish green; basal leaves ovate-triangular to oblong-obovate; distal leaves lanceolate, dorsiventrally flattened, cymbiform; surface glabrous; margin ciliate; apex acute; base cuneate. Inflorescence a terminal, flat-topped thyrse bearing many dichasia; pedicels up to 6 mm long. Calyx lobes linear-triangular, up to 1 mm long. Corolla tubular, up to 5 mm long, shortly fused at base; lobes up to 4 mm long, lanceolate, spreading, becoming recurved. Anthers black.

Phenology: Flowering from early summer to early autumn (December–March).

Pollinators: The conspicuous white flowers suggest a day-flying insect.

Habitat and aspect: Cliffs on the southern margin of the Waterberg (Limpopo Province). Also deeply dissected kloofs of the escarpment (southern aspects). Plants are rooted in crevices and on ledges. Winters are cool but frost is absent or light. Temperature moderate, the average daily maximum about 27°C and the average daily minimum for the region about 15°C. Rainfall mainly in summer, ranging from 700–800 mm per annum.

Altitude: 1000–1750 m.

Associated vegetation: Waterberg-Magaliesberg Summit Sourveld of the Grassland Biome (Mucina *et al.* 2005).

Associated cremonophytes: *Aeollanthus buchnerianus*, *A. parvifolius*, *Agapanthus coddii*, *Aloe arborescens*, *Bulbine natalensis*, *Crassula cymbiformis*, *C. sarcocaulis*, *C. setulosa*, *C. swaziensis*, *Delosperma waterbergensis*, *Lobelia aquamontana*, *Teedia pubescens* and *Tetradenia brevispicata*.

Geology: Quartzitic sandstone Matlabas Subgroup (Waterberg Group).

DISTRIBUTION

Known only from the Waterberg, east of Thabazimbi (Limpopo Province), confined to sheer cliffs.

RELATED SPECIES

Crassula cymbiformis belongs to section *Rosulares*, which contains 22 species of which eight are cremonophilous. Members of the section are characterised by ciliate leaves in a basal rosette. *Crassula cymbiformis* is at once distinguished by its compact, triangular-ovate, reddish leaves (in four ranks), flat-topped thyrse and flowering time in summer.

ADAPTATIONS TO THE CLIFF ENVIRONMENT

Habit: Tight, compact mats.

Size and weight: Clusters of light weight.

Stem: Short, usually unexposed.

Leaves

Orientation: Compact, in opposite pairs (decussate), becoming reddish during dry periods. The compact nature can be viewed as an adaptation to the dry conditions on the cliff face.

Colour: Epidermis green, becoming reddish purple (during dry periods) owing to anthocyanins which reduce penetration of excessive light.

Age and persistence: Plants long-lived perennials.

Armament: Soft-leaved plant bodies without conspicuous armament.

Sexual reproduction

Flowers: Flowering from early summer to early autumn.

Fruit/Seed

Size: Seed minute and ideal for establishment in crevices.

Dispersal: Follicles dehiscent, with seeds spontaneously released and dispersed by wind.

Time: Seeds released in summer and autumn, during the rainy season.

Vegetative reproduction: *Crassula cymbiformis* is prolific from the base, forming dense vegetative clusters. As in most other *Crassula* taxa, these offshoots will root if they become detached and fall into other crevices (as a result of heavy wind or other disturbances), a vegetative reproductive backup system ensuring long-term survival.

CONSERVATION STATUS

Although classified as critically rare (Raimondo *et al.* 2009), it is common in its habitat. It is also not threatened owing to the undisturbed habitat and protection within the borders of the Marakele National Park.

ADDITIONAL NOTES

Lost and found: This species was named in 1985. It was lost after its discovery by Mr Dave Hardy but found again in 2003 by Mr Andrew Hankey and the author on the south-facing cliffs of the Marakele National Park.

Horticulture: Best for highveld gardens, grown in rockeries or containers. Easily cultivated, its vigour viewed as maximising survival. Propagate from cuttings or division. Plant fairly fast-growing, dividing annually and forming small, dense clusters.

VOUCHER

Van Jaarsveld 17952 (NBG).

ILLUSTRATIONS AND MAP

Figures 117a–117c, Map 117.

118. *Crassula exilis* Harv. subsp. *cooperi* (Regel) Toelken in Journal of South African Botany 41: 104 (1975).

Cremonophyte growth form: Dwarf-sized, mat-forming cluster (of light weight, cliff hugger).

Growth form formula: A:S:Lper:R:C:Ts:La (vb)

Etymology: After Thomas Cooper (1815–1913), British traveller and plant collector who collected at the Cape from 1859–1862.

DESCRIPTION AND HABITAT

Plants dwarf-sized, rosulate, proliferating from base to form dense cushions up to about 100 mm in diameter. Roots fibrous. Branches often with adventitious roots. Leaves oblanceolate, ovate to linear-elliptic, 6.0–35 × 3–10 mm, spirally arranged, spreading, dorsiventrally flattened, light to dark green becoming purplish with drought stress, glabrous; upper surface flat to convex, with conspicuous purplish indentations (pitted), lower surface convex; margin ciliate; apex acute. Inflorescence a terminal, flat-topped thyrse; peduncle covered with recurved hairs.

Pollinators: The conspicuous diurnal flowers suggest a day-flying insect.

Habitat and aspect: Sheltered cliffs of mainly shady southern and eastern aspects at higher altitudes. Plants grow in shallow soil on shady rocky ledges. Temperature high in summer, mild in winter. Average daily maximum temperature 23–25°C, average daily minimum 8–10°C. Rainfall mainly in summer (thunder showers), ranging from 500–1000 mm per annum.

Altitude: 900–1500 m.

Associated vegetation: Karoo Escarpment Grassland of the Grassland Biome (Mucina *et al.* 2005).

Associated cremonophytes: Species recorded at the Valley of Desolation: *Cotyledon orbiculata* var. *orbiculata*, *Crassula lanceolata* subsp. *lanceolata*, *C. nemorosa*, *C. perforata*, *Delosperma* spp., *Drimia uniflora* and *Haemanthus humilis* subsp. *hirsutus*.

Geology: Beaufort shales (Adelaide Subgroup, Karoo Supergroup).

DISTRIBUTION

Crassula exilis subsp. *cooperi* is confined to the Eastern Cape between Graaff-Reinet and Aliwal North, its distribution just entering the Northern Cape (Aliwal North district).

RELATED SPECIES

Crassula exilis subsp. *cooperi* belongs to section *Rosulares*, which contains 22 species (Toelken 1985). It can immediately be separated from any other *Crassula* by its follicles spreading at right angles at maturity. It can be distinguished from the other two subspecies by its larger, oblanceolate, less succulent, mottled leaves. *Crassula exilis* is related to *C. capitella* subsp. *thyrsiflora* (not a cremnophyte) but can at once be distinguished by its very dwarf-sized stature and terminal, flat-topped thyrse. *Crassula capitella* has an elongated inflorescence.

ADAPTATIONS TO THE CLIFF ENVIRONMENT

Habit: Dense mats and cushions, plants fairly conspicuous. The tightly arranged leaves and prolific, mat-forming nature suggest an adaptation to the xeric cliff face, filling the crevice rapidly lowering establishment of other cremnophytes.

Size and weight: Clusters small, of light weight.

Stem: Short, usually unexposed.

Leaves

Orientation: Compact, spreading, becoming reddish during dry periods. The compact nature can be viewed as an adaptation to the dry conditions on the cliff face. Leaves pitted, purplish and attractive, soft texture and fragile nature suggesting adaptation to the sheltered, undisturbed cliff face.

Colour: Epidermis dark green, mottled, green becoming reddish, indentations remaining purplish. The reddish colour under dry conditions blocks excessive light, an adaptation resulting from the well-drained habitat.

Age and persistence: Rapid vegetative growth leading to constant renewal of populations, plants thus long-lived perennials.

Armament: Soft-leaved plant bodies without conspicuous armament.

Sexual reproduction

Flowers: Flowering in summer and autumn, pollinated by insects.

Fruit/Seed

Size: Seed minute and ideal for establishment in crevices.

Dispersal: Follicles dehiscent, with seeds spontaneously released and dispersed by wind.

Time: Seeds released in autumn at the onset of cooler conditions, maximising establishment.

Vegetative reproduction: *Crassula exilis* subsp. *cooperi* proliferates, forming dense mats and cushions, an efficient vegetative backup strategy helping the plants to survive the harsh conditions on the cliff face. When an offshoot becomes detached (as a result of heavy wind or some other disturbance), it will root if it falls into a new crevice, ensuring long-term survival.

CONSERVATION STATUS

Locally common and not threatened owing to the undisturbed cliff habitat.

ADDITIONAL NOTES

Horticulture: Best for dry karoo gardens, grown in miniature succulent gardens, roof gardens or containers. Easily cultivated, its vigour viewed as maximising survival. Propagate from cuttings or division. Grows best in sandy, slightly acid soil, preferably in dappled shade.

VOUCHER

Van Jaarsveld 18273 (NBG).

ILLUSTRATIONS AND MAP

Figures 118a & 118b, Map 118.

119. *Crassula exilis* Harv. subsp. *exilis*, Harvey, *Flora capensis* 2: 347 (1862).

Cremonophyte growth form: Dwarf-sized, mat-forming cluster (of light weight, cliff hugger).

Growth form formula: A:S:Lper:R:C:Ts:La (vb)

Etymology: Latin *exilis*, weak, thin and slender, pertaining to the plants.

DESCRIPTION AND HABITAT

Plants dwarf-sized, rosulate, proliferating from base to form dense cushions up to about 50 mm in diameter. Roots fibrous. Branches often with adventitious roots; main branch up to 10 mm in diameter. Leaves linear-elliptic to linear-obovate, 4–15 × 2–3 mm, spirally arranged or decussate, ascending-spreading, dorsiventrally flattened; upper surface flat to convex; lower surface markedly convex; surface light to dark green, uniform, glabrous; margin ciliate; apex acute. Inflorescence a terminal dichasium with pedicellate flowers. Calyx lobes up to 2.5 mm long, narrow to broadly triangular; margin ciliate; apex acute, with a firm apical hair. Corolla white, tubular, 5 mm long; lobes oblong-obovate, up to 4 mm long, apices acute. Anthers yellow.

Pollinators: The conspicuous diurnal flowers suggest a day-flying insect.

Habitat and aspect: Vertical sheltered south-facing cliffs (shady southern and eastern aspects). Plants grow in shallow soil on shady rocky ledges. Temperature is high in summer and mild in winter. The average daily maximum temperature is 25–26°C and the average daily minimum 10–12°C. Rainfall occurs mainly in winter (mainly cyclonic cold fronts) and summer (thunder showers in spring and autumn) and ranges from 100–200 mm per annum.

Altitude: 900–1100 m.

Associated vegetation: Namaqualand Blomveld of the Namaqualand Hardeveld Bioregion of the Succulent Karoo Biome (Mucina *et al.* 2005).

Associated cremnophytes: *Adromischus alstonii*, *Cotyledon orbiculata*, *Haworthia arachnoidea*, *Tylecodon paniculatus* and *T. tuberosum*.

Geology: Quartz of the Khurisberg Subgroup, Bushmanland Group.

DISTRIBUTION

Crassula exilis subsp. *exilis* is confined to northern Namaqualand between Ratelpoort and Steinkopf, just north of Springbok (Northern Cape). It is also known from Dabenorisberg.

RELATED SPECIES

Crassula exilis subsp. *exilis* belongs to section *Rosulares*, which includes 22 species (Toelken 1985). *Crassula exilis* can immediately be separated from any other *Crassula* by its follicles spreading at right angles at maturity. The subsp. *exilis* can be distinguished from the other two subspecies by its leaves, which are not pitted (indentations absent). The leaves are also fleshier than those of the other two related subspecies. *Crassula exilis* is related to *C. capitella* subsp. *thyrsiflora* (non-cremnophilous) and can at once be distinguished by its very dwarf-sized stature and terminal, flat-topped thyrse. *Crassula capitella* has an elongated inflorescence.

ADAPTATIONS TO THE CLIFF ENVIRONMENT

Habit: Dense cushions, plants conspicuous and not camouflaged. The tightly arranged leaves are not camouflaged and can be seen as an adaptation to the xeric cliff face in absence of larger herbivores.

Size and weight: Clusters small, of light weight.

Stem: Short, usually unexposed, main branch up to 10 mm, succulent.

Leaves

Orientation: Compact, ascending-spreading, frail and fragile, becoming reddish during dry periods. The fragile and compact nature can be viewed as an adaptation to the dry, undisturbed conditions on the cliff face.

Colour: Epidermis green, becoming reddish. The reddish colour (production of anthocyanins) under dry conditions protects the plants by preventing penetration of excessive light, an adaptation to the xeric cliff habitat.

Age and persistence: Plants long-lived perennials.

Armament: Soft-leaved plant bodies without conspicuous armament.

Sexual reproduction

Flowers: Conspicuous in when flowering from autumn to spring, pollinated by insects.

Fruit/Seed

Size: Seed minute and ideal for establishment in crevices.

Dispersal: Follicles dehiscent, with seeds spontaneously released and dispersed by wind.

Time: Seeds released in winter and spring under cool, moist conditions, maximising establishment.

Vegetative reproduction: *Crassula exilis* subsp. *exilis* proliferates, forming dense mats and cushions, an efficient vegetative backup strategy helping the plants to survive the harsh conditions on the cliff face. When an offshoot becomes detached, it will root if it falls into a new crevice (as a result of heavy wind or some other disturbance), ensuring long-term survival.

CONSERVATION STATUS

Classified as rare (Raimondo *et al.* 2009). Locally common and well protected by the cliff habitat.

ADDITIONAL NOTES

Horticulture: Best for dry succulent karoo gardens, grown in miniature succulent gardens, roof gardens or containers. Easily cultivated, its vigour viewed as maximising survival. Propagate from cuttings or division. Grows best in sandy, slightly acid soil, preferably in dappled shade.

VOUCHER

Van Jaarsveld 22160 (NBG).

ILLUSTRATIONS AND MAP

Figures 119a–119d, Map 119.

120. *Crassula exilis* Harv. subsp. *sedifolia* (N.E.Br.) Toelken in Journal of South African Botany 41: 104 (1975).

Cremonophyte growth form: Dwarf-sized, mat-forming cluster (of light weight, cliff hugger).

Growth form formula: A:S:Lper:R:C:Ts:La (vb)

Etymology: The epithet *sedifolia* (*sedes*, position, and *folium*, leaf) perhaps pertains to the position of the leaves.

DESCRIPTION AND HABITAT

Plants dwarf-sized, rosulate, proliferating from base to form dense cushions up to about 60 mm in diameter. Roots fibrous. Branches often with adventitious roots; main branch thickened, up to 10 mm in diameter. Leaves linear-elliptic, 4–15 × 1–3 mm, spirally arranged, spreading, dorsiventrally flattened, light to dark green becoming purplish with drought stress, glabrous; upper surface flat to convex with conspicuous purplish indentations (pitted), lower surface keeled; margin ciliate; apex acute. Inflorescence a terminal flat-topped thyrse; peduncle glabrous.

Pollinators: The conspicuous diurnal flowers suggest a day-flying insect.

Habitat and aspect: Sheltered cliffs, growing mainly on shady southern and eastern aspects, in shallow soil on shady rocky ledges. Temperature high in summer and mild in winter. The average daily maximum temperature is 27–28°C and the average daily minimum 11–12°C. Rainfall occurs mainly in summer (mainly thunder showers) and winter (cyclonic winter rain) and ranges from 200–300 mm per annum.

Altitude: 500–900 m.

Associated vegetation: Eastern Gariiep Rocky Desert of the Desert Biome (Mucina *et al.* 2005).

Associated cremonophytes: On Pellaberg, the following species have been recorded: *Adromischus diabolicus*, *Aloe dabenorisana*, *Crassula garibina* and *Tylecodon sulphureus* var. *armianus*.

Geology: Quartz (Aggeneys Formation, Bushmanland Group, Proterozoic).

DISTRIBUTION

Crassula exilis subsp. *sedifolia* is confined to the lower Orange River Valley between Pella and Kakamas (Northern Cape) as well as southern Namibia, from Auros to Riemvasmaak.

RELATED SPECIES

At once distinguished from the other subspecies by its glabrous peduncle and thickened main branch. *Crassula exilis* subsp. *sedifolia* belongs to section *Rosulares*, which includes 22 species (Toelken 1985). It can immediately be separated from its related subspecies by the thickened main branch and glabrous peduncles.

ADAPTATIONS TO THE CLIFF ENVIRONMENT

Habit: Dense cushions, plants conspicuous and not camouflaged. The tightly arranged leaves and prolific, mat-forming nature suggests an adaptation to the xeric cliff face, filling the crevice rapidly lowering establishment of other dwarf-sized cremnophytes.

Size and weight: Clusters dwarf-sized, of light weight.

Stem: Short, usually unexposed, main stem succulent, up to 10 mm in diameter.

Leaves

Orientation: Compact, becoming reddish during dry periods. The compact nature can be viewed as an adaptation to the dry conditions on the cliff face. Leaves pitted, purplish and attractive, soft texture and fragile nature suggesting adaptation to the sheltered, undisturbed cliff face.

Colour: Epidermis green, becoming reddish, indentations remaining purplish. The reddish colour (production of anthocyanins) under dry conditions reduces penetration of excessive light, an adaptation to the xeric cliff environment.

Age and persistence: Rapid vegetative growth leading to constant renewal of populations, plants thus long-lived perennials.

Armament: Soft-leaved plant bodies without conspicuous armament.

Sexual reproduction

Flowers: Flowering in summer and autumn, pollinated by insects.

Fruit/Seed

Size: Seed minute and ideal for establishment in crevices.

Dispersal: Follicles dehiscent, with seeds spontaneously released and dispersed by the wind.

Time: Seeds released in autumn at onset of cooler conditions, maximising establishment.

Vegetative reproduction. *Crassula exilis* subsp. *sedifolia* proliferates, forming dense mats and cushions, an efficient vegetative backup strategy helping the plants to survive the harsh conditions on the cliff face. When an offshoot becomes detached, it will root if it falls into a new crevice (as a result of heavy wind or some other disturbance), ensuring long-term survival.

CONSERVATION STATUS

Locally common and not threatened owing to the undisturbed cliff habitat.

ADDITIONAL NOTES

Horticulture: Best for dry karoo gardens, grown in miniature succulent gardens, roof gardens or containers. Easily cultivated, its vigour viewed as maximising survival. Propagate from cuttings or division. Grows best in sandy, slightly acid soil, preferably in dappled shade.

VOUCHER

Van Jaarsveld 19154 (NBG).

ILLUSTRATIONS AND MAP

Figures 120a–120d, Map 120.

121. *Crassula expansa* Dryand. subsp. *fragilis* (Baker) Toelken in Journal of South African Botany 41: 105 (1975).

Cremonophyte growth form: Dwarf-sized, mat-forming (of light weight, cliff hugger).

Growth form formula: E:F:P:Els (vb)

Etymology: Latin *fragilis*, fragile, pertaining to its soft delicate nature.

DESCRIPTION AND HABITAT

Spreading, delicate, mat-forming, succulent herbs up to 100 mm high and 250 mm in diameter, rooting at nodes. Roots fibrous. Branches decumbent, green to reddish, glabrous to tomentose, up to 2.5 mm in diameter. Leaves shortly petiolate or with cuneate base; blade 2–10 × 4–6 mm, dorsiventrally compressed, ovate to broadly elliptic, rarely obovate, green to greyish green; upper surface flat; lower surface convex; margin often reddish with a ring of hydathodes; apex acute; base cuneate. Flowers axillary in terminal clusters or solitary; pedicels 6–18 mm. Calyx lobes 2–5 mm long, linear. Corolla star-shaped, 4 mm long, up to 6 mm in diameter, petals white.

Phenology. Flowering in summer (November–April).

Pollinators: The small white flowers suggest an insect as possible pollinator.

Habitat and aspect: Shady wooded cliffs (mostly southern aspects) in river valleys and kloofs. Plants grow in shallow soil on shady rocky ledges. Temperatures are high in summer and warm to mild in winter. Average daily maximum temperature is 24–30°C and daily minimum 8–10°C. Rainfall mainly in summer (thunder showers), ranging from 450–1000 mm per annum.

Altitude: 50–1800 m.

Associated vegetation: Savanna Biome (Mucina *et al.* 2005).

Associated cremnohytes: At Penge (Mpumalanga), the following plants have been recorded on a cliff face: *Delosperma vandermerwei*, *Gasteria batesiana* var. *dolomitica*, *Orbeanthus hardyi* and *Plectranthus dolomiticus*.

Geology: It has been recorded as occurring on rock of the following formations: Mesozoic rhyolite (Jozini Formation) of the Lebombo Group, Palaeozoic sandstone and shale (Madzaringwe Formation) of the Karoo Sequence and quartzitic sandstone (Mozaan Formation) of the Pongola Sequence, dolomite of the Malmani Subgroup and Vaalian dolomites of the Chuniespoort Group (Transvaal Supergroup).

DISTRIBUTION

Widespread from the Eastern Cape to Limpopo Province, usually associated with savanna vegetation. It also occurs further north to Tanzania and on Madagascar.

RELATED SPECIES

Crassula expansa subsp. *fragilis* can be distinguished from the non-cremnophilous subspecies by its dorsiventrally flattened leaves. The subsp. *peculiaris* has a procumbent habit and is very similar to the subsp. *fragilis*.

ADAPTATIONS TO THE CLIFF ENVIRONMENT

Habit: Mat-forming, fragile, filling crevices, sometimes pendulous. The mat-forming and pendulous nature, compared to that of the level-ground species, suggests an adaptation to the undisturbed cliff habitat.

Size and weight: Clusters dwarf-sized, of light weight.

Stem: Erect, 100–300 mm in diameter, soft, fragile and flaccid.

Leaves

Orientation: Ascending-spreading to spreading, dwarf-sized, fragile, an adaptation to the undisturbed cliff face. The tomentose forms of the savanna regions suggest adaptation to the hot summers and xeric conditions on the cliff face.

Colour: Green to light green, turning reddish during dry periods as a result of the production of anthocyanins, reducing penetration of light.

Age and persistence: The plants are relatively rapid-growing, leading to constant vegetative renewal.

Armament: Branches soft and fragile without conspicuous armament, an adaptation to the cliff habitat.

Sexual reproduction

Flowers: Flowers axillary in terminal clusters, or solitary, white.

Fruit/Seed

Size: Seed minute and ideal for establishment in crevices.

Dispersal: Follicles dehiscent, with seeds spontaneously released and dispersed by wind.

Time: Seeds released in late summer.

Vegetative reproduction: Stems of *Crassula expansa* subsp. *fragilis* root where they come into contact with the soil. New branches are continuously formed during the growing season, filling crevices—an ideal long-term survival backup on the sheer cliff face. Branches that have become detached will root when landing on other ledges or in new crevices.

CONSERVATION STATUS

Locally common and well protected in the cliff habitat, not threatened.

ADDITIONAL NOTES

Horticulture: Best for bushveld and subtropical coastal gardens, on embankments and miniature rock gardens. Grow in dappled shade, in a sandy mixture. Thriving and popular as a pot plant. Easily cultivated, its vigour viewed as maximising survival. Propagate from cuttings or by division.

VOUCHERS

Van Jaarsveld 17456, 19307 (NBG).

ILLUSTRATIONS AND MAP

Figures 121a & 121b, Map 121.

122. *Crassula foveata* Van Jaarsv., in Van Jaarsveld & Van Wyk in *Bothalia* 33,1: 116–117 (2003e).

Cremonophyte growth form: Mat-forming cluster (of light weight, cliff hugger).

Growth form formula: A:S:Lper:R:C:Ts:La (vb)

Etymology: Latin *foveatus*, pitted, pertaining to the pitted leaves.

DESCRIPTION AND HABITAT

Plants proliferating from base, forming small, dense mats to clusters 100 mm in diameter. Roots fibrous. Branches short, herbaceous, 20–40 mm long, terete, sparsely strigose, glabrous lower down, 1–1.5 mm in diameter, green, becoming reddish when exposed. Leaves in a loose rosette, sessile, crowded, compact, decussately arranged, sometimes falcate and spreading, slightly recurved, becoming smaller distally, linear-lanceolate to triangular-lanceolate, 12–24 × 3–7

mm; surface glabrous, green becoming reddish, distinctly pitted (shallow leaf depressions), the pits consisting of rounded, reddish depressions 0.3–0.5 mm in diameter, abaxial surface rounded, foveate, adaxial surface canaliculate; margin rounded, thickened, sparsely beset with recurved translucent cilia; apex acute, apiculate. Inflorescence a conspicuous rounded to flat-topped thyrse up to 50 mm high and 50 mm in diameter, bearing 1–several dichasia; peduncle with translucent recurved hairs and a gradual transition of leaves to bracts, reddish; bracts ascending-spreading, distal bracts cymbiform, sparsely pitted, margin entire to sparsely ciliate. Flowers diurnal, sweetly scented, white to light pink, buds 3 mm long, open flowers 4 mm in diameter. Calyx lobes triangular with stout hair at apex, 1.5×0.8 mm. Corolla lobes spreading, oblong-ovate white to pink, apices apiculate. Corolla tubular; petals white, ovate-lanceolate, spreading, 2 mm long, acute. Stamens 1.5 mm long; anthers yellowish, 0.1 mm long. Squamae transversely oblong, 0.4×0.1 mm, yellowish orange. Carpel and style 2 mm long.

Phenology: Flowering in early autumn (March–April). Flowers diurnal, strongly scented.

Pollinators: The conspicuous diurnal flowers suggest a day-flying insect.

Habitat and aspect: Cliffs along river valleys (all aspects but mainly exposed northern and western aspects). Plants grow among leaf litter in shallow soil on rocky ledges and often in the shade of cliff-dwelling shrubs or trees. Temperatures are high in summer and mild in winter. The average daily maximum temperature is about 24°C and the average daily minimum about 12°C. Rainfall occurs mainly in summer and ranges from 800–1000 mm per annum (thunder showers, October–May).

Altitude: 300–800 m.

Associated vegetation: Eastern Valley Bushveld of the Savanna Biome (Mucina *et al.* 2005).

Associated cremnophytes: At Collywobbles, *Crassula foveata* grows with *Aptenia cordifolia*, *Cotyledon orbiculata*, *Crassula cordata*, *C. lactea*, *C. perfoliata* var. *minor*, *C. perforata*, *Delosperma* sp., *Drimia anomala* and *Ornithogalum longibracteatum*.

Geology: Sandstone and mudstone (Adelaide Subgroup, Karoo Supergroup).

DISTRIBUTION

Crassula foveata appears to be endemic to the dry river valleys of the Eastern Cape (Mbashe and Mzimvubu Rivers).

RELATED SPECIES

Crassula foveata belongs to section *Rosulares*, which contains 22 species of which eight are cremnophilous. It can immediately be distinguished by its reddish, densely pitted leaves. The leaves are variable in shape, almost subulate to dorsiventrally compressed.

ADAPTATIONS TO THE CLIFF ENVIRONMENT

Habit: Compared to other species in section *Rosulares*, there is a reduction in size and the plants tend to form compact mats, typical of so many cremnophytes.

Size and weight: Clusters small, of light weight.

Stem: Short, ascending to spreading.

Leaves

Orientation: Ascending-spreading, almost subulate, compact, decussately arranged, becoming reddish during dry periods. The rounded, almost subulate leaves, reduction in size and compact nature so typical of many cremnophytes can be viewed as adaptations to the dry conditions on the cliff face.

Colour: Epidermis green, becoming reddish purple, darker pitted surface resulting in a mottled appearance. Margin sparsely ciliate. The reddish colour (production of anthocyanins) under dry conditions reduces penetration of excessive light, an adaptation resulting from the well-drained habitat.

Age and persistence: Plants long-lived perennials.

Armament: Soft-leaved plant bodies without conspicuous armament as opposed to the level-ground species of which some, such as *Crassula capitella* subsp. *capitella* and subsp. *nodulosa*, have a solitary habit or a few branches, the compact clusters suggesting adaptation to the largely undisturbed cliff-face habitat.

Sexual reproduction

Flowers: Flowering in autumn, the strong scent suggesting a day-flying specialist pollinating agent (insect).

Fruit/Seed

Size: Seed minute, and ideal for establishment in crevices.

Dispersal: Follicles dehiscent, with seeds spontaneously released and dispersed by wind.

Time: Seeds released in autumn and winter at the onset of cooler conditions, maximising establishment.

Vegetative reproduction: *Crassula foveata* is prolific from the base, forming dense vegetative clusters. When an offshoot becomes detached, it will root if it falls into a new crevice (as a result of heavy wind or some other disturbance), a vegetative reproductive backup strategy ensuring long-term survival.

CONSERVATION STATUS

Classified as rare (Raimondo *et al.* 2009). Locally common, well protected in the cliff habitat.

ADDITIONAL NOTES

Horticulture: Best for subtropical coastal gardens, in dappled shade in rockeries or containers. Easily cultivated, its vigour viewed as maximising survival. Propagate by division or cuttings.

VOUCHER

Van Jaarsveld, Xaba & Harrower 13 (NBG).

ILLUSTRATIONS AND MAP

Figures 122a & 122b, Map 122.

123. *Crassula intermedia* Schönland in Transactions of the Royal Society of South Africa 17: 244 (1929).

Cremnophyte growth form: Small to dense clusters (of light to medium weight, cliff hugger).

Growth form formula: A:S:Lper:R:C:Ts:La (vb)

Etymology: Latin *intermedius*, pertaining to its relationships with others in the group such as *Crassula montana* subsp. *quadrangularis* and *C. orbicularis*.

DESCRIPTION AND HABITAT

Plants rosulate, usually proliferating from base to form dense groups up to 60 mm high (without inflorescence). Roots fibrous. Leaves obovate to oblong-obovate, dorsiventrally flattened, 20–50 × 13–25 mm, distal leaves ascending, tightly imbricate, forming hollow cup, basal leaves spreading, not imbricate; surface grey-green to pale green, glabrous; margin ciliate; apex acute to obtuse. Inflorescence a terminal, elongate to round-topped thyrse bearing many clustered dichasia; peduncle up to 150 mm long. Calyx lobes up to 1.5 mm, ovate, ciliate. Corolla tubular, up to 3 mm long; lobes oblong-obovate, up to 2.5 mm long, fused shortly at base, apex rounded. Anthers yellow.

Phenology: Flowering in spring (August to October).

Pollinators: The small white flowers suggest a flying insect.

Habitat and aspect: *Crassula intermedia* is most often associated with sheltered south-facing cliffs. It occurs in large numbers and is easily detected. Summers are hot and humid but winters are cooler. The average daily maximum temperature is about 21–22°C and the average daily minimum for the region 12–13°C. Rainfall mainly in summer, ranging from 400–1000 mm per annum.

Altitude: 50–500 m.

Associated vegetation: Mainly Eastern Valley Bushveld (Mucina *et al.* 2005).

Associated cremnophytes: At Mzimvubu River cliffs near the Welch Bridge (northeastern part of the Eastern Cape), *Crassula pellucida* subsp. *alsinoides*, *Gasteria excelsa*, *Haemanthus albiflos* and *Ornithogalum longibracteatum* have been recorded.

Geology: Varied, shale and sandstone (Cape Supergroup).

DISTRIBUTION

Crassula intermedia occurs widespread in the Eastern Cape, especially in dry river valleys.

RELATED SPECIES

Related to *Crassula montana* subsp. *quadrangularis* but immediately distinguished by its pale grey-green, cup-shaped rosettes.

ADAPTATIONS TO THE CLIFF ENVIRONMENT

Habit: Conspicuous clusters, an adaptation to the undisturbed cliffs.

Size and weight: Clusters of light to medium weight.

Stem: Short, not visible.

Leaves

Orientation: In a dense cup-shaped rosette, the open rosettes maximising absorption of light on the south-facing cliffs.

Colour: Epidermis glaucous to pale green.

Age and persistence: Plants long-lived perennials. Leaves also persistent and long-lived, suggesting adaptation to the xeric cliff conditions.

Armament and camouflage: Leaves soft, bodies without conspicuous armament or camouflage properties.

Sexual reproduction

Flowers: Conspicuous when in flower, insect-pollinated.

Fruit/Seed

Size: Seed minute and ideal for establishment in crevices.

Dispersal: Follicles dehiscent, with seeds spontaneously released and dispersed by wind.

Time: Seeds dispersed during spring rains, maximising establishment.

Vegetative reproduction: Many forms proliferate from the base, forming dense groups, a vegetative backup survival strategy and adaptation to the sheer cliffs and high run-off. Detached offshoots will root where they fall into crevices below.

CONSERVATION STATUS

Locally common and well protected in the cliff habitat.

ADDITIONAL NOTES

Horticulture: Best for thicket and subtropical coastal gardens, grown in rockeries or containers, in dappled shade. Easily cultivated, its vigour viewed as maximising survival. Grow from cuttings or by division.

VOUCHERS

Van Jaarsveld 17815, 18756 (NBG).

ILLUSTRATIONS AND MAP

Figures 123a–123c, Map 123.

124. *Crassula lanuginosa* Harv. var. *lanuginosa*, Harvey, Flora capensis 2: 347 (1862).

Cremonphyte growth form: Dwarf-sized, mat-forming (of light weight, cliff hugger).

Growth form formula: E:F:P:Els (vb)

Etymology: Latin *lana*, wool, pertaining to the wool-like hairs on the leaves.

DESCRIPTION AND HABITAT

Densely branched, decumbent to prostrate, mat-forming plant up to 50 mm high and 200 mm in diameter. Roots fibrous. Branches about 1 mm in diameter, hairy, sometimes internodes not visible on short side branches owing to dense leaf arrangement, sometimes with aerial roots. Leaves elliptic to obovate, 2–10 × 1–4.5 mm, spreading ascending, dorsiventrally compressed, biconvex; epidermis with spreading hairs; apex acute, with long cilia. Inflorescence a thyse up to 15 × 5 mm, bearing 3–7 flowers and usually with 1 pair of bracts below inflorescence; peduncle 3–15 mm long; bracts triangular-oblong, 1 × 0.3 mm. Corolla up to 3 mm long, tubular; lobes fused at base, becoming recurved, lorate-obovate bearing a dorsal appendage, white to cream. Anthers black.

Phenology: Flowering in summer (January–March).

Pollinators: The white to cream corolla suggests a flying insect.

Habitat and aspect: Mainly shady cliffs, sometimes exposed. Plants grow in shallow soil on shady rocky ledges. Temperatures hot in summer and warm to mild in winter. Average daily maximum temperature is 24–25°C and daily minimum 9–10°C. Rainfall occurs mainly in summer (thunder showers) but with some winter rainfall (cyclonic) and occasional snow during cold fronts. It ranges from 200–450 mm per annum.

Altitude: 1000–3000 m.

Associated vegetation: Karoo Escarpment Grassland of the Grassland Biome (Mucina *et al.* 2005).

Associated cremnohytes: At Danielshoek (between Cradock and Pearston), the following plants have been recorded on a cliff face: *Crassula lanceolata* var. *lanceolata*, *C. nemorosa*, *Delosperma* sp., *Drimia uniflora* and *Haemanthus albiflos*.

Geology: Mainly Beaufort shales (Adelaide Subgroup, Karoo Supergroup).

DISTRIBUTION

Crassula lanuginosa var. *lanuginosa* is distributed from Graaff-Reinet, Cradock to Aliwal North in the Eastern and Northern Cape Provinces.

RELATED SPECIES

Differs from other members in section *Argyrophylla* in its soft fragile texture, small leaf size and mat-forming habit. Differs from *C. lanuginosa* var. *pachystemon* in its smaller leaves with sharply acute apices with apical cilia. In comparison, its level-ground relatives have firm, sturdy leaves, and the soft texture of var. *lanuginosa* can be interpreted as the result of a lack of disturbance by herbivores, having evolved in the absence of such disturbances.

ADAPTATIONS TO THE CLIFF ENVIRONMENT

Habit: Mat-forming, filling crevices, sometimes pendulous. This mat-forming, dwarf-sized, pendulous nature, compared to that of the level-ground species, suggests an adaptation to the sheer cliff face, where the plants often fill small crevices.

Size and weight: Clusters, dwarf-sized, of light weight.

Stem: Erect, 40–100(–150) mm long.

Leaves

Orientation: Ascending-spreading, soft, hairy.

Colour and texture: Grey-green to green. The soft texture is an adaptation to the undisturbed environment, and the hairiness an adaptation to the xeric conditions on the cliff face.

Age and persistence: The plants are relatively rapid-growing, but long-lived perennials.

Armament: Branches soft and fragile without conspicuous armament, an adaptation to the cliff habitat.

Sexual reproduction

Flowers: Inflorescence a thyrse, bearing 3–7 white to cream flowers.

Fruit/Seed

Size: Seed minute and ideal for establishment in crevices.

Dispersal: Follicles dehiscent, with seeds spontaneously released and dispersed by wind.

Time: Seeds released in late summer.

Vegetative reproduction: Stems of *Crassula lanuginosa* var. *lanuginosa* root where they come into contact with the soil. New branches are continuously formed during the growing season, filling crevices—an ideal long-term survival backup strategy on the sheer cliff face. Detached branches will root when they land on other ledges or in new crevices.

CONSERVATION STATUS

Locally common and well protected by the cliff habitat.

ADDITIONAL NOTES

Horticulture: Best for miniature succulent gardens or small containers in karoo and thicket gardens. Outside the habitat, it is best grown under controlled conditions in a greenhouse. Easily cultivated, its vigour viewed as maximising survival. Easily grown from seed or by division.

VOUCHER

Van Jaarsveld 18268 (NBG).

ILLUSTRATIONS AND MAP

Figures 124a–124d, Map 124.

125. *Crassula montana* Thunb. subsp. *montana*, Thunberg in Nova Acta Physico-Medica Academiae Caesareae Leopoldino-Carolinae ... 6: 329, 332 (1778).

Crempnophyte growth form: Mat-forming cluster (of light weight, cliff hugger).

Growth form formula: A:S:Lper:R:C:Ts:La (vb)

Etymology: Latin *montana*, mountain, pertaining to the habitat where this species grows.

DESCRIPTION AND HABITAT

Plants rosulate, usually proliferating from base to form small, dense groups up to 30 mm high (without inflorescence). Roots fibrous. Leaves ovate to broadly obovate, 15–25 × 10–16 mm, decussate, in dense basal rosette, becoming smaller distally, light to dark green, with dark green dots, glabrous but with short marginal cilia; apex acute to obtuse. Inflorescence a terminal spike-like thyrses, occasionally flat-topped, 50–90 mm high, bearing sessile dichasia; peduncle 10–80 mm long; bracts leaf-like, obovate to lanceolate 5–14 × 6–8 mm, ciliate. Calyx lobes 2–4 mm long, triangular-lanceolate, ciliate. Corolla tubular, 6 mm long; lobes oblong, 5 mm long, fused shortly at base.

Phenology: Flowering in spring (August–October).

Pollinators: The conspicuous diurnal flowers suggest a day-flying insect.

Habitat and aspect: Sheltered cliffs on mountain ranges and kloofs. Plants grow in shallow soil on shady rocky ledges and often in shade. Temperatures are high in summer and mild in winter. Average daily maximum temperature is 25–27°C and the average daily minimum 10–12°C. Rainfall occurs mainly in winter (cyclonic winter rain) and summer (thunder showers) and ranges from 200–300 mm per annum.

Altitude: 200–2000 m.

Associated vegetation: Agter-Sederberg Shrubland (Fynbos Biome) and Western Gwarrieveld (Succulent Karoo Biome) (Mucina *et al.* 2005).

Associated cremnoophytes: On the Wolfberg, the following cliff dwellers have been recorded: *Bulbine* sp., *Crassula nudicaulis*, *C. tomentosa* var. *glabrifolia* and *Senecio crassulaefolius*.

Geology: Quartzitic sandstone (Table Mountain Formation, Cape Supergroup).

DISTRIBUTION

Crassula montana subsp. *montana* is distributed from the southern Cedarberg to Badspoort south of Calitzdorp. Also recently reported from the Piekenierskloof Pass.

RELATED SPECIES

Crassula montana subsp. *montana* can be distinguished by its tight cushions of 4-ranked, obovate, mottled leaves forming almost cup-shaped rosettes.

ADAPTATIONS TO THE CLIFF ENVIRONMENT

Habit: The dense clusters can be viewed as vegetative output on the cliff face, filling crevices in absence of disturbances by larger herbivores.

Size and weight: Clusters small, of light weight.

Stem: Short, usually unexposed.

Leaves

Orientation: Spreading, in open rosettes, compact, decussately arranged. The compact nature can be viewed as an adaptation to the dry conditions on the cliff face.

Colour: Epidermis green, mottled, becoming reddish during dry periods. The reddish colour (production of anthocyanins) reduces penetration of light, an adaptation resulting from the well-drained, dry habitat.

Age and persistence: Plants long-lived perennials.

Armament: Soft-leaved plant bodies without conspicuous armament.

Sexual reproduction

Flowers: Flowering in spring, pollinated by insects.

Fruit/Seed

Size: Seed minute and ideal for establishment in crevices.

Dispersal: Follicles dehiscent, with seeds spontaneously released and dispersed by wind.

Time: Seeds released in summer at the onset of thunder showers, maximising establishment.

Vegetative reproduction. Plants proliferating, forming dense cushions, a vegetative backup strategy enabling the plants to survive the harsh conditions on the cliff face.

CONSERVATION STATUS

Locally common and well protected in the undisturbed cliff habitat, not threatened.

ADDITIONAL NOTES

Horticulture: Best for dry fynbos and succulent karoo gardens, grown in rockeries or containers. Outside its habitat, it is best grown under controlled conditions in a greenhouse. Keep dry during the summer months. Grow in a sandy soil, feed in autumn. Easily cultivated, its vigour viewed as maximising survival. Propagate by division. Dividing annually, rapidly forming dense clusters.

VOUCHERS

Van Jaarsveld 17167, 19545 (NMG).

ILLUSTRATIONS AND MAP

Plate 125, Figures 125a–125g, Map 125.

126. *Crassula montana* Thunb. subsp. *quadrangularis* (Schönland) Toelken in Journal of South African Botany 41: 109 (1975).

Cremonophyte growth form: Mat-forming cluster (of light weight, cliff hugger).

Growth form formula: A:S:Lper:R:C:Ts:La (vb)

Etymology: The epithet *quadrangularis*, with four angles, refers to the four-ranked arrangement of the leaves.

DESCRIPTION AND HABITAT

Plants rosulate, proliferating from base to form small, dense mats up to 30 mm high. Roots fibrous. Leaves in basal rosette, 4-ranked, obovate, 7–20 × 4–15 mm, abruptly tapering towards apex, forming a flat square rosette, light to dark green, with dark green dots, glabrous but with short marginal cilia; apex acute to obtuse. Inflorescence a terminal flat-topped thyrse 50–70 mm high, bearing sessile dichasia; bracts leaf-like, obovate to lanceolate, 5–14 × 6–8 mm, ciliate. Calyx lobes 4–5 mm long, triangular-lanceolate, ciliate. Corolla tubular, 6 mm long; lobes oblong, 5 mm long, fused shortly at base, apices spreading, white.

Phenology: Flowering in spring (August–October).

Pollinators: The conspicuous diurnal flowers suggest a day-flying insect.

Habitat and aspect: Sheltered cliffs, mainly on southern aspects. Plants grow in shallow soil among leaf litter on shady rocky ledges. Temperature high in summer and mild in winter. The average daily maximum temperature is 25–27°C and average daily minimum 10–12°C. Rainfall occurs in winter (cyclonic winter rain) and summer (thunder showers) and ranges from 200–300 mm per annum.

Altitude: 1000–1400 m.

Associated vegetation: Steytlerville Karoo (Rainshadow Valley Karoo Bioregion) of the Succulent Karoo Biome (Mucina *et al.* 2005).

Associated cremnophytes: *Cotyledon orbiculata*, *Crassula lactea*, *C. perfoliata* var. *minor*, *C. perforata*, *Drimia anomala* and *Ornithogalum longibracteatum*.

Geology: Quartzitic sandstone (Table Mountain Formation, Cape Supergroup).

DISTRIBUTION

Crassula montana subsp. *quadrangularis* is confined to the eastern Great Karoo and southwards to the lower slopes of the Cape Fold Belt mountains bordering the southern Great Karoo, from Laingsburg in the west to the Baviaanskloof in the east.

RELATED SPECIES

Crassula montana subsp. *quadrangularis* is related to *C. cremnophila* (section *Rosulares*). It is at once distinguished from this species by its square bodies, green leaves and white flowers. *Crassula cremnophila* has spherical, grey leaves and pinkish flowers. It is also related to *C. hemisphaerica* growing in non-cliff habitats, usually solitary, with mottled leaves and well camouflaged.

ADAPTATIONS TO THE CLIFF ENVIRONMENT

Habit: Dense, compact clusters and mat-forming on cliffs and rock overhangs. The dense clusters can be viewed as vegetative output on the cliff face, filling crevices in absence of disturbances by larger herbivores.

Size and weight: Clusters small, of light weight.

Stem: Short, usually unexposed.

Leaves

Orientation: Compact, decussately arranged, ascending, spreading, in tight rosettes. The dwarf-sized rosettes and compact nature can be viewed as an adaptation to the dry conditions on the cliff face.

Colour: Epidermis green, becoming reddish. The reddish colour (production of anthocyanins) appears under dry conditions, reducing penetration of excessive light, an adaptation resulting from the xeric conditions of the cliff habitat.

Age and persistence: Plants long-lived perennials.

Armament: Soft-leaved plant bodies without conspicuous armament.

Sexual reproduction

Flowers: Flowering in spring, pollinated by insects.

Fruit/Seed

Size: Seed minute and ideal for establishment in crevices.

Dispersal: Follicles dehiscent, with seeds spontaneously released and dispersed by wind.

Time: Seeds released in summer at the onset of rainy conditions, maximising establishment.

Vegetative reproduction: *Crassula montana* subsp. *quadrangularis* proliferates, forming dense mats and cushions, an efficient vegetative backup strategy enabling the plants to deal with the harsh conditions on the cliff face. When an offshoot becomes detached (as a result of heavy wind or other disturbance), it will root if it falls into a new crevice, ensuring long-term survival.

CONSERVATION STATUS

Crassula montana subsp. *quadrangularis* is common in the habitat, well protected by the cliff environment.

ADDITIONAL NOTES

Horticulture: Best for thicket gardens, grown in rockeries, miniature succulent gardens, roof gardens or containers. Grow in dappled shade. Easily cultivated, its vigour viewed as maximising survival. Propagate from cuttings or by division. Grows best in sandy, slightly acid soil.

VOUCHER

Van Jaarsveld 22356 (NBG).

ILLUSTRATIONS AND MAP

Figures 126a–126c, Map 126.

127. *Crassula nemorosa* (Eckl. & Zeyh.) Endl. ex Walp., *Repertorium botanices systematicae* 2: 253 (1843).

Cremonophyte growth form: Geophyte, compact cluster (of light weight, cliff hugger).

Growth form formula: A:S:Lar:D (vb)

Etymology: Latin *nemorosa*, woods and groves, perhaps pertaining to its wooded cliff-face habitat.

DESCRIPTION AND HABITAT

Geophytes with erect, branched to unbranched stems up to 150 mm high. Tuber spherical, with fibrous adventitious roots. Leaves broadly ovate to orbicular, 3–15 × 4–13 mm, dorsiventrally flattened; margin entire; surface glabrous, grey-green with brown lines; petiole 3–15 mm long; apex rounded to truncate; base cordate to abruptly cuneate. Inflorescence a lax terminal thyrse without peduncle. Calyx lobes triangular-ovate, up to 2.5 mm; apices acute to obtuse. Corolla stellate, shallowly cup-shaped, up to 8 mm in diameter, yellowish green; lobes lanceolate, up to 3.5 mm long; apices becoming recurved. Anthers yellow.

Phenology. Flowering from May–August.

Pollinators: The pale yellow corolla suggests a flying insect.

Habitat and aspect: Sheltered to somewhat exposed cliffs on mountain slopes and kloofs. Plants grow in shallow soil on shady rocky ledges. Temperatures hot in summer and warm to mild in winter. The average daily maximum temperature is 22–24°C and daily minimum 9–14°C. Rainfall occurs mainly in summer (thunder showers) in the eastern part, with winter rainfall in Namaqualand (cyclonic), ranging from 200–450 mm per annum.

Altitude: 200–1800 m.

Associated vegetation: Albany Thicket, Nama-Karoo and Succulent Karoo Biomes (Mucina *et al.* 2005).

Associated cremonophytes: At Danielshoek (between Cradock and Pearston), the following plants have been recorded on a cliff face: *Crassula lanceolata* var. *lanceolata*, *C. lanuginosa* var. *lanuginosa*, *Delosperma* sp., *Drimia uniflora* and *Haemanthus albiflos*.

Geology: Mainly Beaufort shales (Adelaide Subgroup, Karoo Supergroup), dolomite (Namibia).

DISTRIBUTION

Crassula nemorosa is widely distributed in the Eastern Cape around Queenstown, on the mountains of the southern Great Karoo and again in the Richtersveld and Hunsberg of southern Namibia.

RELATED SPECIES

Differs from other members of section *Petrogeton* (eight species) in its small size, glaucous, distinctly succulent leaves, of which the hydathodes are arranged in a ring on the leaf margin, and in the shallow cup-shaped flowers. This reduction in size and succulent, glaucous leaves can be seen as an adaptation to its xeric cliff-face habitat.

ADAPTATIONS TO THE CLIFF ENVIRONMENT

Habit: Forming small, loose clusters, often filling hairline cracks. The often dwarf size and unarmed, soft texture of the plants are adaptations to the undisturbed cliff-face habitat. The perennial succulent geophytic base ensures survival during dry periods.

Size and weight: Clusters dwarf-sized, of light weight.

Stem: Erect, 40–100(–150) mm long, flaccid, fragile.

Leaves

Orientation: Ascending-spreading.

Colour: Glaucous.

Age and persistence: Summer-deciduous, long-lived perennials.

Armament: Branches soft and fragile without conspicuous armament, an adaptation to the cliff habitat.

Sexual reproduction

Flowers: Inflorescence a lax terminal thyrse without peduncle, the flowers with a stellate, shallowly cup-shaped, yellowish green corolla, up to 8 mm in diameter. The flowers are relatively large, suggesting a specialist pollinator.

Fruit/Seed

Size: Seed minute and ideal for establishment in crevices.

Dispersal: Follicles dehiscent, with seeds spontaneously released and dispersed by wind.

Time: Seeds released in late summer.

Vegetative reproduction: Proliferates from its subterranean tubers, filling crevices, an efficient vegetative backup strategy enabling the plants to deal with the harsh conditions on the cliff face.

CONSERVATION STATUS

Classified as rare in Namibia (Loots 2005). Locally common and well protected in the cliff habitat.

ADDITIONAL NOTES

Horticulture: Best for miniature succulent gardens and containers. Allow for a resting period. Keep in dappled shade. Easily cultivated, its vigour viewed as maximising survival.

VOUCHER

Van Jaarsveld 21079 (NBG).

ILLUSTRATIONS AND MAP

Figures 127a–127d, Map 127.

128. *Crassula orbicularis* L., Species plantarum, edn 1: 283 (1753). (Luputana form.)

Cremonophyte growth form: Rarely solitary, small clusters, mat-forming (of light weight, cliff hugger).

Growth form formula: A:S:Lper:R:C:Ts:La (vb)

Etymology: The epithet *orbicularis*, rounded, pertains to the round leaves of some forms.

DESCRIPTION AND HABITAT

Plants rosulate, solitary or forming small to dense clusters of up to about 50 plants by vegetative arboreal stolons. Roots fibrous. Main branch short. Leaves in a dense rosette 30–60 mm in diameter consisting of 10–12 leaves; blade dorsiventrally flattened, green to reddish on undersurface, broadly ovate, 20–35 × 15–25 mm; margin ciliate; adaxial surface convex, with a distinct off-centre groove from close to apex and parallel to margin for a third to two thirds of leaf length, lower surface concave; apex subacute. Inflorescence a terminal, ascending, elongated, lax thyrse up to 150 mm high, bearing several dichasia; peduncle 20 mm long, reddish green; pedicels short, up to 1 mm long. Corolla 3 mm in diameter, shortly tubular; lobes white, ovate-lanceolate, up to 3 mm long. Stamens 2 mm long.

Phenology: Flowering from midwinter to early summer (June–November).

Pollinators: The small white flowers suggest a flying insect.

Habitat and aspect: *Crassula orbicularis* is often associated with cliffs, some forms confined solely to cliff faces, usually on sheltered southern aspects. It occurs in large numbers

and is easily detected. Summers are hot and humid but it is cooler in winter. The average daily maximum temperature is about 20–24°C and the average daily minimum for the region 12–15°C. Rainfall in the south is in winter and summer and in the north it occurs mainly in summer, ranging from 400–1000 mm per annum.

Altitude: 50–1800 m.

Associated vegetation: Mainly Succulent Karoo, Albany Thicket and Eastern Valley Bushveld (Mucina *et al.* 2005).

Associated cremnophytes: At Luputana Gorge in the northeastern part of the Eastern Cape, the following plants have been recorded: *Begonia dregei*, *Crassula pellucida* subsp. *alsinoides*, *Haemanthus albiflos*, *Ornithogalum longibracteatum*, *Peperomia rotundifolia*, *Plectranthus saccatus* subsp. *pondoensis* and *Streptocarpus liliputana*.

Geology: Varied, shale and sandstone and often associated with quartzitic sandstone of the Table Mountain Group (Cape Supergroup).

DISTRIBUTION

Crassula orbicularis occurs widespread from near Worcester to northern KwaZulu-Natal.

RELATED SPECIES

Crassula orbicularis var. *orbicularis* (Luputana form) belongs to section *Argyrophylla*. It differs from other members in its small rosettes of smooth (margin crenulate, hyaline), unequally bilobed leaves with acute apices.

ADAPTATIONS TO THE CLIFF ENVIRONMENT

Habit: Conspicuous clusters, an adaptation to the undisturbed cliffs.

Size and weight: Clusters of medium weight.

Stem: Short, not visible.

Leaves

Orientation: Spreading, in dense rosettes, the open rosettes maximising penetration of light on the south-facing cliffs.

Colour: Epidermis light green.

Age and persistence: Plants long-lived perennials. Leaves also persistent and long-lived, an adaptation to the xeric cliff conditions.

Armament and camouflage: Plants with soft leaves and bodies without conspicuous armament or camouflage properties.

Sexual reproduction

Flowers: Inflorescence conspicuous, the reddish stems and white flowers contrasting against the light green leaves.

Fruit/Seed

Size: Seed minute and ideal for establishment in crevices.

Dispersal: Follicles dehiscent, with seeds spontaneously released and dispersed by wind.

Time: Seeds dispersed during spring rains, maximising establishment.

Vegetative reproduction: Many forms with runners forming dense groups, a vegetative survival backup and adaptation to the sheer cliffs and high run-off.

CONSERVATION STATUS

Locally common and well protected in the cliff habitat.

ADDITIONAL NOTES

Variability: Although as a species it is not an obligate cremnohyte, it is extremely variable, with some obligate cremnophilous forms, and therefore incorporated in this study.

Horticulture: Often grown by lovers of succulent plants. Best grown in succulent karoo, thicket and subtropical coastal gardens. Grow in dappled shade in rockeries or containers. Easily cultivated and a popular succulent plant. Its vigour can be viewed as maximising survival. Propagate by division or from stolons.

VOUCHER

Van Jaarsveld 16421 (NBG).

ILLUSTRATIONS AND MAP

Figures 128a–128c, Map 128.

129. *Crassula peculiaris* (Toelken) Toelken & Wickens in *Journal of South African Botany* 41: 105 (1975).

Cremnohyte growth form: Dwarf-sized, mat-forming (of light weight, cliff hugger).

Growth form formula: E:F:P:Els (vb)

Etymology: Latin *peculiaris*, peculiar, perhaps pertaining to its peculiar habitat in the Western Cape, as opposed to that of its close relative, var. *fragilis*, from the warm subtropical summer-rainfall region.

DESCRIPTION AND HABITAT

Spreading, delicate, mat-forming, succulent herbs up to 300 mm in diameter, with aerial roots and rooting at nodes. Roots fibrous. Branches decumbent, tomentose, green to reddish, glabrous to tomentose, up to 2.5 mm in diameter. Leaves shortly petiolate (3 mm); blade ovate to broadly elliptic, 2–10 × 4–6 mm, tomentose, dorsiventrally compressed, green; upper surface flat, lower surface convex; margin with a ring of hydathodes; apex acute; base cuneate. Flowers solitary in leaf axils; pedicels 6–18 mm long. Calyx lobes 2–5 mm long, linear. Corolla star-shaped, 4 mm long, up to 6 mm in diameter.

Phenology: Flowering in late spring and summer (November–March).

Pollinators: The small white flowers suggest an insect as possible pollinator.

Habitat and aspect: Shady sheltered cliffs and boulders at high altitudes. Plants grow in shallow soil on shady rocky ledges. Temperatures hot in summer and cool in winter, with occasional snow. The average daily maximum temperature is 17–20°C and average daily minimum 6–8°C. Rainfall occurs mainly in winter (cyclonic) and summer (thunder showers) and ranges from 800–2000 mm per annum.

Altitude: 1200–1800 m.

Associated vegetation: North Swartberg Sandstone Fynbos (Mucina *et al.* 2005).

Associated cremnophytes: Solitary and not sharing with other succulent plants.

Geology: Quartzitic sandstone of the Table Mountain Group (Cape Supergroup).

DISTRIBUTION

Crassula peculiaris is restricted to the Groot Swartberg (Western Cape).

RELATED SPECIES

Crassula peculiaris differs from the other level-ground species in its distinctly papillose seeds. It has solitary flowers in the leaf axils.

ADAPTATIONS TO THE CLIFF ENVIRONMENT

Habit: Mat-forming, fragile, flaccid stems, filling crevices, sometimes pendulous. The safe cliff environment allows for its survival (absence of larger herbivores).

Size and weight: Clusters small, of light weight.

Stem: Ascending to spreading, flaccid, 100–300 mm in diameter.

Leaves

Orientation: Ascending-spreading.

Colour: Green.

Age and persistence: Plants relatively rapid-growing, with constant vegetative renewal.

Armament: Branches soft and fragile without conspicuous armament, an adaptation to the cliff habitat.

Sexual reproduction

Flowers: Flowers solitary in leaf axils. Corolla star-shaped, 4 mm long, up to 6 mm in diameter.

Fruit/Seed

Size: Seed minute, distinctly papillate and ideal for establishment in crevices (becoming stuck in crevices).

Dispersal: Follicles dehiscent, with seeds spontaneously released and dispersed by wind.

Time: Seeds released in late summer.

Vegetative reproduction: The vigorous mat-forming growth ensures vegetative increase. Branches occupy new crevices by active growth or when they drop from the cliff face, landing and rooting in new crevices. This vegetative increase represents effective backup growth, ensuring long-term survival on the cliff.

CONSERVATION STATUS

Classified as rare (Raimondo *et al.* 2009). Locally common, well protected in the cliff habitat.

ADDITIONAL NOTES

Horticulture: Best for cool, moist fynbos gardens. Outside the habitat, it is best grown under controlled conditions in a greenhouse (cool, moist atmosphere). Easily cultivated, thriving in containers. Propagation from cuttings or by division.

VOUCHER

Van Jaarsveld 19510 (NBG).

ILLUSTRATIONS AND MAP

Figures 129a & 129b, Map 129.

130. *Crassula pellucida* L. subsp. *spongiosa* Toelken in Journal of South African Botany 41: 114 (1975).

Cremonophyte growth form: Mat-forming cluster (of light weight, cliff hugger).

Growth form formula: E:F:P:Els (vb)

Etymology: Latin *spongia*, a sponge, pertaining to the lower part of the ovaries which become spongy.

DESCRIPTION AND HABITAT

Procumbent, mat-forming, with branches up to about 200 mm high, often rooting at nodes. Roots fibrous. Branches terete, green up to 3 mm in diameter; internodes 10–30 mm long. Leaves ovate to broadly ovate, grey-green, 10–22 × 7–18 mm; margin entire, papillose; apex obtuse or acute; base cuneate, decurrent on stem and fused shortly at base to opposite leaf pair. Inflorescence an irregular terminal dichasium up to 30 mm long; pedicels 5–7 mm long. Calyx lobes linear-triangular, up to 2 × 1 mm. Corolla star-shaped, white to pink, up to 10 mm in diameter; lobes ovate, 3 × 2 mm; apices acute. Stamens 2 mm long; anthers yellow.

Phenology: Flowering in late spring (October–November).

Pollinators: The conspicuous diurnal flowers suggest a day-flying insect.

Habitat and aspect: Sheltered cliffs on mountains and kloofs. Plants grow in shallow soil among leaf litter on shady rocky ledges. It is cool in summer and cold in winter. The average daily maximum temperature is 19–21°C and average daily minimum 10–11°C. Rainfall is mainly in winter (cyclonic) and ranges from 800–2000 mm per annum.

Altitude: 800–1600 m.

Associated vegetation: Peninsula Sandstone Fynbos and Western Altimontane Sandstone Fynbos (Mucina *et al.* 2005).

Associated cremnophytes: *Cotyledon orbiculata*, *Crassula coccinea*, *Scopelogena verruculata* and *Senecio serpens*.

Geology: Quartzitic sandstone (Table Mountain Formation, Cape Supergroup).

DISTRIBUTION

Crassula pellucida subsp. *spongiosa* is confined to the higher cliffs of Table Mountain, Du Toits Kloof, Matroosberg, southern Cedarberg and occurs northwards to Calvinia and Nieuwoudtville (Western Cape).

RELATED SPECIES

Crassula pellucida subsp. *spongiosa* can be distinguished from subsp. *pellucida* by its smaller stature, fragile nature, glaucous leaves and spongy basal part of the ovary.

ADAPTATIONS TO THE CLIFF ENVIRONMENT

Habit: Small mats of procumbent stems (rooting at nodes), sometimes becoming drooping.

Size and weight: Clusters small, of light weight.

Stem: Up to 200 mm long.

Leaves

Orientation: Fused at the base, spreading at right angles (decussately arranged). The reduction in size (in comparison to other subspecies of *Crassula pellucida*), compact arrangement and glaucous colour can be viewed as adaptations to the dry conditions on the cliff face.

Colour: Epidermis glaucous, becoming purplish. The purplish colour under dry conditions (production of anthocyanins) reduces penetration of excessive light, an adaptation resulting from the well-drained habitat.

Age and persistence: Plants short-lived perennials.

Armament: Soft-leaved plant bodies without conspicuous armament.

Sexual reproduction

Flowers: Flowering in spring, pollinated by insects.

Fruit/Seed

Size: Seed minute and ideal for establishment in crevices.

Dispersal: Follicles dehiscent, with seeds spontaneously released and dispersed by wind.

Time: Seeds released in summer.

Vegetative reproduction. Plants proliferating and forming dense mats, soon filling new crevices—an effective vegetative backup for continued existence under the harsh conditions on the cliff face. Detached parts that fall into adjacent crevices will root in the new spot.

CONSERVATION STATUS

Locally common and well protected in the undisturbed cliff habitat, not threatened.

ADDITIONAL NOTES

Horticulture: Best for dry fynbos gardens, grown in rockeries in dappled shade. Outside its habitat, it is best grown under controlled greenhouse conditions. Easily cultivated, its vigour viewed as maximising survival. Propagate from cuttings. Plants soon forming dense mats.

VOUCHER

Van Jaarsveld 17740 (NBG).

ILLUSTRATIONS AND MAP

Figures 130a–130d, Map 130.

131. *Crassula perforata* Thunb. subsp. *kougaensis* Van Jaarsv. & A.E. van Wyk in Aloe 46,1: 22–23 (2009b).

Cremonophyte growth form: Cluster of drooping, leafy stems (of light weight, cliff hugger).

Growth form formula: E:F:P:Els (vb)

Etymology: After its habitat along the Kouga River in the Eastern Cape.

DESCRIPTION AND HABITAT

Plants dwarf-sized, drooping, sparsely to moderately branched shrublets, 80 × 40 mm. Roots fibrous. Branches flaccid, leafy, pendent, 0.8 mm in diameter (usually not visible owing to crowded leaves), grey; younger branches purplish, succulent. Leaves decussate, persistent, ovate to broadly ovate, 8–10 × 8–10 mm, fused at base, closely clasping around stem, forming 4-angled column; blade 3–7 × 2.5–6.0 mm, cymbiform, keeled towards apex; surface smooth, grey- to bluish green, becoming yellowish to reddish towards base, with waxy layer, adaxial surface flattened to convex, abaxial surface convex; margin entire, purplish red with hydathodes (0.4 mm apart); apices acute; oldest leaves withering. Inflorescence a rounded thyrse 6–10 mm in diameter; peduncle curved, up to 5–8 mm long; bracts clasping, 1.0–1.5 mm long, amplexicaul at base. Calyx lobes triangular 0.5 × 0.4 mm long. Corolla 3.5 mm in diameter, tubular, pale yellow; lobes oblong, 2 × 1 mm long, shortly fused at base. Stamens 1.75 mm long; anthers versatile, 0.5 mm long, yellow. Squamulae rectangular, 0.25 mm long. Follicles 1.5 mm long, tapering. Seed pear-shaped, 0.25 × 0.20 mm; surface verrucose.

Pollinators: The conspicuous diurnal flowers suggest a day-flying insect. Bluebottles have been observed visiting flowers in habitat.

Habitat and aspect: Exposed cliffs (mainly northern and western aspects). Plants are firmly rooted in crevices (often very small hairline cracks), often solitary in small crevices or socially with other cremonophytes. It is warm to hot in summer and temperatures can reach 40°C. The average daily maximum temperature is about 23–25°C and the average daily minimum for the region 10–12°C. Winters are cooler but frost is absent. Rainfall in winter and summer, ranging from 300–400 mm per annum (cyclonic winter rain or thunder showers).

Altitude: 400–800 m.

Associated vegetation: Gamtoos Thicket of the Albany Thicket Biome (Mucina *et al.* 2005).

Associated cremonophytes: *Adromischus cristatus* var. *schonlandii*, *Aloe pictifolia*, *Centella* sp., *Cotyledon tomentosa* var. *tomentosa* and *Crassula perfoliata* var. *minor*.

Geology: Quartzitic sandstone of the Peninsula Formation (Cape Supergroup).

DISTRIBUTION

Restricted to cliffs adjacent to the Kouga River, near Hankey (Eastern Cape).

RELATED SPECIES

Distinguished from the normal forms of *Crassula perforata* by its dwarf-sized stature, flexible and drooping stems, tight 4-ranked leaves forming a rectangular oblong body, and short rounded thyrses. This dwarf-sized Kouga form occurs sympatrically with *C. perforata* and *C. rupestris* subsp. *rupestris*. *Crassula perforata* and *C. rupestris* usually occur on steep rocky slopes below or above the cliff face or on well-vegetated larger ledges. No intermediates or hybridisation have been observed. Grown in cultivation, plants retain their dwarf size. The Kouga form is closely related to *C. perforata*, which has similar flowers, and to *C. rupestris*, both with woody stems. Branches of the subsp. *kougaensis* are flaccid, drooping from cliff faces, and not woody.

ADAPTATIONS TO THE CLIFF ENVIRONMENT

Habit: Pendent clusters (leafy, flaccid branches) with compact growth.

Size and weight: Clusters dwarf-sized, of light weight. The dwarf size enables plants to occupy small vertical rock crevices.

Stem: Branches flaccid, pendulous to subpendulous. This less woody and pendent nature of the stems can be viewed as an adaptation to the cliff environment.

Leaves

Orientation: Leaves spreading, closely packed and forming an oblong, rectangular body about 8×8 mm, becoming distinctly purplish reddish during dry periods. This columnar feature is typical of many cremnophytes and can be viewed as an adaptation to the extreme xeric conditions of the cliff face.

Colour: Epidermis grey-green to glaucous (covered with powdery bloom). The reddish colour under dry conditions reduces penetration of light, an adaptation resulting from the extreme xeric conditions of the cliff habitat.

Age and persistence: Plants long-lived perennials. The long-lived leaves and slow growth rate can be viewed as an adaptation to the mineral-poor quartzitic sandstone soil.

Armament and camouflage: Soft-leaved plant bodies without conspicuous armament or camouflage properties as opposed to the level-ground species, which are more woody (*Crassula perforata*).

Sexual reproduction

Flowers: Flowering from summer to early autumn (December–March), diurnal, scented, about 3.5 mm in diameter, pale yellow. Bluebottles have been observed visiting flowers in the habitat.

Fruit/Seed

Size: Seed pear-shaped, 0.25×0.20 mm, with verrucose surface ideal for establishment in crevices.

Dispersal: Follicles dehiscent, with seeds spontaneously released and dispersed by wind.

Time: Summer and autumn, just in time for the winter rains, maximising establishment.

Vegetative reproduction: Like most other *Crassula* taxa, this species will root when stems find new crevices or when pieces become detached (as a result of heavy wind or other disturbances), a vegetative reproductive backup system ensuring long-term survival.

CONSERVATION STATUS

Locally common and well protected in the cliff habitat.

ADDITIONAL NOTES

Horticulture: *Crassula perforata* subsp. *kougaensis* is best grown in thicket gardens, on rockeries but owing to the small size, rather in containers. It can be grown in full sun or dappled shade in sandy, acidic soil. Add ample compost and feed in spring. Easily propagated from seed, cuttings or division.

VOUCHER

Van Jaarsveld 9905 (NBG).

ILLUSTRATIONS AND MAP

Plate 131, Figures 131a–131d, Map 131.

132. *Crassula perforata* Thunb. subsp. *perforata*, Thunberg in Nova Acta Physico-Medica Academiae Caesareae Leopoldino-Carolinae ... 6: 319, 338 (1778). (Eastern Cape and KwaZulu-Natal forms.)

Cremonophyte growth form: Loose clusters with spreading to drooping, flaccid stems (of medium weight, cliff hanger).

Growth form formula: E:F:P:Els (vb)

Etymology: Latin *perforata*, pierced with holes, pertaining to the fused leaf pairs.

DESCRIPTION AND HABITAT

Spreading and scrambling to pendulous, branched shrub up to 500 mm high, variable in size and leaf shape. Roots fibrous. Branches grey-brown, up to 3 mm in diameter, flaccid. Leaves 14–33 × 12–20 mm, dorsiventrally flattened to cymbiform, decussate, abruptly constricted and fused basally to opposite leaf; lamina ovate; surface glabrous, grey-green; margin reddish; apices acute or obtuse; older leaves persistent. Inflorescence an elongated thyse up to 80 mm long, bearing sessile flowers; peduncle with gradual change from leaves to bracts. Calyx triangular, up to 1 mm long, acute. Corolla tubular, yellowish, shortly fused at base; lobes oblong, up to 2.5 mm long. Anthers brown.

Phenology: Flowering in summer and autumn (November–April).

Pollinators: The small yellowish flowers suggest a flying insect.

Habitat and aspect: Cliffs at altitudes of up to about 800 m (all aspects, common on northern and western aspects). Plants firmly rooted in crevices and size often depends on the growing space allowed by the crevice. It is warm to hot in summer and temperatures can reach 40°C. The average daily maximum temperature is about 22–24°C and the average daily minimum for the region 12–14°C. Winters are colder but frost is absent. Rainfall in the eastern parts (Eastern Cape and KwaZulu-Natal) ranges from 400–800 mm per annum (mainly summer rain).

Altitude: 300–800 m.

Associated vegetation: Mainly Eastern Valley Bushveld of the Savanna Biome (Mucina *et al.* 2005).

Associated cremnophytes: At Collywobbles (Eastern Cape), the following plants have been recorded: *Aloe reynoldsii*, *Cotyledon orbiculata*, *Crassula cordata*, *Drimia anomala*, *Haworthia cymbiformis* var. *setulifera* and *Ornithogalum longibracteatum*.

Geology: Shale of the Beaufort Subgroup (Beaufort Group, Karoo Supergroup), quartzitic sandstone of the Peninsula Formation (Cape Supergroup).

DISTRIBUTION

From Worcester in the Western Cape eastwards and northeastwards to the dry river valleys of southern KwaZulu-Natal.

RELATED SPECIES

A very variable species and distinguished from the level-ground forms by its more flexible, flaccid stems and less woody growth.

ADAPTATIONS TO THE CLIFF ENVIRONMENT

Habit: Conspicuous, spreading branches drooping from the cliff face.

Size and weight: Clusters smaller (of medium weight and about 200 mm in diameter) compared to the more robust woody level-ground forms (shrubs up to 600 mm in diameter).

Stem: Flaccid and flexible, shorter, pendulous or subpendulous. The softer, less woody and pendulous nature of the stems can be viewed as an adaptation to the cliff environment.

Leaves

Orientation: Leaves spreading at right angles. Compared to other karoo forms of this species, the cliff face forms are more closely packed (genotypic) than level-ground forms, often becoming distinctly purplish reddish during dry periods. This reduction in size and compact growth can be viewed as adaptations to the xeric conditions found on the cliff face.

Colour: Epidermis grey-green to glaucous (covered with powdery bloom). The reddish colour under dry conditions reduces penetration of light, an adaptation resulting from the extreme run-off in its sheer habitat.

Age and persistence: Plants long-lived perennials. Leaves also persistent and long-lived, suggesting adaptation to the xeric cliff conditions.

Armament and camouflage: Soft-leaved plant bodies without conspicuous armament or camouflage properties as opposed to the level-ground species, which are more woody.

Sexual reproduction

Flowers: Flowering from midsummer to autumn (November–April), diurnal.

Fruit/Seed

Size: Seed minute and ideal for establishment in crevices.

Dispersal: Follicles dehiscent, with the seeds spontaneously released and dispersed by the wind.

Time: Seeds dispersed in time for autumn rains, maximising establishment.

Vegetative reproduction: The vigorous, spreading growth ensures vegetative increase. Branches will occupy new crevices by active growth or branches blown from the cliff face will root in crevices where they land. This vegetative increase is an effective backup growth ensuring long-term survival on the cliff.

CONSERVATION STATUS

Locally common and well protected in the cliff habitat.

ADDITIONAL NOTES

Horticulture: Best for thicket and succulent karoo gardens, grown in rockeries, on embankments or as a pot plant. Outside the native habitat, it is best grown under controlled conditions in a greenhouse. Easily cultivated, its vigour viewed as maximising survival. Propagate from cuttings or seed.

VOUCHER

Van Jaarsveld 17060 (NBG).

ILLUSTRATIONS AND MAP

Figures 132a–132c, Map 132.

133. *Crassula pseudohemisphaerica* Friedrich in *Mitteilungen der Botanischen Staatssammlung München* 3: 594 (1960).

Cremonophyte growth form: Mat-forming cluster (of light weight, cliff hugger).

Growth form formula: A:S:Lper:R:C:Ts:La (vb)

Etymology: Greek *pseudo*, false, and *hemisphaerica*, half a sphere, pertaining to its likeness to *Crassula hemisphaerica*.

DESCRIPTION AND HABITAT

Sparsely branched, decumbent to erect, compact herbs forming small to larger, often dense clusters up to 300 mm in diameter and up to 200 high (when flowering). Roots fibrous. Leaves obovate to orbicular, 8–45 × 10–50 mm, dorsiventrally flattened, 4-ranked, tightly imbricate, forming neat spherical bodies, green to reddish green, mottled; margin ciliate; apex rounded. Inflorescence a terminal elongated thyse bearing many dichasia; peduncle up to 250 mm high. Calyx lobes oblong-triangular, up to 3 mm long. Corolla yellowish, tubular, up to 5 mm long, shortly fused at base. Corolla lobes oblong-oblancheolate, up to 4 mm long, spreading and becoming recurved. Anthers yellow.

Phenology: Flowering from spring to early summer (September–November).

Pollinators: The conspicuous diurnal flowers suggest a day-flying insect.

Habitat and aspect: Sheltered cliffs and mainly on southern aspects. Plants grow in shallow soil on shady rocky ledges. Temperatures high in summer and mild in winter. The average daily maximum temperature is 25–27°C and the average daily minimum 10–12°C. Rainfall occurs mainly in winter (cyclonic) and occasionally in autumn (thunder showers) and ranges from 100–300 mm per annum.

Altitude: 50–900 m.

Associated vegetation: Mainly Succulent Karoo and Desert Biomes (Mucina *et al.* 2005).

Associated cremonophytes: Associated cliff-dwelling succulent plants at Kuamsibberg Mountain (southern Namibia) include *Aloe pavelkae*, *Tylecodon buchholzianus*, *T. racemosa* and *T. rubrovenosus*.

Geology: Sandstone and shale.

DISTRIBUTION

Widespread in the Northern Cape, from north of Vanrhynsdorp to Lüderitz in southwestern Namibia.

RELATED SPECIES

Crassula pseudohemisphaerica is related to *C. hemisphaerica*, a widespread species from the south growing on flats and hills. The latter is at once distinguished by its solitary growth (also

section *Rosulares*). *Crassula pseudohemisphaerica* is also related to *C. orbicularis*, also growing on cliffs and mat-forming. It is at once distinguished from that species by its mottled green, 4-ranked leaves and pointed papillae on the ovary.

ADAPTATIONS TO THE CLIFF ENVIRONMENT

Habit: Small to dense, tight clusters that can be viewed as vegetative output on the cliff face, the plants filling crevices in the absence of disturbance by larger herbivores.

Size and weight: Clusters small, of light weight.

Stem: Short, usually unexposed.

Leaves

Orientation: Spreading to spreading-recurved, the body often dome-shaped. The compact leaves are 4-ranked, mottled and purplish to reddish green, especially during dry periods. The compact nature and open rosettes can be viewed as an adaptation to the dry conditions on the cliff face.

Colour: Epidermis green, often becoming reddish, often mottled. The reddish colour under dry conditions (production of anthocyanins) reduces penetration of light, an adaptation resulting from the well-drained habitat.

Age and persistence: Plants long-lived perennials.

Armament: Soft-leaved plant bodies without conspicuous armament.

Sexual reproduction

Flowers: Flowering in spring, pollinated by insects.

Fruit/Seed

Size: Seed minute and ideal for establishment in crevices.

Dispersal: Follicles dehiscent, with seeds spontaneously released and dispersed by wind.

Time: Seeds released in summer.

Vegetative reproduction: Plants proliferating and forming dense cushions, a vegetative backup enabling the plants to survive the harsh conditions on the cliff face. Crevices are soon occupied by the vegetative growth and by detached plants that fall and root in new crevices, forming new populations.

CONSERVATION STATUS

Not threatened owing to the undisturbed cliff habitat.

ADDITIONAL NOTES

Horticulture: An ornamental species with attractive mottled leaves. Best grown in succulent karoo gardens, on rockeries or containers, in dappled shade. Outside its native habitat, it should rather be grown under controlled conditions in a greenhouse. Sensitive to leaf rust (in moist climates). Propagate by division. Easily cultivated, its vigour viewed as maximising survival.

VOUCHER

Van Jaarsveld 17589 (NBG).

ILLUSTRATIONS AND MAP

Figures 133a–133d, Map 133.

134. *Crassula pubescens* Thunb. subsp. *ratrayi* (Schönland & Baker f.) Toelken in Journal of South African Botany 41: 116 (1975).

Cremonphyte growth form: Dwarf-sized, mat-forming (of light weight, cliff hugger).

Growth form formula: A:S:Lper:Lc:Ts (vb)

Etymology: After George Rattray (1872–1941) a Scotsman, teacher and naturalist.

DESCRIPTION AND HABITAT

Dwarf-sized, much-branched, succulent herbs forming small, tight clusters up to 100 mm high. Roots fibrous. Branches succulent, short, green to reddish green, becoming grey-brown. Leaves in a basal rosette, oblanceolate, obovate to oblanceolate, 15–35 × 5–12 mm, dorsiventrally flattened, spreading; surface pubescent; adaxial side flat to channelled, abaxial surface convex; margin rounded to acute, minutely ciliate; apex obtuse to acute; base cuneate. Inflorescence an erect elongated spike-like thyrse 60–80 mm high, bearing 1–several dichasia in distal half; peduncle with 1–3 pairs of bracts; basal bracts 5 × 4 mm, erect, triangular-ovate. Calyx lobes oblong, 1.5 mm long. Corolla tubular, white; lobes oblong-panduriform, up to 3 mm long, fused shortly at base, with ovoid to globose apical appendage.

Phenology: Flowering in summer (end November–January).

Pollinators: The small white to cream corolla suggests a flying insect.

Habitat and aspect: Sheltered south-facing cliffs more than 800 m above sea level. Plants are firmly rooted in crevices and size often depends on the growing space allowed by the crevice. Temperature high in summer (30°C). Winters are cooler, with occasional frost or snow. The average daily maximum temperature is about 23°C and the average daily minimum 8°C. Rainfall occurs throughout the year but with a peak in spring and summer, ranging from 300–400 mm per annum (thunder showers or cyclonic winter rain).

Altitude: 800–1500 m.

Associated vegetation: Camdebo Escarpment Thicket (Mucina *et al.* 2005).

Associated cremnophytes: At Tandjiesberg (southern escarpment margin) near Graaff-Reinet, the following species have been recorded: *Adromischus fallax*, *Cotyledon orbiculata* var. *orbiculata*, *Crassula exilis* subsp. *cooperi*, *C. lanceolata* subsp. *lanceolata*, *C. nemorosa*, *C. perforata*, *Delosperma* spp., *Haemanthus humilis* subsp. *hirsutus* and *Litanthus pusillus*.

Geology: Beaufort shales (Adelaide Subgroup, Karoo Supergroup).

DISTRIBUTION

Known only from the escarpment mountains near Graaff-Reinet.

RELATED SPECIES

Differs from subsp. *pubescens* and subsp. *radicans* in its small basal rosettes and clustered growth.

ADAPTATIONS TO THE CLIFF ENVIRONMENT

Habit: Basal rosette and clustered growth, a structural adaptation typical of many cremnophytes.

Size and weight: Clusters dwarf-sized, of light weight.

Stem: Short, decumbent.

Leaves

Orientation: Ascending-spreading (rarely almost recurved), in a basal rosette, dorsiventrally flattened.

Colour: Green with a pubescent epidermis.

Age and persistence: The plants are relatively rapid-growing but long-lived perennials.

Armament: Branches soft and fragile without conspicuous armament, an adaptation to the cliff habitat.

Sexual reproduction

Flowers: Inflorescence an erect, elongated, spike-like thyrse bearing white flowers pollinated by insects.

Fruit/Seed

Size: Seed minute and ideal for establishment in crevices.

Dispersal: Follicles dehiscent, with seeds spontaneously released and dispersed by wind.

Time: Seeds released in late summer.

Vegetative reproduction: The brittle, succulent leaves will root when they become detached, forming new plantlets—a vegetative backup strategy and efficient adaptation helping the plants to deal with the harsh cliff-face conditions.

CONSERVATION STATUS

Locally common and well protected in the undisturbed cliff habitat, not threatened.

ADDITIONAL NOTES

Horticulture: Easily cultivated, its vigour viewed as maximising survival. Easily grown from seed or division, thriving in small containers.

VOUCHER

Van Jaarsveld 18283 (NBG).

ILLUSTRATIONS AND MAP

Figures 134a & 134b, Map 134.

135. *Crassula rupestris* Thunb. subsp. *marnieriana* (H.E.Huber & H.Jacobsen) Toelken in Journal of South African Botany 41: 116 (1975).

Cremnophyte growth form: Loose clusters with spreading to drooping stems (of medium weight, cliff hanger).

Growth form formula: E:F:P:Els (vb)

Etymology: After Marnier la Postolle, grower of succulent plants in France.

DESCRIPTION AND HABITAT

Spreading to pendulous, branched shrublets up to 200 mm in diameter, rooting where branches touch ground. Stems 1–2 mm in diameter, spreading and becoming pendulous. Leaves crowded and internodes not visible, sessile, ovate, 3–6 × 4–6 mm, bases fused (over half leaf length) into a disc; surface smooth, glaucous; margins entire; hydathodes concentrated along margins; apex rounded. Inflorescence a short, sessile, rounded thyrse up to 15 mm in diameter, with many flowers in dichasia. Flowers 5-merous, star-shaped, up to 4.5 mm in diameter, white; pedicels 2–5 mm long. Calyx lobes triangular, 1 mm long, apices acute. Corolla lobes oblong-elliptic, 3–4 mm long, recurved; apices obtuse. Stamens up to 3.5 mm long; anthers brown; pollen yellow. Squamae oblong to square, 0.4–0.9 × 0.3–0.6 mm, thick, fleshy, yellowish orange.

Phenology: Flowering in autumn (April–May).

Pollinators: The small white flowers suggest a flying insect.

Habitat and aspect: *Crassula rupestris* subsp. *marnieriana* is confined mainly to south-facing quartzitic sandstone cliffs at 800–1500 m. It is locally abundant, firmly rooted in crevices, size often depending on the growing space allowed by the crevice. It is warm to hot in summer and temperatures can reach 40°C. Winters are cooler but frost is absent. The average daily maximum temperature is about 25–26°C and the average daily minimum for the region 9–10°C. Rainfall occurs mainly in winter (cyclonic) and summer (thunder showers), ranging from 250–350 mm per annum.

Altitude: 800–2000 m.

Associated vegetation: Mainly Gamka Thicket, Albany Thicket Biome (Mucina *et al.* 2005).

Associated cremnophytes: Associated cremnophytes include *Aloe comptonii*, *Crassula cotyledonis*, *C. muscosa*, *C. perforata* and *Haemanthus coccineus*.

Geology: Quartzitic sandstone of the Peninsula Formation, Table Mountain Group (Cape Supergroup).

DISTRIBUTION

Northwestern Little Karoo, Anysberg to Klein Swartberg and mountains along the Huis River Pass (Western Cape).

RELATED SPECIES

Differs from the typical subsp. *rupestris* in its smaller, spreading habit (readily rooting at the nodes) and its short internodes not visible (forming a cylindrical ‘body’), and in the opposite, round-ovate leaves fused into an orbicular disk obtuse at the apices.

ADAPTATIONS TO THE CLIFF ENVIRONMENT

Habit: Conspicuous, spreading branches drooping from the cliff face.

Size and weight: Clusters of medium weight and smaller (about 200 mm in diameter) compared to the larger and more woody level-ground forms of *Crassula rupestris*.

Stem: Flaccid, shorter and pendulous or subpendulous. The softer, less woody and pendulous nature of the stems (compared to the woody subsp. *rupestris* on non-cliff habitats) can be viewed as an adaptation to the cliff environment.

Leaves

Orientation: Spreading, closely packed, forming a cylindrical body. Leaf pairs fused by half or more into a disc, this crowded leaf arrangement an adaptation to the xeric conditions of the cliff face.

Colour: Epidermis glaucous, an adaptation resulting from the extreme run-off in the sheer habitat.

Age and persistence: Plants long-lived perennials. Leaves also persistent and long-lived, suggesting adaptation to the xeric cliff conditions.

Armament and camouflage: Soft-leaved plant bodies without conspicuous armament or camouflage properties as opposed to the level-ground *Crassula rupestris* subsp. *rupestris*, which is more woody.

Sexual reproduction

Flowers: In a large round-topped thyrses, conspicuous, in autumn and winter (April–June).

Fruit/Seed

Size: Seed minute and ideal for establishment in crevices.

Dispersal: Follicles dehiscent, with seeds spontaneously released and dispersed by wind.

Time: Seeds dispersed in time for autumn rains, maximising establishment.

Vegetative reproduction: The spreading growth ensures vegetative increase and branches will occupy new crevices by active growth. This vegetative increase is an effective backup growth ensuring long-term survival on the cliff.

CONSERVATION STATUS

Classified as rare (Raimondo *et al.* 2009). Locally common and well protected in the cliff habitat.

ADDITIONAL NOTES

Variability: Plants variable in size, with many different forms.

Horticulture: Best for succulent karoo and dry fynbos gardens, in rockeries or containers. Propagate from cuttings or by division. Grow in full sun or dappled shade, preferably in slightly acid, sandy soil.

VOUCHER

Van Jaarsveld 17431 (NBG).

ILLUSTRATIONS AND MAP

Figures 135a–135d, Map 135.

136. *Crassula rupestris* Thunb. subsp. *rupestris*, Thunberg in Nova Acta Physico-Medica Academiae Caesareae Leopoldino-Carolinae ... 6: 329, 337 (1778). (Olifantsrivier and Peninsula forms.)

Cremnophyte growth form: Cluster with spreading to drooping stems (of light to medium weight, cliff hanger).

Growth form formula: E:F:P:Els (vb)

Etymology: Latin *rupes*, a cliff or rock, pertaining to its often rock or cliff habitat.

DESCRIPTION AND HABITAT

Plants small, drooping to rounded, branched shrublets up to 180 × 180 mm. Roots fibrous. Branches leafy, flaccid, pendent, becoming woody at base, up to 4 mm in diameter; bark peeling; younger branches 2 mm in diameter, succulent. Leaves 10–14 × 9–14 mm, dorsiventrally flattened; adaxial surface flat to convex, concave towards base, abaxial surface convex; blade broadly ovate; surface glabrous grey-green to glaucous, with powdery bloom, constricted towards base, fused with opposite leaf pair basally; margin entire, reddish; apex acute or obtuse. Inflorescence a rounded thyrses, 25 × 25 mm; peduncle up to 10 mm long; basal bracts spreading, up to 7 mm long. Calyx lobes oblong-triangular, up to 1 mm long. Corolla 5 mm in diameter, tubular, white to light pink, sweetly scented; lobes oblong, 3 mm long, shortly fused at base. Anthers brown. Seed minute.

Pollinators: The conspicuous diurnal flowers suggest a day-flying insect.

Habitat and aspect: Cliffs at altitudes of up to about 700 m (mainly northern and western aspects). Plants grow firmly rooted in crevices, size often depending on the space allowed by the crevice. Warm to hot in summer, temperatures reaching 40°C. Winters are cooler but frost is absent. Average daily maximum temperature 22–24°C, average daily minimum for the region 12–14°C. Rainfall mainly in winter, 400–1000 mm per annum (mainly cyclonic winter rain).

Altitude: 400–700 m.

Associated vegetation: Mainly fynbos.

Associated cremnoophytes: On Karbonkelberg (Cape Peninsula), the plants have been recorded with *Aloe succotrina*, *Bulbine lagopus*, *Cotyledon orbiculata* var. *orbiculata*, *Crassula coccinea*, *Scopelogena verruculata* and *Tylecodon paniculatus*.

Geology: Quartzitic sandstone of the Peninsula Formation (Cape Supergroup).

DISTRIBUTION

Table Mountain and Karbonkelberg (Cape Peninsula), Piketberg, Hottentots Holland and Olifantsrivier Mountains of the Western Cape.

RELATED SPECIES

Distinguished from the non-cremnophilous forms of *Crassula rupestris* by its smaller, compact and flaccid growth and internodes that are 2–3 mm long (as opposed to 7–10 mm in other forms). Branches often droop from cliff faces and plants are less woody.

ADAPTATIONS TO THE CLIFF ENVIRONMENT

Habit: Conspicuous, with reduction in size and compact growth.

Size and weight: Clusters of small to medium weight.

Stem: Shorter but pendulous or subpendulous. The softer, less woody (flaccid stems) and pendulous nature of the stems can be viewed as an adaptation to the cliff environment.

Leaves

Orientation: Closely packed, almost forming a subcylindrical body about 15–18 mm in diameter, often becoming distinctly purplish reddish during dry periods. The reduction in size and the compact growth can be viewed as adaptations to the xeric conditions on the cliffs.

Colour: Epidermis grey-green to glaucous (covered with powdery bloom). The reddish colour under dry conditions reduces penetration of light, an adaptation resulting from the extreme run-off in the sheer habitat.

Age and persistence: Plants long-lived perennials. Leaves also persistent and long-lived.

Armament and camouflage: Soft-leaved plant bodies without conspicuous armament or camouflage properties as opposed to the level-ground species, which are more woody.

Sexual reproduction

Flowers: Flowering in early autumn (February–March), diurnal, scented, about 5 mm in diameter, white to light pink. This suggests a day-flying specialist pollinating agent (insect).

Fruit/Seed

Size: Seed minute and ideal for establishment in crevices.

Dispersal: Follicles dehiscent, with seeds spontaneously released and dispersed by wind.

Time: Autumn, just in time for the winter rains and thus maximising establishment.

Vegetative reproduction: As in most other *Crassula* taxa, stems or detached pieces (as a result of heavy wind or other disturbances) of this species will root when finding a crevice, a vegetative reproductive backup strategy ensuring long-term survival.

CONSERVATION STATUS

Locally common and well protected in the undisturbed cliff habitat, not threatened.

ADDITIONAL NOTES

Horticulture: Best for fynbos gardens, grown on steep embankments and rockeries, and it also thrives in containers, in sandy soil. Easily cultivated, its vigour viewed as maximising survival. Propagate from cuttings or division.

VOUCHER

Van Jaarsveld 18418 (NBG).

ILLUSTRATIONS AND MAP

Figures 136a & 136b, Map 136.

137. *Crassula sediflora* (Eckl. & Zeyh.) Endl. ex Walp. var. *sediflora*, Walpers, Repertorium botanices systematicae 2: 254 (1843).

Cremnophyte growth form: Loose cluster (of light weight, cliff hugger).

Growth form formula: E:F:P:Els (vb)

Etymology: The epithet *sediflora* pertains to the flowers resembling the genus *Sedum*.

DESCRIPTION AND HABITAT

Decumbent, branched, wiry perennials, up to 400 mm high. Branches with internodes 4–15 mm long. Leaves linear, 10–35 × 1–2 mm, dorsiventrally flattened; leaf pairs alternately arranged; surface slightly papillose (becoming smooth), green to yellowish green; margin ciliate towards base; apex acute. Inflorescence an erect, terminal, round-topped thyrse bearing 1–many dichasia; bracts leaf-like, becoming shorter distally. Flowers shortly pedicellate, lax. Calyx lobes broadly triangular, up to 2 mm long, surface glabrous. Corolla tubular, cream to white, up to 3 mm long; lobes oblong-obovate, up to 2.5 mm long, fused shortly at base; apices rounded, slightly hooded, recurved. Anthers yellow.

Pollinators: The conspicuous diurnal white to cream flowers suggest a day-flying insect.

Habitat and aspect: Mainly on sheltered south-facing cliffs, in shallow soil on sunny rocky ledges. Temperatures moderate in summer and mild to low in winter. The average daily maximum temperature is 22–23°C and the average daily minimum 6–7°C. Rainfall occurs mainly in summer (mainly thunder showers) and ranges from 700–1000 mm per annum.

Altitude: 350–950 m.

Associated vegetation: Midlands Mistbelt Grassland of the Grassland Biome (Mucina *et al.* 2005).

Associated cremnophytes: *Crassula* species, *Ledebouria* sp. and *Merwillia plumbea*.

Geology: Mainly sandstone (Natal Group).

DISTRIBUTION

Crassula sediflora var. *sediflora* is distributed from near Seymour (Eastern Cape) to eastern, central KwaZulu-Natal.

RELATED SPECIES

Differs from var. *amatolica* in its thinner, longer leaves without the distinct cilia on the leaf margin. The latter variety is a grassland species with shorter, broader leaves (Toelken 1975). Differs from the related *Crassula southii* in its leaf apices lacking the long central hair.

ADAPTATIONS TO THE CLIFF ENVIRONMENT

Habit: Loose clusters, becoming drooping. Plants conspicuous and not camouflaged. The unarmed, soft texture of the plants is an adaptation to the undisturbed cliff-face habitat.

Size and weight: Clusters small, of light weight.

Stem: Decumbent, flaccid, up to 400 mm long.

Leaves

Orientation: Leaves spreading to recurved, linear, soft, dorsiventrally flattened and with a slightly papillose (becoming smooth) surface. Margin ciliate only towards base; apex acute.

Colour and texture: Epidermis green to yellowish green. The soft texture and fragile nature suggest adaptation to the sheltered and undisturbed cliff face.

Age and persistence: The plants are fast-growing, long-lived perennials.

Armament: Soft-leaved plant bodies without conspicuous armament.

Sexual reproduction

Flowers: Flowering in summer (February) and autumn (to May), pollinated by insects.

Fruit/Seed

Size: Seed minute and ideal for establishment in crevices.

Dispersal: Follicles dehiscent, with seeds spontaneously released and dispersed by wind.

Time: Seeds released in late autumn or winter.

Vegetative reproduction: Stems will root when coming into contact with the soil. The prolific nature of the plants (vegetative backup) ensures long-term survival on the cliffs.

CONSERVATION STATUS

Locally common and well protected by the cliff-face habitat.

ADDITIONAL NOTES

Horticulture: For subtropical coastal gardens; shady embankments or containers. Easily cultivated, its vigour viewed as maximising survival. Propagate from cuttings. Keep moist in summer.

VOUCHER

Van Jaarsveld 22391 (NBG).

ILLUSTRATIONS AND MAP

Figures 137a & 137b, Map 137.

138. *Crassula sericea* Schönland var. *sericea*, Schönland in Botanische Jahrbücher 45: 254 (1910). (Cliff-face form from the Richtersveld.)

Cremnophyte growth form: Rounded cluster to mat-forming (of light weight, cliff hugger).

Growth form formula: A:S:Lper:Lc:Ts (vb)

Etymology: Latin *sericea*, with closely depressed silky hairs, pertaining to the leaves of the species.

DESCRIPTION AND HABITAT

Plants much-branched, forming rounded, spreading tufts, 60 × 200 mm. Leaves very fragile, variable, mainly broadly obovate, oblanceolate to orbicular, 10–25 × 10–25 mm; blade very swollen, somewhat dorsiventrally compressed; surface grey-green with spreading to recurved hairs, adaxial surface flat to convex, abaxial surface convex; margin reddish distally; apex obtuse; base cuneate. Inflorescence an elongated thyrses, 40–100 mm, with few to many dichasia; peduncle hairy, purplish, 2 mm in diameter at base; bracts triangular, clasping, 2 mm high. Calyx lobes triangular-lanceolate, 1 mm high. Corolla tubular, sessile, 4 × 2 mm; lobes oblanceolate, 3 × 1.3 mm, ascending-spreading, white. Anthers brown.

Phenology: Flowering mainly in winter (May–August).

Pollinators: The conspicuous diurnal flowers suggest a day-flying insect.

Habitat and aspect: Sheltered cliffs, at altitudes of up to about 800 m. Plants grow in shallow soil on shady rocky ledges. Temperatures are high in summer and mild in winter. The average daily maximum temperature is about 24°C and daily minimum about 10–12°C. Rainfall in the western Richtersveld region occurs mainly in winter (cyclonic winter rain) and in the eastern part (Bushmanland) mainly in summer. It ranges from 75–250 mm per annum.

Altitude: 100–800 m.

Associated vegetation: Western Gariiep Hills Desert, Noms Mountain Desert and Richtersveld Mountain Desert. Also Bushmanland Arid Grassland of the Nama-Karoo Biome (Mucina *et al.* 2005).

Associated cremnophytes: In the upper reaches of the Gannakouriep River (Richtersveld Transfrontier National Park), *Crassula sericea* var. *sericea* has been recorded with other cliff-

dwelling succulent plants such as *Aloe meyeri*, *Bulbine pendens*, *Ornithogalum suaveolens* and *Tylecodon ellaphieae*.

Geology: Quartzitic sandstone, Rosyntjieberg Formation (Orange River Group; Proterozoicum).

DISTRIBUTION

Crassula sericea var. *sericea* is confined to the lower Orange River Valley, from Kakamas to the Richtersveld, also Karasberg and Witputz region.

RELATED SPECIES

Crassula sericea var. *sericea* is related to var. *hottentotta* but the latter is not as fragile and the leaves have rounded trichomes.

ADAPTATIONS TO THE CLIFF ENVIRONMENT

Habit: Dense, rounded, compact clusters.

Size and weight: Clusters small, of light weight.

Stem: Short, usually unexposed.

Leaves

Orientation: Ascending-spreading, very fragile, compact. Compared to other varieties of *Crassula sericea*, which are larger, the reduction in size and compact nature can be viewed as an adaptation to the dry conditions on the cliff face.

Colour: Epidermis greyish to brownish green, becoming brownish or reddish green. The reddish colour under dry conditions (production of anthocyanins) reduces penetration of light, an adaptation resulting from the well-drained habitat.

Age and persistence: Plants long-lived perennials.

Armament: Soft-leaved plant bodies without conspicuous armament.

Sexual reproduction

Flowers: Flowering mainly in winter and early spring and pollinated by insects. Inflorescence is an elongated thyrse (indication of wind-dispersed seed). Corolla tubular, ascending-spreading, white-flowered.

Fruit/Seed

Size: Seed minute and ideal for establishment in crevices.

Dispersal: Follicles dehiscent, with seeds spontaneously released and dispersed by wind.

Time: Seeds released in spring and summer.

Vegetative reproduction. Plants proliferating and forming dense cushions, a vegetative backup strategy enabling the plants to survive the harsh conditions on the cliff face. When becoming detached, the fragile leaves will root if they fall into a crevice.

CONSERVATION STATUS

Locally common and well protected in the undisturbed cliff habitat, not threatened.

ADDITIONAL NOTES

Horticulture: Best for succulent karoo gardens, in shady rockeries or grown as a pot plant. Outside its habitat, it should preferably be grown under controlled conditions in a greenhouse. Easily cultivated, its vigour viewed as maximising survival. Propagate from leaf cuttings or division. Tends to get fungal rust in coastal parts (Cape Town coast).

VOUCHER

Van Jaarsveld 22258 (NBG).

ILLUSTRATIONS AND MAP

Figures 138a–138d, Map 138.

139. *Crassula setulosa* Harv. var. *jenkinsii* Schönland in Transactions of the Royal Society of South Africa 17: 239 (1929).

Cremonophyte growth form: Dwarf-sized, mat-forming cluster (of light weight, cliff hugger).

Growth form formula: A:S:Lper:R:C:Ts:La (vb)

Etymology: After T.J. Jenkins, assistant at the Transvaal Museum during Mrs Leendertz's time.

DESCRIPTION AND HABITAT

Plants with erect, irregularly arranged leaves, proliferating to form dense, untidy clusters up to 250 mm in diameter. Roots fibrous. Leaves lanceolate to linear lanceolate, 10–30 × 6–14 mm, dorsiventrally flattened; upper surface flat, glabrous, lower surface convex, glabrous, green to reddish when exposed; margin ciliate; apex acute. Inflorescence a terminal cyme with 1–5 flowers; axillary buds below flowers characteristic of this variety, brittle, rooting when becoming detached. Corolla white, tubular, up to 4 mm long; lobes oblong to oblanceolate, fused shortly at base, apices spreading to recurved. Anthers dark purple to black.

Pollinators: The conspicuous diurnal flowers suggest a day-flying insect.

Habitat and aspect: Exposed cliffs above altitudes of 500 m. Plants grow in shallow soil on rocky ledges. Temperatures are high in summer and mild in winter. The average daily maximum temperature is 27–28°C and the average daily minimum 10–12°C. Rainfall occurs mainly in summer (mainly thunder showers) and ranges from 500–1000 mm per annum.

Altitude: 1000–1800 m.

Associated vegetation: Waterberg-Magaliesberg Summit Sourveld of the Grassland Biome (Mucina *et al.* 2005).

Associated cremnophytes: On the Blouberg (Limpopo Province), plants grow with *Adromischus umbraticola* subsp. *umbraticola*, *Aloe mutabilis*, *Cotyledon barbeyi* and *Crassula swaziensis*.

Geology: Mainly quartzitic sandstone on various formations.

DISTRIBUTION

Crassula setulosa var. *jenkinsii* is widely distributed in Gauteng and the Limpopo Province, from the Magaliesberg range to Soutpansberg in the north.

RELATED SPECIES

At once distinguished from the other varieties or *Crassula* species by its erect leaves and untidy mats.

ADAPTATIONS TO THE CLIFF ENVIRONMENT

Habit: Dense and often untidy cushions, plants conspicuous and not camouflaged. The tightly arranged leaves and mat-forming prolific nature suggest an adaptation to the xeric cliff face, the plants rapidly filling crevices and thus lowering establishment of other dwarf-sized cremnophytes.

Size and weight: Clusters dwarf-sized, of light weight.

Stem: Lengthening and becoming spreading, adpressed against the rocks.

Leaves

Orientation: Ascending to erect. The compact nature can be viewed as an adaptation to the dry conditions on the cliff face.

Colour and texture: Epidermis green, becoming reddish. The reddish colour (production of anthocyanins) under dry conditions reduces penetration of light, an adaptation resulting from the well-drained habitat. The soft texture and fragile nature suggest adaptation to the sheltered and undisturbed cliff face.

Age and persistence: Rapid vegetative growth leading to constant renewal of populations, plants thus long-lived perennials.

Armament: Soft-leaved plant bodies without conspicuous armament.

Sexual reproduction

Flowers: Sparsely flowering, and vegetative buds on inflorescence distinct. Flowering in late summer and autumn, pollinated by insects.

Fruit/Seed

Size: Seed minute and ideal for establishment in crevices.

Dispersal: Follicles dehiscent, with seeds spontaneously released and dispersed by wind.

Time: Seeds released in late autumn or winter.

Vegetative reproduction: The inflorescence has axillary buds that are brittle and when they become detached and fall into crevices below they will root, thus spreading by vegetative means, filling crevices. This differs from the situation in solitary rosulate forms on level ground and represents an adaptation to the cliff habitat.

CONSERVATION STATUS

Locally common and well protected in the cliff habitat.

ADDITIONAL NOTES

Horticulture: *Crassula setulosa* var. *jenkinsii* is best for highveld gardens, grown in miniature rockeries. Plants can be grown in full sun or dappled shade. Easily cultivated, fast-growing and its vigour can be viewed as maximising survival. Propagate from cuttings (rosettes) or division.

VOUCHERS

Van Jaarsveld 18019, 18038 (NBG).

ILLUSTRATIONS AND MAP

Figures 139a–139d, Map 139.

140. *Crassula setulosa* Harv. var. *longiciliata* Toelken in Journal of South African Botany 41: 119 (1975).

Cremonophyte growth form: Mat-forming cluster (of light weight, cliff hugger).

Growth form formula: A:S:Lper:R:C:Ts:La (vb)

Etymology: Latin *longi*, long, and *cilium*, an eyelash, pertaining to the leaves with long hairs on the margins.

DESCRIPTION AND HABITAT

Plants rosulate, forming erect branches up to 150 mm high, often with rosette-like buds on main branch in winter. Roots fibrous. Leaves elliptic-oblong to oblanceolate, 3–10 × 2–3 mm, dorsiventrally flattened; upper surface flat, glabrous, lower surface convex, glabrous, green to

reddish when exposed; margin ciliate; apex acute. Inflorescence a terminal flat-topped thyrse with many flowers. Corolla white, tubular, up to 4 mm long; lobes oblong-ob lanceolate, fused shortly at base; apices spreading to recurved, rounded. Anthers dark purple to black.

Pollinators: The conspicuous diurnal flowers suggest a day-flying insect.

Habitat and aspect: Exposed cliffs above altitudes of 1000 m. Plants grow in shallow soil on rocky ledges. Temperatures are moderate in summer and mild to low in winter. The average daily maximum temperature is 18–20°C and daily minimum 6–8°C. Rainfall occurs mainly in summer (mainly thunder showers) and ranges from 1000–1500 mm per annum.

Altitude: 1000–3000 m.

Associated vegetation: Lydenburg Montane Grassland of the Grassland Biome (Mucina *et al.* 2005).

Associated cremnophytes: *Aloe challisii*, *Ledebouria* spp., *Rhodohypoxis baurii* and *Senecio orbicularis*.

Geology: Mainly quartzitic sandstone on various formations.

DISTRIBUTION

Crassula setulosa var. *longiciliata* is distributed from the northern Drakensberg in KwaZulu-Natal to Mount Anderson in Mpumalanga.

RELATED SPECIES

Differs from var. *setulosa* by its woody branches up to 150 mm long and the rosulate buds along the stem in winter.

ADAPTATIONS TO THE CLIFF ENVIRONMENT

Habit: Dense cushions, plants conspicuous and not camouflaged. The tightly arranged leaves clasping the stem and prolific nature are an adaptation to the xeric cliff face, the plants rapidly filling crevices and thus lowering establishment of other dwarf-sized cremnophytes.

Size and weight: Clusters small, of light weight.

Stem: Erect, woody, with rosettes in leaf axils.

Leaves

Orientation: Ascending-spreading.

Colour and texture: Epidermis green, becoming reddish. The reddish colour under dry conditions reduces penetration of excessive light, an adaptation resulting from the well-drained habitat. The soft texture and fragile nature suggest adaptation to the sheltered and undisturbed cliff face.

Age and persistence: Rapid vegetative growth leading to constant renewal of populations, plants thus long-lived perennials.

Armament: Soft-leaved plant bodies without conspicuous armament.

Sexual reproduction

Flowers: Flowering in late summer and autumn, pollinated by insects.

Fruit/Seed

Size: Seed minute and ideal for establishment in crevices.

Dispersal: Follicles dehiscent, with the seeds spontaneously released and dispersed by the wind.

Time: Seeds released in late autumn or winter.

Vegetative reproduction: Stems lengthening and forming rosettes in the axils. These brittle vegetative propagules break loose and will root if they fall into a crevice or come into contact with the soil. This differs from the situation in solitary rosulate forms on level ground and represents an adaptation to the cliff habitat.

CONSERVATION STATUS

Locally common and well protected by the undisturbed cliff habitat, not threatened.

ADDITIONAL NOTES

Horticulture: Easily cultivated, its vigour viewed as maximising survival. Propagate from rosettes. Not often grown.

VOUCHER

Van Jaarsveld 16986 (NBG).

ILLUSTRATIONS AND MAP

Figures 140a & 140b, Map 140.

141. *Crassula setulosa* Harv. var. *setulosa*, Harvey, Flora capensis 2: 347 (1862).

Cremonophyte growth form: Dwarf-sized, mat-forming cluster (of light weight, cliff hugger).

Growth form formula: A:S:Lper:R:C:Ts:La (vb)

Etymology: Latin *seta*, a bristle, and pertaining to the leaves.

DESCRIPTION AND HABITAT

Plants rosulate, proliferating from procumbent branches to form dense clusters up to 250 mm in diameter. Roots fibrous. Leaves elliptic, broadly elliptic to ovate-lanceolate, 10–30 × 6–14 mm, dorsiventrally flattened, recurved, in a tight rosette (when exposed to sun) at first, becoming more lax in flower; surface variable in colour and vestiture, with recurved hairs, to glabrous, green to reddish when exposed, upper surface flat to slightly channelled, lower surface convex; margin ciliate; apex acute; base cuneate. Inflorescence a terminal round-topped thyrse bearing 1–few dichasia. Flowers sessile. Calyx lobes triangular, up to 3 mm long, margin ciliate; apices with sturdy apical hair. Corolla tubular, up to 4 mm long, white; lobes oblong-lanceolate, up to 3.5 mm long, shortly fused at base; apices acute, spreading to recurved. Anthers yellow to brown.

Pollinators: The conspicuous diurnal flowers suggest a day-flying insect.

Habitat and aspect: Sheltered cliffs above altitudes of 1000 m (mainly exposed northern and western aspects). Plants grow in shallow soil on exposed rocky ledges. Temperatures are moderate in summer and low in winter, with snow on the high escarpments. The average daily maximum temperature is 18–22°C and daily minimum 6–10°C. Rainfall occurs mainly in summer (mainly thunder showers) and ranges from 800–2000 mm per annum.

Altitude: 1000–3000 m.

Associated vegetation: Southern Drakensberg Highland Grassland of the Grassland Biome (Mucina *et al.* 2005).

Associated cremnoophytes: On Aasvoëlkop (Northcliff, Johannesburg) plants grow with *Adromischus umbraticola* subsp. *umbraticola* and *Crassula swaziensis*.

Geology: Mainly quartzitic sandstone on various formations.

DISTRIBUTION

Crassula setulosa var. *setulosa* is widely distributed from the higher eastern Drakensberg escarpment mountains in South Africa and northwards to Mount Mulanje in Malawi.

RELATED SPECIES

At once distinguished from the other varieties by its regular rosettes of ovate to elliptic, usually hairy leaves. *Crassula setulosa* var. *setulosa* belongs to section *Rosulares*, which includes 22 species (Toelken 1985). Var. *jenkinsii* has indistinct basal rosettes. The var. *deminuta* has smaller and less cauline leaves. Differs from the other related level-ground *Crassula* species in its dwarf size and dense habit of brittle leaves.

ADAPTATIONS TO THE CLIFF ENVIRONMENT

Habit: Dense cushions, plants fairly conspicuous. The tightly arranged leaves and prolific, mat-forming nature suggest an adaptation to the xeric cliff face.

Size and weight: Clusters small, of light weight.

Stem: Short, adpressed against the rocks.

Leaves

Orientation: Ascending-spreading, compact. The compact nature can be viewed as an adaptation to the dry conditions on the cliff face.

Colour and texture: Epidermis green, becoming reddish. The reddish colour (production of anthocyanins) under dry conditions reduces penetration of light, an adaptation resulting from the well-drained habitat. The soft texture and fragile nature reflect the sheltered habitat on the undisturbed cliff face.

Age and persistence: Rapid vegetative growth leading to constant renewal of populations, plants thus long-lived perennials.

Armament: Soft-leaved plant bodies without conspicuous armament.

Sexual reproduction

Flowers: Flowering in summer and autumn, pollinated by insects.

Fruit/Seed

Size: Seed minute and ideal for establishment in crevices.

Dispersal: Follicles dehiscent, with seeds spontaneously released and dispersed by wind.

Time: Seeds released in autumn and winter.

Vegetative reproduction: *Crassula setulosa* var. *setulosa* proliferates, forming dense mats and cushions, an efficient vegetative backup strategy for surviving the harsh conditions on the cliff face. A detached offshoot will root if it falls into a new crevice (as a result of heavy wind or some other disturbance), ensuring long-term survival.

CONSERVATION STATUS

Locally common and well protected by the cliff habitat.

ADDITIONAL NOTES

Horticulture: *Crassula setulosa* var. *setulosa* is best for highveld gardens, grown in miniature rockeries. Plants can be grown in full sun or dappled shade. Easily cultivated, its vigour viewed as maximising survival. Propagate from cuttings (rosettes) or division.

VOUCHER

Van Jaarsveld 17339 (NBG).

ILLUSTRATIONS AND MAP

Figures 141a–141c, Map 141.

142. *Crassula sladenii* Schönland in Annals of the South African Museum 9: 46 (1912).

Cremonophyte growth form: Cluster of drooping, leafy stems (of medium weight, cliff hanger).

Growth form formula: E:F:P:Els (vb) (e)

Etymology: After the Percy Sladen Expedition. Funds provided with the help of the Percy Sladen Memorial Trust (William Percy Sladen, a British naturalist who died in 1900).

DESCRIPTION AND HABITAT

Spreading, somewhat scrambling, sparsely branched shrub up to 500 mm high. Roots fibrous. Branches grey-brown, 4 mm in diameter. Leaves ovate to ovate-lanceolate, 25–40 × 15–25 mm, dorsiventrally flattened, basally fused with opposite leaf; surface glabrous, grey-green or pale green, with a powdery bloom, upper surface flat, lower surface convex; margin reddish; apices obtuse or acute; older leaves persistent. Inflorescence an elongated, round-topped thyrse; peduncle short, up to 20 mm long, with sessile flowers. Calyx triangular-lanceolate, up to 2 mm long, acute. Corolla tubular, white, shortly fused at base; lobes oblong-elliptic, up to 5 mm long. Anthers black.

Phenology: Flowering in midsummer.

Pollinators: The conspicuous diurnal flowers suggest a day-flying insect.

Habitat and aspect: Cliffs at altitudes of up to about 1000 m (all aspects). Plants are firmly rooted in crevices (often very small hairline cracks), often solitary in small crevices or socially with other cremonophytes. Temperatures are moderate to high in summer and can reach 40°C. Winters are cooler but frost is absent. The average daily maximum temperature is 27°C and the average daily minimum for the region is 13°C. Rainfall occurs mainly in winter, ranging from 75–200 mm per annum (thunder showers or cyclonic winter rain).

Altitude: 500–1100 m.

Associated vegetation: Western Gariep Lowland Desert of the Desert Biome as well as Succulent Karoo Biome.

Associated cremonophytes: On Kuansibberg in southern Namibia, *Crassula sladenii* grows in association with *Aloe pavelkae*, *Crassula macowanii*, *Hartmanthus* sp., *Haworthia tessellata* and *Tylecodon racemosus*.

Geology: Dolomite and sandstone of the Kuibis and Schwarzrand Subgroups (Nama Group). Substrate rough, with many ledges, crevices and fissures, ideal for the establishment of plants.

DISTRIBUTION

Restricted to cliffs along the lower Orange River Valley (Northern Cape in South Africa and in southern Namibia), mainly on dolomite, but also sandstone.

RELATED SPECIES

Related to *Crassula perforata*, *C. rupestris* and *C. badspoortense*. Immediately distinguished from them by its larger, more robust stature.

ADAPTATIONS TO THE CLIFF ENVIRONMENT

Habit: Clusters of pendent, leafy branches

Size and weight: Clusters of medium weight.

Stem: Branches bending down at the apices, becoming pendulous to subpendulous. This epinastic growth, becoming pendent, can be viewed as an adaptation to the cliff environment.

Leaves

Orientation: Spreading, decussate, closely packed and fused at the bases.

Colour: Grey-green to glaucous, covered with a powdery bloom (becoming distinctly purplish reddish during dry periods), suggesting adaptation to the extreme xeric conditions of the cliff face. The reddish colour under dry conditions reduces penetration of light, another adaptation resulting from the extreme run-off in the sheer habitat.

Age and persistence: Plants long-lived perennials. Leaves also persistent and long-lived.

Armament and camouflage: Soft, flaccid, leafy plant bodies without conspicuous armament or camouflage properties as opposed to the level-ground species, which are more woody.

Sexual reproduction

Flowers: Flowering in midsummer.

Fruit/Seed

Size: Seed very fine dust diaspores, ideal for establishment in crevices.

Dispersal: Follicles dehiscent, with seeds spontaneously released and dispersed by wind.

Time: Summer and autumn, just in time for the winter rains and thus maximising establishment.

Vegetative reproduction: Stems will root when coming in close contact with crevices, an efficient vegetative backup strategy for surviving the harsh conditions on the cliff face. A detached branch will root.

CONSERVATION STATUS

Classified as near threatened (Raimondo *et al.* 2009). However, locally abundant and well protected in the cliff habitat.

ADDITIONAL NOTES

Horticulture: Best for desert and succulent karoo gardens and ideal for steep embankments. Grow in a sandy soil, keep dry in summer. Outside the desert habitat, it should be grown under controlled conditions in a greenhouse. *Crassula sladenii* is easily propagated from cuttings.

VOUCHER

Van Jaarsveld 19917 (NBG).

ILLUSTRATIONS AND MAP

Plate 142, Figures 142a–142c, Map 142.

143. *Crassula smithii* Van Jaarsv., D.G.A.Styles & G.McDonald in *Aloe* 45,4: 90–92 (2008).

Cremonophyte growth form: Compact small clusters (of medium weight, cliff hugger).

Growth form formula: A:S:Lper:R:C:Ts:La (vb)

Etymology: After Professor Gideon Smith (1959–), current Chief Director, Biosystematics Research and Biodiversity Collections, at the South African National Biodiversity Institute, who discovered this species.

DESCRIPTION AND HABITAT

Perennials forming compact, rosulate, basal clusters, when in flower up to 250 mm tall, 200 mm in diameter. Roots fibrous. Stems erect to decumbent, succulent, glabrous, terete, up to 8 mm in diameter, yellowish green at first, becoming reddish brown with age. Leaves sessile, firm, distinctly succulent, linear-triangular, 40–160 × 8–12 mm; adaxial surface flat to slightly channelled, lower surface rounded, yellowish to reddish green; margin entire; apex acute, bearing a mucro. Inflorescence a terminal, round-topped thyrse with many pedicellate, 5-merous flowers in 1–many dichasia; basal part of inflorescence glabrous, distal parts with scattered, recurved, scabrid hairs; bracts triangular-subulate, becoming smaller distally; basal bracts 10 × 4 mm, distal bracts 4 × 1.5 mm; pedicels 7–25 mm long. Sepals triangular, 4 × 1.5 mm, surface subglabrous, with scattered recurved translucent scabrid hairs, with distinct marginal cilia; apex acute. Petals triangular, 5 × 1.8 mm, spreading, slightly recurved at tip; apex reddish with distinct subulate dorsal appendage, 0.5 mm long. Stamens 5 × 0.8 mm, tapering towards apex; anthers 0.8 × 0.5 mm, brown; pollen yellow. Squamae 0.3 × 0.5 mm, slightly emarginate, orange. Carpels tapering into subulate styles.

Phenology: Flowering in summer (January–March).

Pollinators: The conspicuous diurnal white flowers suggest a day-flying insect.

Habitat and aspect: Exposed cliffs at altitudes of up to about 1000 m. Plants grow in shallow soil on sunny rocky ledges. Temperature moderate in summer and mild to lower in winter. Average daily maximum temperature is about 24°C and daily minimum about 12°C. Rainfall mainly in summer (mainly thunder showers), ranging from 700–800 mm per annum.

Altitude: 800–1300 m.

Associated vegetation: KwaZulu-Natal Sandstone Sourveld of the Savanna Biome (Mucina *et al.* 2005).

Associated cremnophytes: According to David Styles (pers. comm.) who recently visited the habitat, the following cliff dwellers occur there: *Aeollanthus parvifolius*, *Aloe arborescens*, *Crassula perfoliata* var. *heterotricha*, *Cyanotis* sp., *Delosperma* sp. (white flowers), *Plectranthus purpuratus* subsp. *purpuratus* and *Senecio rhyncholaenus*.

Geology: Mainly quartzitic sandstone of the Natal Group (Cape Supergroup).

DISTRIBUTION

Crassula smithii is known only from the Noodsberg, northwest of Durban, KwaZulu-Natal.

RELATED SPECIES

Differs from *Crassula alba* (flat terrain) by its subulate, very succulent leaves (increase in succulence). The leaf margin in *C. smithii* is not ciliate, there are fewer bracts on the inflorescence and the peduncle is glabrous. The calyx lobes are smaller (half the length of those of *C. alba*).

ADAPTATIONS TO THE CLIFF ENVIRONMENT

Habit: Cluster-forming, plants conspicuous and not camouflaged. The aloe-like leaves in a rosette are well adapted to the undisturbed cliff face.

Size and weight: Clusters small, of medium weight.

Stem: Ascending to decumbent, very short.

Leaves

Orientation: Ascending-spreading to erect, compact, in a basal rosette. The compact, rosulate nature and subulate form can be viewed as an adaptation to the dry conditions on the cliff face.

Colour and texture: Epidermis green to yellowish green, becoming reddish. The reddish colour under dry conditions reduces penetration of light, an adaptation resulting from the well-drained habitat. The soft texture and fragile nature reflect the sheltered, undisturbed cliff face.

Age and persistence: The plants are relatively slow-growing, long-lived perennials.

Armament: Soft-leaved plant bodies without conspicuous armament.

Sexual reproduction

Flowers: Flowering in late summer and autumn (March–April), pollinated by insects.

Fruit/Seed

Size: Seed minute and ideal for establishment in crevices.

Dispersal: Follicles dehiscent, with seeds spontaneously released and dispersed by wind.

Time: Seeds released in autumn or winter.

Vegetative reproduction: Plants proliferating and cluster-forming, filling up crevices. This differs from the situation in solitary rosulate forms (*Crassula alba* var. *alba*) on level ground and can be viewed as an adaptation to the cliff habitat.

CONSERVATION STATUS

Locally common and well protected in the undisturbed cliff habitat, not threatened.

ADDITIONAL NOTES

Horticulture: Easily cultivated, its vigour viewed as maximising survival. Easily grown from seed or division. Dividing and rapidly forming dense clusters.

VOUCHER

Smith s.n. (NBG).

ILLUSTRATIONS AND MAP

Plate 143, Figures 143a & 143b, Map 143.

144. *Crassula socialis* Schönland in Transactions of the Royal Society of South Africa 17: 241 (1929).

Cremonophyte growth form: Dwarf-sized, mat-forming cluster (of light weight, cliff hugger).

Growth form formula: A:S:Lper:R:C:Ts:La (vb)

Etymology: Latin *socialis*, social, pertaining to its prolific nature, occurring in dense groups.

DESCRIPTION AND HABITAT

Plants rosulate, proliferating from base to form dense, rounded clusters up to 40 mm high (without inflorescence). Roots fibrous. Leaves ovate to elliptic, 4–11 × 8–16 mm, dorsiventrally compressed, 4-ranked, light to dark green, glabrous but with marginal cilia; apex acute. Inflorescence a terminal rounded thyrse bearing 1–3 dichasia up to 70 mm high,

with sessile flowers. Calyx lobes triangular-ovate, up to 1.5 mm long, ciliate. Corolla tubular, 6 mm long, white; lobes oblong-obovate, up to 2.5 mm long, fused shortly at base; apices spreading. Anthers yellow. Carpels with reniform ovaries and short, reflexed styles.

Phenology: Flowering in spring (August–October).

Pollinators: The conspicuous diurnal flowers suggest a day-flying insect.

Habitat and aspect: South-facing cliffs. Plants firmly rooted in crevices. Temperatures are high in summer (35–40°C). Winters are cooler but frost is absent. The average daily maximum temperature is about 29°C and daily minimum 14°C. Rainfall occurs throughout the year but with a peak in spring and summer, ranging from 300–400 mm per annum (thunder showers or cyclonic winter rain).

Altitude: 800–1200 m.

Associated vegetation: Mainly Great Fish Noorsveld of the Albany Thicket Biome (Mucina *et al.* 2005)

Associated cremnophytes: North of Grahamstown along the Great Fish River, the following plants have been recorded: *Bulbine latifolia*, *Crassula cultrata*, *C. perfoliata* var. *minor*, *Gasteria excelsa* and *Ornithogalum juncifolium* var. *emsii*.

Geology: Dark-coloured and smooth-textured Ecca shale (Fort Brown Formation) of the Karoo Supergroup.

DISTRIBUTION

Confined to the Eastern Cape, between King William's Town and Kommadagga.

RELATED SPECIES

Crassula socialis belongs to section *Rosulares*, which includes 22 species (Toelken 1985). It can be confused with *C. montana* subsp. *quadrangularis* but is at once distinguished by its much smaller heads and flowers with reflexed styles. It is distinguished from related non-cremnophilous *Crassula* species by its dwarf-sized, compact growth.

ADAPTATIONS TO THE CLIFF ENVIRONMENT

Habit: Dense, rounded clusters, plants conspicuous and not camouflaged. The tight, imbricate leaves that are not camouflaged and the dwarf-sized, compact nature can be seen as an adaptation to the xeric conditions on the cliff face.

Size and weight: Clusters small, of light weight.

Stem: Short, usually unexposed.

Leaves

Orientation: Spreading, compact, 4-ranked. The compact nature can be viewed as an adaptation to the dry conditions on the cliff face.

Colour: Epidermis green, becoming reddish. The reddish colour under dry conditions is due to the production of anthocyanins (reducing excessive penetration of light), an adaptation resulting from the well-drained cliff habitat.

Age and persistence: Plants long-lived perennials.

Armament: Soft-leaved plant bodies without conspicuous armament.

Sexual reproduction

Flowers: Flowering in spring, pollinated by insects.

Fruit/Seed

Size: Seed minute and ideal for establishment in crevices.

Dispersal: Follicles dehiscent, with seeds spontaneously released and dispersed by wind.

Time: Seeds released in late spring at the onset of summer rain conditions and thus maximising establishment.

Vegetative reproduction: *Crassula socialis* proliferates, forming dense mats and cushions, an efficient vegetative backup strategy for surviving the harsh conditions on the cliff face. When an offshoot becomes detached, it will root if it falls into a new crevice (as a result of heavy wind or some other disturbance), ensuring long-term survival.

CONSERVATION STATUS

Classified as rare (Raimondo *et al.* 2009). Locally common and well protected in the undisturbed cliff habitat.

ADDITIONAL NOTES

Horticulture: Best for thicket gardens, grown in rockeries, miniature succulent gardens, roof gardens and containers. Easily cultivated, its vigour viewed as maximising survival. Propagate from cuttings or division. Grows best in sandy slightly acid soil, preferably in dappled shade.

VOUCHER

Van Jaarsveld 16806 (NBG).

ILLUSTRATIONS AND MAP

Figures 144a–144d, Map 144.

145. *Crassula streyi* Toelken in The Flowering Plants of Africa 42: t. 1672 (1973).

Cremonophyte growth form: Cluster (of medium weight, cliff squatter).

Growth form formula: E:F:As:S/H:Es (vb)

Etymology: After Rudolf Georg Strey (1907–1988) farmer and botanist who first collected this species.

DESCRIPTION AND HABITAT

Decumbent to erect, sparsely branched, succulent herbs 100–200 high (without inflorescence). Roots fibrous. Branches 5–10 mm in diameter, reddish. Leaves sessile, 40–65 × 25–40 mm ascending-spreading, becoming slightly recurved, flat; blade ovate to elliptic, dark green, often mottled above, purplish below; margin entire to subcrenulate, slightly revolute to revolute; apex rounded to acute, cuspidate. Inflorescence an ascending rounded thyrse bearing several dichasia; peduncle up to 80 mm long. Calyx lobes linear-triangular, up to 2 mm long. Corolla 4- or 5-merous, star-shaped, 10 mm in diameter; lobes fused at base, lanceolate, up to 4.5 × 2 mm, yellowish green. Anthers yellow.

Phenology: Flowering in midwinter (May–June).

Pollinators: The conspicuous diurnal flowers suggest a day-flying insect.

Habitat and aspect: Cliffs, at altitudes of up to 250 m. Plants grow in shallow soil among leaf litter on shady rocky ledges, often in the shade of cliff-dwelling shrubs. Temperature high in summer and mild in winter. The average daily maximum temperature is about 24°C and average daily minimum about 15°C. Rainfall occurs mainly in summer, ranging from 800–1000 mm per annum.

Altitude: 50–250 m.

Associated vegetation: KwaZulu-Natal Coastal Belt of the Indian Ocean Coastal Belt (Mucina *et al.* 2005).

Associated cremonophytes: *Cotyledon orbiculata*, *Crassula perfoliata* var. *minor*, *C. perforata*, *Delosperma* sp., *Gasteria croucheri*, *Ornithogalum longibracteatum*, *Plectranthus ernstii* and *P. saccatus* subsp. *pondoensis*.

Geology: Quartzitic sandstone of the Natal Group (Cape Supergroup).

DISTRIBUTION

Crassula streyi is confined to quartzitic sandstone gorges in southern KwaZulu-Natal and into the adjacent northern Eastern Cape.

RELATED SPECIES

Crassula streyi is related to *C. multicava* but is at once distinguished by its larger, mottled leaves and less vigorous nature.

ADAPTATIONS TO THE CLIFF ENVIRONMENT

Habit: Small clusters of very fleshy leaves. The very succulent nature of the clusters can be viewed as an adaptation to the dry cliff-face conditions, the plants able to fill crevices in the absence of disturbances by larger herbivores.

Size and weight: Clusters of medium weight.

Stem: Short, ascending to decumbent, usually purplish.

Leaves

Orientation: Ascending-spreading, compact, decussately arranged.

Colour: Epidermis green, becoming reddish. The upper side often white-mottled and very attractive. The reddish colour under dry conditions (production of anthocyanins) reduces penetration of light, an adaptation resulting from the well-drained habitat.

Age and persistence: Plants long-lived perennials.

Armament: Soft-leaved plant bodies without conspicuous armament.

Sexual reproduction

Flowers: Flowering in spring, pollinated by insects.

Fruit/Seed

Size: Seed minute and ideal for establishment in crevices.

Dispersal: Follicles dehiscent, with seeds spontaneously released and dispersed by wind.

Time: Seeds released in spring at the onset of rainy conditions and thus maximising establishment.

Vegetative reproduction: Plants proliferating and forming small cushions. Branches or detached leaves touching the soil will root, a vegetative backup strategy enabling the plants to survive the harsh conditions on the cliff face.

CONSERVATION STATUS

Locally common and well protected in the undisturbed cliff habitat, not threatened.

ADDITIONAL NOTES

Horticulture: Best for subtropical coastal gardens, grown in rockeries or as a pot plant in dappled shade. Outside the habitat, it is best grown as a pot plant under controlled conditions in a greenhouse. Propagate from leaf or stem cuttings.

VOUCHER

Van Jaarsveld 18258 (NBG).

ILLUSTRATIONS AND MAP

Plates 145 & 145a, Figures 145a–145d, Map 145.

146. *Crassula tabularis* Dinter in Repertorium Specierum Novarum Regni Vegetabilis 19: 146 (1923).

Cremonophyte growth form: Mat-forming cluster (of light weight, cliff hugger).

Growth form formula: A:S:Lper:R:C:Ts:La (vb)

Etymology: Latin *tabularis*, horizontally flattened, pertaining to the plant body.

DESCRIPTION AND HABITAT

Plants rosulate, solitary or proliferating from base to form small clusters up to 300 mm high (inflorescence included). Roots fibrous. Leaves lanceolate to ovate, 10–45 × 5–15 mm, ascending-spreading, dorsiventrally compressed; surface glabrous, upper surface flat, lower surface somewhat keeled; margin ciliate; apex acute to acuminate. Inflorescence a terminal elongated thyrse bearing many dichasia; peduncle not distinct. Flowers sessile. Calyx lobes triangular, up to 3 mm long; margin ciliate; apex acute, bearing a larger apical hair. Corolla tubular, 5 mm long, white; lobes oblong-obovate, up to 4.5 mm long; apices acute, spreading, becoming reflexed. Anthers yellow.

Phenology: Flowering in summer and autumn (February–April).

Pollinators: The conspicuous diurnal flowers suggest a day-flying insect.

Habitat and aspect: Sheltered cliffs, at altitudes of about 1000–2000 m. Plants grow in shallow soil on shady rocky ledges. Temperatures are high in summer and mild in winter. The average daily maximum temperature is 25–27°C and daily minimum 10–12°C. Rainfall occurs mainly in summer (thunder showers) and ranges from 300–400 mm per annum.

Altitude: 1200–2000 m.

Associated vegetation: Dry Grassland, Nama-Karoo and dry Savanna (Mucina *et al.* 2005).

Associated cremonophytes: On the Auasberg Mountains it has been recorded with *Adromischus schuldianus*, *Ceterach cordatum*, *Cotyledon orbiculata* var. *orbiculata* and *Crassula sericea* var. *sericea*.

Geology: Mainly sandstone and mudstone.

DISTRIBUTION

Crassula tabularis is confined to the northern parts of the Great Karoo (Northern Cape, southern Free State) extending northwards to central Namibia, especially the Auasberg south of Windhoek.

RELATED SPECIES

Crassula tabularis is related to *C. capitella* subsp. *thyrsiflora* but is immediately distinguished by its flat rosettes of mottled leaves. The two species also do not overlap in distribution. *Crassula capitella* subsp. *thyrsiflora* occurs in the Succulent Karoo and Albany Thicket Biomes and is a more robust species.

ADAPTATIONS TO THE CLIFF ENVIRONMENT

Habit: With compact growth, often forming small, dense clusters typical of so many cremnophilous species.

Size and weight: Clusters small, of light weight.

Stem: Short, usually unexposed.

Leaves

Orientation: Spreading, in flat compact rosettes (of spirally arranged leaves).

Colour: Epidermis green, becoming reddish. The reddish colour under dry conditions (production of anthocyanins) reduces penetration of light, an adaptation resulting from the well-drained habitat.

Age and persistence: Plants long-lived perennials.

Armament: Soft-leaved plant bodies without conspicuous armament.

Sexual reproduction

Flowers: Flowering in summer and early autumn (February–April), pollinated by insects.

Fruit/Seed

Size: Seed minute and ideal for establishment in crevices.

Dispersal: Follicles dehiscent, with seeds spontaneously released and dispersed by wind.

Time: Seeds released in summer and autumn at the onset of cooler conditions, maximising establishment.

Vegetative reproduction: Plants proliferating and forming dense cushions, a vegetative backup strategy for continued existence despite the harsh conditions on the cliff face.

CONSERVATION STATUS

Well protected by the undisturbed cliff-face habitat, not threatened.

ADDITIONAL NOTES

Horticulture: Easily cultivated from seed or division. Dividing annually and forming dense clusters.

VOUCHER

Van Jaarsveld 17469 (NBG).

ILLUSTRATIONS AND MAP

Figures 146a–146c, Map 146.

147. *Crassula tomentosa* Thunb. var. *glabrifolia* (Harv.) Toelken in Flora of southern Africa 14: 188 (1985).

Cremnophyte growth form: Compact cluster (of light weight, cliff hugger).

Growth form formula: A:S:Lper:R:C:Ts:La (vb) (r)

Etymology: The epithet *glabrifolia*, smooth leaves, pertains to the leaf surface without hairs.

DESCRIPTION AND HABITAT

Plants proliferating from base, cluster-forming, rosulate, up to 300 mm high (with inflorescence). Roots fibrous. Leaves 2-ranked, tightly packed, broadly obovate, 5–25 × 5–30 mm, dorsiventrally flattened; surface grey-green to green, tomentose, with marginal cilia; apex truncate. Inflorescence a terminal branched spike-like thyrses 300 mm high, bearing many dichasia, with basal dichasia pedunculate; peduncle indistinct, with leaf-like bracts becoming smaller distally; flowers spreading in sessile, decussate, glomerate dichasia. Calyx lobes triangular-ovate, up to 3 mm long, tomentose, with marginal cilia. Corolla tubular; lobes oblong-panduriform, 4.5 mm long, fused in basal part, off-white to pale yellow, spreading, becoming slightly recurved. Anthers black.

Phenology: Flowering in spring and summer (October–December).

Pollinators: The pale yellow corolla suggests a flying insect.

Habitat and aspect: Shady sheltered cliffs of the northern Cape Fold Belt mountains. Plants grow in shallow soil on shady rocky ledges. Temperatures hot in summer and mild in winter. The average daily maximum temperature is 24–26°C and average daily minimum 8–10°C. Rainfall occurs mainly in winter (cyclonic winter rain) and summer (thunder showers), ranging from 75–300 mm per annum.

Altitude: 400–1700 m.

Associated vegetation: Vanrhynsdorp Shale Renosterveld of the Fynbos Biome (Mucina *et al.* 2005).

Associated cremnophytes: Associated plants on the Gifberg include *Aloe perfoliata*, *Crassula nudicaulis* and *Oscularia alba*.

Geology: Mainly quartz (Khurisberg Subgroup, Aggeneys and Hom Formation) (Bushmanland Group), dolomite of the Holgat Formation (Gariep Supergroup) sandstone and shale of the Ecca Formation (Karoo Supergroup).

DISTRIBUTION

Crassula tomentosa var. *glabrifolia* is widely distributed along the margin of the winter-rainfall Karoo region, from Matjiesfontein in the south to the Gifberg and Bushmanland in the north and entering southern Namibia.

RELATED SPECIES

This variety of *Crassula tomentosa* differs from the non-cremnophytes in its smaller size (up to 300 mm in flower), and densely branched, tight, fragile rosettes. Leaves are shorter than 15 mm, broadly obovate, with truncate apices. The inflorescence is an unbranched, spike-like thyrse with pedunculate flowers. As in *C. tomentosa* var. *tomentosa*, each rosette is monocarpic, dying after flowering.

ADAPTATIONS TO THE CLIFF ENVIRONMENT

Habit: Forming tight clusters, rosettes flowering in succession, plants conspicuous and not camouflaged. The unarmed, soft texture of the plants is an adaptation to the undisturbed cliff-face habitat.

Size and weight: Clusters small, of light weight.

Stem: Decumbent, up to 100 mm long.

Leaves

Orientation: Ascending, in a tight rosette. The leaves are much shorter than those of the typical variety, broadly obovate with truncate apices. The reduction in size, soft texture and rosulate orientation suggest an adaptation to the undisturbed cliff face. The truncate apices might be an adaptation to the chasmophytic life style in areas where herbivores can reach.

Colour and texture: Green to dark green, soft-textured.

Age and persistence: The plants are relatively slow-growing, long-lived perennials.

Armament: Soft, fragile rosettes without conspicuous armament, an adaptation to the cliff habitat.

Sexual reproduction

Flowers: Spring to summer (October–December). Heads monocarpic but not all flowering in the same season, the plants thus with a longer life than those of var. *tomentosa*, suggesting an adaptation to the cliff face where establishment of seed is more difficult than on level ground. It is advantageous for the plants not being fully monocarpic.

Fruit/Seed

Size: Seed minute and ideal for establishment in crevices.

Dispersal: Follicles dehiscent, with seeds spontaneously released and dispersed by wind.

Time: Seeds released in late summer.

Vegetative reproduction: *Crassula tomentosa* var. *glabrifolia* continuously proliferates from the base, forming small dense clusters, an ideal long-term survival backup strategy on the sheer cliff face. When becoming detached, these rosettes will root where they land on other ledges or in new crevices.

CONSERVATION STATUS

Locally common and well protected by the cliff habitat.

ADDITIONAL NOTES

Horticulture: Best grown in succulent karoo gardens, in rockeries and miniature succulent gardens. Easily cultivated, its vigour viewed as maximising survival. Easily grown from seed or division. Dividing and rapidly forming dense clusters.

VOUCHER

Van Jaarsveld 19104 (NBG).

ILLUSTRATIONS AND MAP

Figures 147a–147d, Map 147.

TYLECODON Toelken

148. *Tylecodon aurusbergensis* G.Will. & Van Jaarsv., in Williamson in Aloe 29,3 & 4: 60–62 (1992).

Cremonphyte growth form: Dwarf-sized, tapering stem (of light weight, cliff squatter).

Growth form formula: E:F:As:S/H:Ca:D (vb)

Etymology: After the Aurusberg in the Sperrgebiet in southern Namibia, where the species was found.

DESCRIPTION AND HABITAT

Sparsely branched, erect plant up to 80 mm high, with conical, smooth to knobbly, succulent caudex up to 40 mm in diameter; bark grey, peeling, exposing green tissue. Leaf-bearing branches 2–3 mm in diameter, grey, with short, sharp, bract-like leaves up to 0.5 mm long; phyllopodia rounded, truncate, up to 1 mm long. Stem sparsely branched, with 1–several erect, succulent stems with grey bark and short, truncate phyllopodia. Leaves ovate to obovate-spathulate, 18–20 × 15–35 mm, crowded at apices; adaxial surface concave to channelled, abaxial surface with maroon striations, glandular hairy; apex obtuse; base cuneate. Inflorescence a short, almost sessile monochasium with 1–3 glandular hairy flowers; peduncle 2–20 mm long; pedicels 2–3 mm long. Corolla tubular, about 10 mm long, tube light green, glandular pubescent; lobes pink to pink-lilac, becoming recurved.

Phenology: Flowering from summer through to early autumn (March–April).

Pollinators: Insects.

Habitat and aspect: *Tylecodon aurusbergensis* grows mainly on quartzitic sandstone cliffs, the plants occurring in crevices, on ledges and in shady rock veins on southern aspects. Temperature moderate to high in summer but mild to warm in winter (frost absent). The average daily maximum temperature is about 22–24°C and the average daily minimum for the region 10–12°C. Rainfall is mainly in winter and autumn, ranging from 50–75 mm per annum (mainly cyclonic winter rain). Regular fog provides extra moisture.

Altitude: 600–900 m.

Associated vegetation: Succulent Karoo and Desert Biomes.

Associated cremnophytes: *Conophytum taylorianum* subsp. *taylorianum*, *Crassula aurusbergensis* and *Holothrix filicornis*.

Geology: Quartzitic sandstone cliffs (Gariiep Complex).

DISTRIBUTION

Endemic to the Aurusberg in southern Namibia.

RELATED SPECIES

Tylecodon aurusbergensis is related to *T. torulosus*, a related cremnophilous species from near Lekkering. The latter is larger and more robust. Compared to non-cremnophilous species, the small size and lack of defence mechanisms suggest adaptation to the undisturbed cliff-face.

ADAPTATIONS TO THE CLIFF ENVIRONMENT

Habit: Small, with lax, slender growth (single-stemmed or sparsely branched) from a tuberous base.

Size and weight: Dwarf-sized, up to 80 mm high, of light weight.

Roots: Fleshy at the base, otherwise fibrous. The fleshy nature can be viewed as an adaptation to the xeric conditions on the cliff face.

Stem: Succulent, grey-green with peeling bark and up to 3 mm in diameter, covered with grey phyllopodia.

Leaves

Orientation: Ascending-spreading. The rosulate presentation maximises absorption of light.

Colour and texture: Epidermis dark green. The very soft, fragile, succulent nature reflects a lack of disturbance by larger animals.

Age and persistence: Plants slow-growing, long-lived perennials. Leaves becoming deciduous during the long, dry summer, an adaptation to the moist conditions in winter.

Armament and camouflage: Plants fleshy and fragile without conspicuous armament or camouflage properties as opposed to the non-cremnophilous *Tylecodon* species, the reduction in camouflage and armament due to the undisturbed conditions on the cliff face.

Sexual reproduction

Flowers: The small, tubular flowers suggest a pollinator such as a flying insect with a long proboscis.

Fruit/Seed

Size: Seed minute and ideal for establishment in crevices.

Dispersal: Follicles dehiscent, with seeds spontaneously released and dispersed by wind.

Time: Seeds dispersed in autumn at the onset of the rainy season, maximising establishment.

Vegetative reproduction: *Tylecodon aurusbergensis* will root from branches that touch the soil.

CONSERVATION STATUS

Classified as near threatened (Loots 2005). It is rare and confined to the Aurusberg in southern Namibia, a region that falls within a protected reserve.

ADDITIONAL NOTES

Horticulture: Best for dry succulent karoo gardens, grown in dappled shade in containers. Keep dry in summer. Propagate from stem cuttings in autumn or winter.

VOUCHER

Williamson 4417 (NBG).

ILLUSTRATIONS AND MAP

Map 148.

149. *Tylecodon bleckiae* G.Will. in *Cactus and Succulent Journal* (U.S.) 70,3: 127–128 (1998).

Cremnophyte growth form: Cluster-forming (of medium weight, cliff squatter).

Growth form formula: E:F:As:S/H:Ca:D (vb)

Etymology: In honour of Ms Mary Bleck, Curator of the succulent plant collection of the Johannesburg Botanical Gardens from 1983–1990, who collected the plant together with Mr John Lavranos.

DESCRIPTION AND HABITAT

Dwarf-sized, cluster-forming, succulent shrublet up to 80 mm tall, from an elongated spreading tuberous base. Tubers up to 70 × 30 mm. Stems numerous, often tangled and not branched, up to 70 × 2.5–4 mm, ascending to spreading, grey with raised black plaques. Leaves 3–7 in a terminal rosette, 6–8 × 3–4 mm, elliptical, with centric groove on upper surface, dull green, glandular hairy. Inflorescence with 1 or 2 dichasia on erect peduncle 10 × 1.2 mm. Calyx lobes ovate-triangular, up to 2.5 × 1.8 mm, glandular pubescent. Corolla cylindrical, 12 × 4.5 mm, pale green, with spreading lobes, becoming recurved; lobes ovate-acute, light red with dark pink to red streaks and white margins. Squamae narrowly ovate, emarginate, cream-yellow.

Phenology: Flowering from mid- to late summer.

Pollinators: Insects.

Habitat and aspect: Quartzite cliffs, occurring mainly on eastern and south-facing slopes. Plants occur in crevices and on ledges on southern and southwest-facing aspects. Temperature moderate to high in summer and mild to warm in winter (frost absent), but occasionally lowered by fog from the Atlantic Ocean. The average daily maximum temperature is about 22°C and the average daily minimum for the region 14°C. Rainfall is mainly in winter and autumn, about 50–150 mm per annum (mainly cyclonic winter rain and thunder showers in autumn). Regular fog provides extra moisture.

Altitude: 600–900 m.

Associated vegetation: Succulent Karoo.

Associated cremnophytes: *Gasteria pillansii* var. *ernesti-ruschii*.

Geology: Quartzite, lava, tuff (Richtersveld Suite).

DISTRIBUTION

Restricted to the lower Orange River Valley adjacent to Rosh Pinah and Rooiberg in the Richtersveld Transfrontier National Park (Northern Cape).

RELATED SPECIES

Tylecodon bleckiae is at once distinguished from the related *T. buchholzianus* var. *buchholzianus* by its elongated, tuberous roots and unbranched to little-branched, tangled stems up to 70 mm long. Generally it is smaller and plants are about 120 mm in diameter. It differs further by its branches of 2.5–4.0 mm in diameter. The branches are soft and fragile. The var. *buchholzianus* is a larger, ascending, sturdy and robust plant without tuberous roots.

ADAPTATIONS TO THE CLIFF ENVIRONMENT

Habit: Densely clustered and with spreading branches, but not pendulous. The reduction in size (compared to its sister taxon *Tylecodon buchholzianus* var. *buchholzianus*) and spreading nature can be viewed as an adaptation to the cliff environment.

Size and weight: Clusters medium-sized, up to 120 mm in diameter, of medium weight.

Roots: Tuberous roots viewed as an adaptation to the extreme xeric conditions on the cliff face.

Stem: Numerous, often tangled, not branched, up to 70 × 2.5–4.0 mm, ascending to spreading, grey, with raised black plaques, fragile.

Leaves

Orientation: Ascending-spreading, 3–7 in a terminal rosette.

Colour and texture: Dull green and glandular hairy.

Age and persistence: Plants slow-growing, long-lived perennials. Leaves fragile, becoming deciduous during the long, dry summer, suggesting an adaptation to the moist conditions in winter.

Armament and camouflage: Plants fleshy and fragile without conspicuous armament or camouflage properties as opposed to the larger, robust, single-stemmed level-ground *Tylecodon buchholzianus* var. *buchholzianus*, the reduction in camouflage and armament due to the undisturbed conditions on the cliff face.

Sexual reproduction

Inflorescence and flowers: Inflorescence with 1 or 2 dichasia on an erect peduncle 10 × 1.2 mm. Calyx lobes ovate-triangular, up to 2.5 × 1.8 mm, glandular pubescent. Corolla cylindrical, 12 × 4.5 mm, pale green with spreading lobes, becoming recurved; lobes ovate-acute, light red with dark pink to red streaks and white margins.

Fruit/Seed

Size: Seed minute and ideal for establishment in crevices.

Dispersal: Follicles dehiscent, with seeds spontaneously released and dispersed by wind.

Time: Seeds dispersed in autumn at the onset of the rainy season, maximising establishment.

Vegetative reproduction: Densely branched, the branches rooting where they touch the ground or where they find new crevices (vegetative spread), an efficient vegetative backup for surviving the harsh cliff environment.

CONSERVATION STATUS

Rare but well protected owing to the cliff habitat.

ADDITIONAL NOTES

Horticulture: Best grown in succulent karoo gardens, in rockeries or containers. Outside the habitat, it is best suited to a greenhouse, grown under controlled conditions. Propagate from stem cuttings. Easily cultivated, its vigour viewed as maximising survival.

VOUCHER

Bleck & Lavranos s.n. (NBG).

ILLUSTRATIONS AND MAP

Figures 149a–149c, Map 149.

150. *Tylecodon bodleyae* Van Jaarsv. in *Cactus and Succulent Journal* (U.S.) 64,2: 57–61 (1992b).

Cremonophyte growth form: Erect shrublet (of light weight, cliff squatter).

Growth form formula: E:F:As:S/H:Ca:D (vb)

Etymology: Commemorates Mrs Elise Bodley (1922–1997), well known illustrator of succulents and who illustrated most known *Tylecodon* and *Cotyledon* species (Van Jaarsveld & Koutnik 2004).

DESCRIPTION AND HABITAT

Dwarf-sized, erect, sparsely branched succulent, up to 100 mm high, from tuberous base up to 60 mm in diameter; bark yellow-brown, peeling. Branches ascending, grey-green, with dark longitudinal striations, articulated at nodes; younger branches 4–5 mm in diameter; phyllopodia short, truncate. Leaves obovate to elliptic, 8–15 × 6–14 mm, green to pale green, sparsely glandular hairy or glabrous; apex acute; base cuneate. Inflorescence a thyrse up to

40 mm high, of 1 or 2 monochasia each bearing 1 or 2 flowers; pedicels 6–16 mm long, glandular pubescent; bracts linear, acute, 1–1.5 mm long. Calyx 4 mm long, 2.5 mm in diameter; lobes triangular-lanceolate, 3 × 1 mm. Corolla 11–15 mm long; tube funnel-shaped, yellowish green, 3 mm wide at base, expanding to 4 mm at throat, glandular hairy; lobes oblong, 5 × 2.5 mm, spreading, becoming recoiled, with long hairs on inner surface, white. Stamens erect, 13 mm long. Squamulae oblong, 1 × 0.5 mm, emarginate, erect, yellowish green.

Phenology: Flowering in midsummer (January–February).

Pollinators: Insects.

Habitat and aspect: Quartzitic sandstone cliffs, plants occurring in crevices and on ledges on eastern and southern aspects. Temperatures are moderate to high in summer and mild to warm in winter (frost absent), but are regularly lowered by fog from the Atlantic Ocean. The average daily maximum temperature is about 18°C and the average daily minimum for the region 10°C. Rainfall is mainly in winter, about 50 mm per annum (mainly cyclonic winter rain). Regular fog provides extra moisture.

Altitude: 350–470 m.

Associated vegetation: Vyftienmyl se Berge Succulent Shrubland of the Richtersveld Bioregion of the Succulent Karoo Biome (Mucina *et al.* 2005).

Associated cremnophytes: *Conophytum stephanii*, *Gasteria pillansii* var. *ernesti-ruschii*, *Tylecodon racemosus* and *T. similis*.

Geology: Quartz acetose of the Stinkfontein Formation (Gariiep Supergroup).

DISTRIBUTION

Southern Oograbies Mountains, 23 km east of Port Nolloth (Northern Cape).

RELATED SPECIES

Tylecodon bodleyae is similar to *T. similis* but is at once distinguished by its erect, robust not scandent nature and large, conspicuous, white flowers. It differs further in its articulated stems and larger, dorsiventrally flattened leaves. *Tylecodon similis* is a smaller, inconspicuous species, well camouflaged among the shrublets in succulent karoo.

ADAPTATIONS TO THE CLIFF ENVIRONMENT

Habit: Erect, sparsely branched, dwarf-sized shrublet.

Size and weight: Up to 100 mm high.

Roots: Tuberous.

Stem: Branches ascending, grey-green, with dark longitudinal striations, articulated at nodes; younger branches 4–5 mm in diameter; phyllopodia short, truncate.

Leaves

Orientation: Spreading, in a apical rosette.

Colour and texture: Green to pale green, sparsely glandular hairy or glabrous.

Armament and camouflage: Plants fleshy and fragile without conspicuous armament or camouflage properties as opposed to the smaller *Tylecodon similis* which is well camouflaged among the karoo shrubs. The fragile nature and lack of defence properties reflect the undisturbed cliff habitat.

Sexual reproduction

Inflorescence and flowers: Rich flowering. Inflorescence a conspicuous thyrses up to 40 mm high, with 1 or 2 monochasia, each bearing 1 or 2 flowers; pedicels 6–16 mm long, glandular pubescent; bracts linear, acute, 1–1.5 mm long. Calyx 4 mm long, 2.5 mm in diameter; lobes triangular-lanceolate, 3 × 1 mm. Corolla 11–15 mm long; tube funnel-shaped, yellowish green, 3 mm wide at base, expanding to 4 mm at throat, glandular hairy; lobes oblong, 5 × 2.5 mm, spreading, becoming recoiled, with long hairs on inner surface.

Fruit/Seed

Size: Seed minute and ideal for establishment in crevices.

Dispersal: Follicles dehiscent, with seeds spontaneously released and dispersed by wind.

Time: Seeds dispersed in autumn at the onset of the rainy season, maximising establishment.

Vegetative reproduction: Detached branches will root if they fall into new crevices (vegetative spread), an efficient vegetative backup for survival in the harsh cliff-face environment.

CONSERVATION STATUS

Classified as rare (Raimondo *et al.* 2009), but well protected owing to the cliff habitat.

ADDITIONAL NOTES

Horticulture: Best grown in succulent karoo gardens, in rockeries or containers. Outside its habitat, it is best suited to a greenhouse, grown under controlled conditions. Propagate from stem cuttings. Easily cultivated, its vigour viewed as maximising survival.

VOUCHER

Van Jaarsveld 22311 (NBG).

ILLUSTRATIONS AND MAP

Figures 150a–150f, Map 150.

151. *Tylecodon bruynsii* Van Jaarsv. & S.A.Hammer in *Cactus and Succulent Journal* (US) 81,5: 235–238 (2009).

Cremonophyte growth form: Loose stem clusters (of medium weight, cliff squatter).

Growth form formula: E:F:As:S/H:Ca:D (vb)

Etymology: After Peter Bruyns, mathematician and botanist at the University of Cape Town who first located this species.

DESCRIPTION AND HABITAT

Cluster-forming, much-branched, summer-deciduous, dwarf-sized shrublets, becoming subpendent, up to 400 mm in diameter; base often thickset, up to 40 mm in diameter. Roots fibrous. Branches up to 170 mm long, 15–20 mm in diameter, succulent, grey-green, smooth, light grey, somewhat flaking, exposing grey green epidermis; phyllopodia slightly raised, stem tapering at apex; petiole short, indistinct, up to 2 mm long. Leaves softly succulent, in apical rosettes, spreading, 25–45 × 15–30 mm; blade broadly obovate to subrotund, spreading, 2–4 mm thick, occasionally 3-lobed; both sides covered in short, translucent, glandular hairs; adaxial surface flat to slightly concave, greyish green, abaxial surface flattened, greyish green; margin entire; apex obtuse to rounded to subacute. Inflorescence a sparsely branched, short thyrse up to 30 mm long, bearing 1 or 2 apical monochasia (each with 1–3 flowers), glandular pubescent; peduncle greenish, 15 mm long, 1 mm in diameter at base, glandular pubescent; pedicels 7 mm long. Calyx 3 mm long, glandular pubescent, green; lobes 2 × 1 mm. Corolla funnel-shaped, glandular pubescent; tube 12 mm long, 4 mm at base, expanding to 6 mm at throat, yellowish green; lobes 5 × 3 mm, becoming slightly recurved, white; apices acute. Stamens up to 10 mm long, attached to throat, protruding for 5 mm; anthers 1 mm long. Squamae slightly tapering, 1 × 0.6 mm, emarginate, pale green, translucent. Gynoecium 22 mm long; carpels 5, free, about 10 mm long, tapering into styles 12 mm long and protruding for 12 mm from corolla apex. Follicles 8 × 1.7 mm. Seeds not seen.

Phenology: Flowering in midsummer (January–February).

Pollinators: Insects.

Habitat and aspect: Vertical quartzitic sandstone cliffs, mainly on cooler southern aspects offering shady conditions. Plants are firmly rooted in crevices large enough to support the roots and stem clusters. Temperature high during the day and the average daily summer temperature is about 26°C. Winters are cooler and subject to regular coastal fog from the west coast. Frost is absent. Rainfall mainly from autumn (thunder showers) to spring (cyclonic winter rain), and ranging from about 50–125 mm per annum.

Altitude: 700–800 m.

Associated vegetation: Succulent Karoo.

Associated cremonophytes: *Aloe pavelkae*, *Conophytum ricardianum*, *Crassula macowaniana*, *C. pseudoemisphaerica*, *C. sericea* var. *velutina*, *C. sladenii*, *Tylecodon buchholzianus*, *T. racemosus* and *T. rubrovenosus*.

Geology: Sandstone of the Kuibis and Schwarzrand Subgroups (Nama Group). Substrate rough, with many ledges crevices and fissures, ideal for establishment of plants.

DISTRIBUTION

Tylecodon bruynsii is confined to the upper slopes of the southern mountain range along the Orange River and adjacent area of the same geological formation. It mainly includes the Sonberg and Kuamsibberg.

RELATED SPECIES

Related to both *Tylecodon longipes* and *T. torulosus* (also a cremnohyte) but at once distinguished by its larger size, becoming pendent. Its branches are grey-green, with peeling bark, the obovate to subrotund leaves with a glandular hairy epidermis. The branches of *T. torulosus* are distinctly torulose (young bark dark brown) and the leaves often folded inwards. *Tylecodon longipes* has a compact growth, with many short branches, and plants do not become pendent.

ADAPTATIONS TO THE CLIFF ENVIRONMENT

Habit: Conspicuous, loose, pendent clusters. The summer-deciduous nature is an adaptation to the long, dry summers; the fragile texture not adapted to disturbances by larger herbivores.

Size and weight: Clusters medium-sized, pendent for up to 300 mm, of medium weight.

Roots: Tuberous.

Stem: Branches grey-white, up to 30 mm in diameter at the base; phyllopodia sometimes swollen (not torulose); bark grey, smooth; older branches flaking.

Leaves

Orientation: Spreading, apically grouped.

Colour and texture: Greyish green. The glandular hairy leaf indumentum indicative of adaptation to the regular fog from the Atlantic Ocean.

Age and persistence: Plants slow-growing, long-lived perennials, typical of cremnophilous succulent plants.

Armament and camouflage: Plants conspicuous, fleshy, fragile and without armament or camouflage properties, reflecting the disturbance-free cliff face. In comparison, the related *Tylecodon schaeferianus* of level ground is smaller, inconspicuous and a master of camouflage.

Sexual reproduction

Inflorescence and flowers: Inflorescence a sparsely branched, short thyrses up to 30 mm long, bearing 1 or 2 apical monochasia (each with 1–3 flowers), glandular pubescent; peduncle greenish, 15 mm long, 1 mm in diameter at base, glandular pubescent; pedicels 7 mm long. Calyx 3 mm long, glandular pubescent, green; lobes 2 × 1 mm. Corolla funnel-

shaped, glandular pubescent, tube 12 mm long, 4 mm at base, expanding to 6 mm at throat, yellowish green; lobes 5 × 3 mm, becoming slightly recurved, white; apices acute.

Fruit/Seed

Size: Seed minute and ideal for establishment in crevices.

Dispersal: Follicles dehiscent, with seeds spontaneously released and dispersed by wind.

Time: Seeds dispersed in autumn at the onset of the rainy season, maximising establishment.

Vegetative reproduction: The spreading branches will root where they touch the soil, forming loose, pendent mats (vegetative spread), an efficient vegetative backup for surviving the harsh cliff-face environment.

CONSERVATION STATUS

Rare but well protected owing to the cliff habitat.

ADDITIONAL NOTES

Horticulture: Best grown in succulent karoo gardens, in rockeries or containers. Outside its habitat, it is best suited to a greenhouse, grown under controlled conditions. Propagate from stem cuttings. Easily cultivated, its vigour viewed as maximising survival.

VOUCHER

Van Jaarsveld 21088 (NBG).

ILLUSTRATIONS AND MAP

Plate 151, Figures 151a–151c, Map 151.

152. *Tylecodon buchholzianus* (Schuldt & P.Stephan) Toelken var. *fasciculatus* G.Will. in *Aloe* 29,3 & 4: 62–63 (1992).

Cremnophyte growth form: Cluster-forming stem succulent (of medium weight, cliff squatter).

Growth form formula: E:F:As:S/H:Ca:D (vb)

Etymology: Latin *fasciculus*, a little bundle, pertaining to its clustered (fasciculate) branching.

DESCRIPTION AND HABITAT

Branched, ascending, spreading, summer-deciduous, densely clustered succulent, up to 270 mm in diameter, up to 150 mm high, often with drooping branches from cliff face up to 220 long. Branches grey-green, smooth, brittle, up to 12 mm in diameter at base, tapering to 5–7

mm, much-branched, sometimes remaining leafless and photosynthetically active; bark scaly, exposing green living tissue; leaf scars 1–1.3 mm wide. Leaves 1 or 2 occasionally produced, spreading, linear-terete, 8–10 × 3–5 mm; bract-like leaves reddish, subulate, 1 mm long. Inflorescence an erect, almost sessile thyrse up to 20 mm high, consisting of a solitary monochasium bearing 1–3 flowers. Calyx lobes triangular, 1 × 1.5 mm. Corolla tubular, purplish to yellow-green, 10 × 4 mm; lobes hairy on inside, spreading, becoming recurved. Squamulae 1.5 × 0.6 mm, emarginate, pale white, translucent.

Phenology: Flowering from mid- to late summer (February).

Pollinators: Insects.

Habitat and aspect: Quartzitic sandstone cliffs, the plants occurring in crevices and on ledges on eastern and southern aspects. Temperature moderate to high in summer and mild to warm in winter (frost absent), but regularly lowered by fog from the Atlantic Ocean. The average daily maximum temperature is about 18°C and the average daily minimum for the region 10°C. Rainfall mainly in winter, about 50 mm per annum (mainly cyclonic winter rain). Regular fog provides extra moisture.

Altitude: 50–700 m.

Associated vegetation: Vyftienmyl se Berge Succulent Shrubland of the Succulent Karoo Biome (Mucina *et al.* 2005).

Associated cremnohytes: *Anacampseros scopata*, *Conophytum stephanii*, *Crassula pseudohemisphaerica*, *Gasteria pillansii* var. *ernesti-ruschii* and *Tylecodon similis*.

Geology: Quartz acetose of the Stinkfontein Formation (Gariiep Supergroup).

DISTRIBUTION

Oograbies Mountains, 23 km east of Port Nolloth and running parallel to the coast for approximately 18 km (Northern Cape).

RELATED SPECIES

Tylecodon buchholzianus var. *fasciculatus* is at once distinguished from the typical variety by its densely branched, clustered growth, often with spreading to drooping stems from the cliff face. It differs further by its much-branched, thicker, grey-green photosynthetically active branches (only rarely producing 1 or 2 leaves, soon aborted). The branches are softer and more fragile. The var. *buchholzianus* is a larger, ascending, sturdy plant with a solitary main stem and thinner branches producing leaves in winter. The densely clustered, spreading to drooping and more compact growth with fragile branches can be viewed as an adaptation to the undisturbed cliff face.

ADAPTATIONS TO THE CLIFF ENVIRONMENT

Habit: Densely clustered, often drooping from the cliff face, typical of many cremnohytes. The reduction in size and compact growth can be viewed as adaptations to the cliff environment.

Size and weight: Clusters of medium weight.

Stem: Branches grey-green, smooth, brittle, up to 12 mm in diameter at the base, tapering to 5–7 mm, proliferating and forming dense clusters; bark scaly and exposing the green living tissue; leaf scars 1.0–1.3 mm wide. Branches sometimes remain leafless but photosynthetically active, a character that can be viewed as a xeromorphic adaptation to the dry cliff-face.

Leaves

Orientation: Ascending-spreading, one or two in number, occasionally produced.

Colour: Greyish green to green.

Age and persistence: Plants slow-growing, long-lived perennials. Leaves fragile, becoming deciduous during the long, dry summer, an adaptation to the moist conditions in winter.

Armament and camouflage: Plants fleshy, fragile and without conspicuous armament as opposed to the larger, robust, single-branched, level-ground *Tylecodon buchholzianus* var. *buchholzianus*, the reduction in camouflage and armament properties due to the undisturbed conditions on the cliff face.

Sexual reproduction

Inflorescence and flowers: Inflorescence an erect, almost sessile thyrse up to 20 mm high, consisting of a solitary monochasium with 1–3 flowers. Corolla tubular, purplish to yellow-green, 10 × 4 mm.

Fruit/Seed

Size: Seed minute and ideal for establishment in crevices.

Dispersal: Follicles dehiscent, with seeds spontaneously released and dispersed by wind.

Time: Seeds dispersed in autumn at the onset of the rainy season, maximising establishment.

Vegetative reproduction: The spreading branches root where they touch the soil, forming loose, mats (vegetative spread), an efficient vegetative backup for surviving the harsh cliff-face environment.

CONSERVATION STATUS

Classified as rare (Raimondo *et al.* 2009). Localised, common, but restricted to the Oograbies Mountains in the Richtersveld where it is well protected by the cliff-face habitat.

ADDITIONAL NOTES

Horticulture: Best grown in succulent karoo gardens, in rockeries or containers. Outside its habitat, it is best suited to a greenhouse, grown under controlled conditions. Propagate from stem cuttings. Easily cultivated, its vigour viewed as maximising survival.

VOUCHER

Van Jaarsveld 9456 (NBG).

ILLUSTRATIONS AND MAP

Figures 152a–152d, Map 152.

153. *Tylecodon cordiformis* G.Will. in *Cactus and Succulent Journal* (U.S.) 70,5: 255 (1998).

Cremonophyte growth form: Loose stem clusters (of light weight, cliff hugger).

Growth form formula: E:F:As:S/H:Ca:D (vb) (ft)

Etymology: The epithet *cordiformis*, heart-shaped, pertains to the shape of the leaves.

DESCRIPTION AND HABITAT

Dwarf-sized, spreading, branched, succulent subshrub, 20–50 mm high from tuberous base. Tubers spreading, up to 50 mm in diameter. Branches grey, 5–45 mm long, 4–8 mm in diameter, with phyllopodia present. Leaves 2–4, cordiform to orbicular, up to 35 × 20 mm, shiny, dark green, covered with erect, transparent-white, glandular trichomes; petiole 5–8 mm long. Inflorescence a 1- or 2-flowered dichasium; peduncle up to 10 mm long, glandular hairy; pedicels 10 mm long, glandular hairy. Calyx lobes rectangular, 2 mm long, covered with glandular trichomes. Corolla tube funnel-shaped, light green, covered with glandular trichomes, 10 mm long, yellowish; lobes spreading, 4 mm long, glandular hairy externally. Squamae transversely oblong, 0.5–0.8 mm long.

Phenology: Flowering in midsummer (December–January).

Pollinators: Insects.

Habitat and aspect: Confined to east-facing quartz cliffs where the plants grow in crevices and in ample soil on ledges of the upper slopes. Plants are subject to some amount of fog. Average daily maximum temperature is more or less 20°C and average daily minimum about 10°C, with frost absent from the habitat. Rainfall mainly in winter (cyclonic cold fronts), ranging from 50–100 mm per annum.

Altitude: 400–600 m.

Associated vegetation: Namaqualand Heuweltjie Veld of the Succulent Karoo Biome (Mucina *et al.* 2005).

Associated cremonophytes: Other cremonophytes observed at Haras include *Adromischus montium-klinghardtii*, *Conophytum chrisocruxum*, *Crassula elegans*, *C. pseudohemisphaerica*, *Cyrtanthus herrei*, *Tylecodon buchholzianus* and *T. cordiformis*.

Geology: Nakanas Formation (Bushmanland Group)

DISTRIBUTION

Appears to be confined to Harasberg (Northern Cape).

RELATED SPECIES

Tylecodon cordiformis is similar to *T. bayeri* but is at once distinguished by its larger, heart-shaped leaves and less creeping habit.

ADAPTATIONS TO THE CLIFF ENVIRONMENT

Habit: Spreading, branched, dwarf-sized shrublet.

Size and weight: Up to 50 mm high.

Roots: Tuberous.

Stem: Branches ascending, spreading, grey-green, younger branches 4–8 mm in diameter.

Leaves

Orientation: Spreading and apically grouped, heart-shaped to orbicular and varying according to the source and brightness of light.

Colour and texture: Dark green, glandular hairy and ideal for absorbing fog.

Armament and camouflage: Plants fleshy, fragile and without conspicuous armament or camouflage properties as opposed to the smaller *Tylecodon bayeri* which is well camouflaged among the karoo shrubs. The fragile nature and lack of defence properties reflect the undisturbed cliff habitat.

Sexual reproduction

Inflorescence and flowers: Rich flowering. Inflorescence a conspicuous thyrses bearing 1 or 2 bright yellow, tubular flowers.

Fruit/Seed

Size: Seed minute and ideal for establishment in crevices.

Dispersal: Follicles dehiscent, with seeds spontaneously released and dispersed by wind.

Time: Seeds dispersed in autumn at onset of rainy season, maximising establishment.

Vegetative reproduction: Detached branches will root if they fall into a crevice (vegetative spread), an efficient vegetative backup for survival in the harsh cliff-face environment.

CONSERVATION STATUS

Classified as critically rare (Raimondo *et al.* 2009), but well protected owing to the cliff habitat.

ADDITIONAL NOTES

Horticulture: Best grown in succulent karoo gardens, in rockeries or containers. Outside its habitat, it is best suited to a greenhouse, grown under controlled conditions. Propagate from stem cuttings. Easily cultivated, its vigour viewed as maximising survival.

VOUCHER

Van Jaarsveld 18787 (NBG).

ILLUSTRATIONS AND MAP

Figures 153a–153e, Map 153.

154. *Tylecodon decipiens* Toelken in *Bothalia* 12: 379 (1978).

Cremonphyte growth form: Mat-forming stem succulent (of medium weight, cliff hugger).

Growth form formula: A:S:Lar:D (vb)

Etymology: Latin *decipiens*, deceiving, referring to the misleading superficial resemblance to *Tylecodon schaeferianus*.

DESCRIPTION AND HABITAT

Dwarf-sized, mat-forming, highly branched, summer-deciduous species, from tuberous base. Branches 7–8 mm in diameter, pale grey-green, smooth, without phyllopodia, densely intertwined, often forming dense cushions up to 250 mm in diameter. Leaves oblanceolate, 5–14 × 6–10 mm, dorsiventrally flattened, glabrous; adaxial surface flat to grooved; apex obtuse. Inflorescence an erect thyrse up to 40 mm high with 1 or 2 monochasia, each bearing 1 or 2 flowers; bracts linear, up to 1.5 × 0.3 mm, becoming dry before flowers open; pedicels 10 mm long. Calyx 2–3 mm long; lobes triangular to triangular-lanceolate, about 1 × 1 mm, green. Corolla tubular, 9–10 × 3–4 mm; tube 5-angular, light green purplish on ridges; lobes pink, 5 × 2 mm, spreading, becoming recurved. Anthers yellow. Squamae linear, 1.5 × 0.3 mm, white translucent.

Phenology: Flowering in midsummer (January–February).

Pollinators: Insects.

Habitat and aspect: Quartzitic sandstone cliffs, mainly on southern and east-facing slopes. Plants occur in crevices and on ledges. Temperature moderate to high in summer and mild to warm in winter (frost absent), but regularly lowered by fog from the Atlantic Ocean. The average daily maximum temperature is about 18°C and the average daily minimum for the region 10°C. Rainfall mainly in winter, about 50–75 mm per annum (mainly cyclonic winter rain). Regular fog provides extra moisture.

Altitude: 300–480 m.

Associated vegetation: Namaqualand Strandveld of the Succulent Karoo Biome (Mucina *et al.* 2005).

Associated cremnophytes: *Adromischus caryophyllaceus*, *Conophytum* sp., *Crassula brevifolia*, *C. macowanii*, *C. muscosa* var. *muscosa*, *Gasteria pillansii* var. *ernesti-ruschii*, *Haemanthus coccineus* and *Tylecodon similis*.

Geology: Quartzitic sandstone of the Stinkfontein Formation (Gariiep Supergroup).

DISTRIBUTION

Kleinzee, rocky northern bank of the Buffelsrivier on the Atlantic coast (Northern Cape).

RELATED SPECIES

Tylecodon decipiens is at once distinguished from the closely related *T. schaeferianus* by its conspicuous, densely branched, clustered growth, often with spreading to drooping stems from the cliff face. It differs further by its thicker grey branches 8 mm in diameter. *Tylecodon schaeferianus* usually occurs on accessible flat terrain, well camouflaged among the desert sand and gravel. It is smaller, less branched, with thinner braches. The densely clustered, spreading to drooping, more compact growth with fragile branches can be viewed as an adaptation to the undisturbed cliff face.

ADAPTATIONS TO THE CLIFF ENVIRONMENT

Habit: Conspicuous, densely clustered, often drooping from the cliff face, typical of many cremnophytes.

Size and weight: Clusters medium-sized, up to 250 mm in diameter.

Roots: Tuberous.

Stem: Branches 7–8 mm in diameter, pale grey-green, smooth, without phyllopodia, densely intertwined, often forming dense cushions up to 250 mm in diameter. The dense stem clusters and often pendulous nature can be viewed as an adaptation to the cliff environment.

Leaves

Orientation: Ascending-spreading, apically grouped.

Colour: Glaucous, glabrous.

Age and persistence: Plants slow-growing, long-lived perennials, typical of cremnophilous succulent plants. Summer-deciduous, an adaptation to the dry conditions in summer.

Armament and camouflage: Plants conspicuous, fleshy, fragile and without armament or camouflage properties, reflecting the disturbance-free cliff face. By comparison, the closely related *Tylecodon schaeferianus* is smaller, inconspicuous and a master of camouflage.

Sexual reproduction

Inflorescence and flowers: Conspicuous in flower. Inflorescence an erect thyrses up to 40 mm high, with 1 or 2 monochasia, each bearing 1 or 2 flowers. Corolla tubular, 9–10 × 3–4 mm; tube 5-angular, light purplish green on ridges; lobes pink, 5 × 2 mm, spreading, becoming recurved.

Fruit/Seed

Size: Seed minute and ideal for establishment in crevices.

Dispersal: Follicles dehiscent, with seeds spontaneously released and dispersed by wind.

Time: Seeds dispersed in autumn at onset of rainy season, maximising establishment.

Vegetative reproduction: Densely branched, procumbent and will fill crevices by active growth, forming dense, tight mats (vegetative spread), an efficient vegetative backup for survival in the harsh cliff environment.

CONSERVATION STATUS

Classified as rare (Raimondo *et al.* 2009) but well protected owing to the cliff habitat.

ADDITIONAL NOTES

Horticulture: Best grown in succulent karoo gardens, in rockeries or containers. Outside its habitat, it is best suited to a greenhouse, grown under controlled conditions. Propagate from stem cuttings. Easily cultivated, its vigour viewed as maximising survival.

VOUCHER

Toelken 5252 (BOL).

ILLUSTRATIONS AND MAP

Figures 154a & 154b, Map 154.

155. *Tylecodon ellaphieae* Van Jaarsv. in *The Flowering Plants of Africa* 50: t. 1983 (1989a).

Cremnophyte growth form: Dwarf-sized stem cluster (of light to medium weight, cliff squatter).

Growth form formula: A:S:Lar:D (vb) (r) (ft)

Etymology: After Ellaphie Ward-Hilhorst (1920–1994), botanical artist.

DESCRIPTION AND HABITAT

Compact, solitary, summer-deciduous, cluster-forming plant up to 100 mm in diameter, with swollen base up to 50 mm in diameter, with 2–8 short, erect branches up to 20–50 mm long,

covered with spine-tipped and a few truncate phyllopodia. Caudex peeling in yellowish grey flakes. Phyllopodia green, strigose. Stems grey-green, about 8 mm in diameter. Roots fibrous. Leaves dimorphic; normal leaves soft, fleshy, ascending-spreading, dorsiventrally compressed, oblanceolate-ovate to ovate-spathulate, up to 70 × 70 mm, concave, shortly petiolate, blade decurrent on petiole, base cuneate, somewhat channelled, surface glandular-pubescent; modified leaves rudimentary, spine-tipped, up to 3 mm long, persistent, curving outwards. Inflorescence an erect flat-topped thyrse up to 60–120 mm high, with 1–several dichasia, each bearing 1–3 flowers; peduncle glandular pubescent. Corolla tubular, 15 mm long, 4 mm wide at base; lobes spreading, white and glabrous on inside, glandular-pubescent on outside. Follicles enclosed by dry persistent corolla. Seed fine.

Phenology: Flowering in midsummer (January–February).

Pollinators: Insects.

Habitat and aspect: South-facing quartzitic sandstone cliffs, the plants occurring in crevices, on ledges and in shady rock veins on southern aspects. Temperature moderate to high in summer but mild to warm in winter (frost absent). The average daily maximum temperature is about 22–24°C and the average daily minimum for the region 10–12°C. Rainfall is mainly in winter and autumn, 50–150 mm per annum (mainly cyclonic winter rain and thunder showers in autumn). Regular fog provides extra moisture.

Altitude: 400–1200 m.

Associated vegetation: Rosyntjieberg Succulent Shrubland of the Succulent Karoo Biome (Mucina *et al.* 2005).

Associated cremnophytes: *Aloe meyeri*, *Conophytum taylorianum* subsp. *rosynense*, *Othonna cyclophylla* and *Trachyandra aridimontana*.

Geology: Quartzitic sandstone cliffs (Rosyntjieberg Formation) of the Richtersveld Suite.

DISTRIBUTION

Endemic to the Rosyntjieberg (including the adjacent Oemsberg in the Richtersveld Transfrontier National Park of the Northern Cape).

RELATED SPECIES

Tylecodon ellaphieae is distinct in general morphology. It can be confused with *T. torulosus*, a related cremnophyte from near Lekkersing. Both have white flowers but that is where the resemblance ends. *Tylecodon ellaphieae* has a more compact growth. Normal leaves are produced at the beginning of the season, soon replaced by the rudimentary spine-tipped leaves (Bruyns 1990). The stems of *T. torulosus* are smooth and torulose. *Tylecodon ellaphieae* occurs in the fog zone (500–1200 m above sea level) where the large, spreading, glandular pubescent, concave leaves as well as the phyllopodia and rudimentary, curved, spine-tipped leaves function as a moisture trap. The conspicuous white tubular flowers are thought to be pollinated by insects and the very tiny, light seeds are wind-dispersed.

ADAPTATIONS TO THE CLIFF ENVIRONMENT

Habit: Small, compact clusters typical of many cremnophytes. The reduction in size and compact growth can be viewed as an adaptation to the cliff environment.

Size and weight: Clusters small, up to 100 mm in diameter, of medium weight.

Roots: The fleshy roots can be viewed as an adaptation to the xeric conditions on the cliff face.

Stem: Succulent, grey-green, up to 8 mm in diameter, covered with green, strigose phyllopodia.

Leaves

Orientation: Ascending spreading to spreading from an apically grouped rosette. Dimorphic, normal leaves large, soft, fleshy, fragile, modified leaves rudimentary, spine-tipped, up to 3 mm long, persistent, curving outwards.

Colour and texture: Epidermis light green. The very soft, succulent nature an adaptation to the undisturbed cliff conditions.

Age and persistence: Plants slow-growing, long-lived perennials. Leaves becoming deciduous during the long, dry summer, suggesting an adaptation to the moist conditions in winter.

Armament and camouflage: Plants fleshy, fragile and without conspicuous armament or camouflage properties as opposed to the level-ground *Tylecodon* species, the reduction in camouflage and armament due to the undisturbed conditions on the cliff face.

Sexual reproduction

Inflorescence and flowers: Rich flowering. Inflorescence a conspicuous erect, flat-topped thyrse up to 60–120 mm high, with 1–several dichasia each bearing 1–3 flowers; peduncle glandular pubescent. Corolla tubular, 15 mm long, 4 mm wide at base; lobes spreading, white and glabrous on inside, glandular-pubescent on outside; dry persistent corolla enclosing follicles.

Fruit/Seed

Size: Seed minute and ideal for establishment in crevices.

Dispersal: Follicles dehiscent, with seeds spontaneously released and dispersed by wind.

Time: Seeds dispersed in autumn at onset of rainy season, maximising establishment.

Vegetative reproduction: Plants will root from branches reaching crevices or pockets of soil. Detached parts of branches will root if they fall into adjacent crevices. This is an effective vegetative backup strategy for surviving the harsh conditions on the cliff face.

CONSERVATION STATUS

Localised and rare, confined to the Rosyntjieberg in the Richtersveld Transfrontier National Park, but not threatened.

ADDITIONAL NOTES

Horticulture: Best grown in dry succulent karoo gardens in containers. Outside its habitat, it is best grown under controlled conditions in a greenhouse. Propagate from branch cuttings. Easily grown, keep dry in summer.

VOUCHER

Van Jaarsveld & Drijfhout 5523 (NBG).

ILLUSTRATIONS AND MAP

Plate 155, Figures 155a–155d, Map 155.

156. *Tylecodon longipes* Van Jaarsv. & G.Will. in *Aloe* 31,3 & 4: 56–59 (1994).

Cremnophyte growth form: Mat-forming clusters (of medium weight, cliff hugger).

Growth form formula: A:S:Lar:D (vb)

Etymology: The epithet *longipes* (*longus*, long, and *pes*, a foot) pertains to the long petioles.

DESCRIPTION AND HABITAT

Dwarf-sized, highly branched, mat-forming, summer-deciduous succulents up to 30 mm high and 200 mm in diameter. Branches up to 20 mm in diameter; bark silvery grey, cracking, exposing green tissue. Leaves 1–4 per branch, crowded, spreading, lanceolate, broadly ovate to spatulate, sometimes 3-lobed, 15–35 × 10–20 mm, glandular hairy; petiole up to 5 mm long, rarely somewhat channelled; apex obtuse; base cuneate; bract-like leaves subulate, 1 mm long, drying soon. Inflorescence a short thyrses up to 30 mm high, of 1–3 monochasia; peduncle 10–20 mm long, glandular hairy; pedicels 7 mm long. Calyx lobes triangular, up to 2 × 1 mm. Corolla tubular, up to 15 mm long; tube cylindrical to funnel-shaped, green-white; lobes oblong, 4–6 × 2 mm. Stamens 10 mm long; anthers rectangular to pyriform, 0.5 mm long. Squamae transversely rectangular, 0.70 mm high, pale green.

Phenology: Flowering in midsummer (January–February).

Pollinators: Insects.

Habitat and aspect: Quartzitic sandstone cliffs. Plants occur in crevices and on ledges on eastern and southern aspects. Temperature moderate to high in summer and mild to warm in winter (frost absent), but regularly lowered by fog from the Atlantic Ocean. The average daily maximum temperature is about 18°C and the average daily minimum for the region about

10°C. Rainfall mainly in winter, about 50–75 mm per annum (mainly cyclonic winter rain). Regular fog from the Atlantic Ocean provides extra moisture.

Altitude: 400–800 m.

Associated vegetation: Lekkersing Succulent Shrubland of the Succulent Karoo Biome (Mucina *et al.* 2005).

Associated cremnophytes: *Adromischus caryophyllaceus*, *Conophytum* sp., *Crassula brevifolia*, *C. macowanii*, *C. muscosa* var. *polypodacea*, *Haemanthus coccineus*, *Haworthia arachnoidea*, *Mitrophyllum clivorum*, *Tylecodon buchholzianus* and *T. racemosus*.

Geology: Quartzitic sandstone of the Stinkfontein Formation (Gariiep Supergroup).

DISTRIBUTION

Spitskloof near Lekkersing (Northern Cape).

RELATED SPECIES

Related to *Tylecodon decipiens*, another cremnophyte, but at once distinguished by its thicker and shorter branches covered with short, linear-acute, bract-like leaves. It differs further by its normal leaves which are distinctly petiolate.

ADAPTATIONS TO THE CLIFF ENVIRONMENT

Habit: Conspicuous, densely clustered, typical of many cremnophytes.

Size and weight: Clusters medium-sized, up to 200 mm in diameter, of medium weight.

Roots: Tuberous.

Stem: Branches up to 20 mm in diameter, with silvery grey bark cracking and exposing the green tissue. The thick, clustered, fragile nature can be viewed as an adaptation to the xeric but undisturbed conditions found on the cliff face.

Leaves

Orientation: Ascending spreading, 1–4 per branch, crowded at branch ends.

Colour and texture: Grey-green, the leaf indumentum and somewhat channelled leaf bases indicative of adaptation to the regular fog from the Atlantic Ocean.

Age and persistence: Plants slow-growing, long-lived perennials, typical of cremnophilous succulent plants.

Armament and camouflage: Plants conspicuous, fleshy, fragile, without armament or camouflage, reflecting the disturbance-free cliff face. By comparison, the closely related *Tylecodon schaeferianus* of level ground is smaller, inconspicuous and a master of camouflage.

Sexual reproduction

Inflorescence and flowers: Rich flowering. Inflorescence a short thyrses, up to 30 mm high, with 1–3 monochasia; peduncle 10–20 mm long, glandular hairy; pedicels 7 mm long. Calyx lobes triangular, up to 2×1 mm. Corolla tubular, up to 15 mm long; tube cylindrical to funnel-shaped, green-white; lobes oblong, $4\text{--}6 \times 2$ mm.

Fruit/Seed

Size: Seed minute and ideal for establishment in crevices.

Dispersal: Follicles dehiscent, with seeds spontaneously released and dispersed by wind.

Time: Seeds dispersed in autumn at onset of rainy season, maximising establishment.

Vegetative reproduction: Densely branched, procumbent and will fill crevices by active growth, forming dense, tight mats (vegetative spread), an efficient vegetative backup for survival in the harsh cliff environment.

CONSERVATION STATUS

Classified as critically rare (Raimondo *et al.* 2009), but well protected owing to the cliff habitat.

ADDITIONAL NOTES

Horticulture: Best grown in succulent karoo gardens, in rockeries or containers. Outside its habitat, it is best suited to a greenhouse, grown under controlled conditions. Propagate from stem cuttings. Easily cultivated, its vigour viewed as maximising survival.

VOUCHER

Van Jaarsveld 13063 (NBG).

ILLUSTRATIONS AND MAP

Figures 156a–156d, Map 156.

157. *Tylecodon petrophilus* Van Jaarsv. & A.E.van Wyk in *Aloe* 45,2: 31–33 (2008b).

Cremnophyte growth form: Medium-sized stem cluster (of medium weight, cliff squatter).

Growth form formula: A:S:Lar:D (vb)

Etymology: Greek *petra*, a rock, and *phileein*, to love, after its rock-dwelling habitat.

DESCRIPTION AND HABITAT

Cluster-forming, much-branched, summer-deciduous shrublets, becoming subpendent and up to 400 mm in diameter. Roots fibrous. Branches 10–17 mm in diameter, succulent, densely

covered in short, slightly tapering, grey-green, woody phyllopodia 4–5 mm long and 4–10 mm in diameter at base. Leaves softly succulent, in apical rosettes, spreading, covering stem and base; blade broadly obovate to subrotund, 50–100 × 35–70 mm, about 2–3 mm thick, faintly striate; both surfaces covered in short, translucent glandular hairs up to 0.5 mm long, adaxial surface flat to slightly concave, green to dull green, abaxial surface flat, dull green and purplish, bearing faint midrib; margin entire; apex obtuse to rounded; petiole short, indistinct. Inflorescence a sparsely branched, ascending thyrse up to 350 mm long, bearing 1 or 2 apical monochasia each bearing 2 or 3 flowers, basally with spirally arranged, leaf-like bracts; basal bracts 20 × 5 mm, becoming smaller distally, of same colour and texture as leaves; peduncle reddish brown, glandular pubescent, 3 mm in diameter at base. Flowers ascending-spreading, yellowish green; pedicels 8–10 mm long, green. Calyx 6–7 mm long, glandular tomentose, purplish green; lobes 6–7 × 2 mm. Corolla glandular pubescent; tube cylindrical, 11–12 × 5–6 mm; lobes 12 × 5 mm, distinctly recurved, yellowish green; margins white; apices acute. Stamens up to 10 mm long, attached to throat, protruding for 5 mm; anthers 1 mm long. Squamae slightly tapering 1 × 0.6 mm, emarginate, pale green, translucent. Gynoecium 22 mm long; carpels 5, free, about 10 mm long, tapering into styles 12 mm long and protruding for 12 mm from corolla apex. Follicles 8 × 1.7 mm. Seeds not seen.

Phenology: Flowering in midsummer (December–January).

Pollinators: Insects.

Habitat and aspect: South-facing quartzitic sandstone cliffs, the plants occurring in crevices, on ledges and in shady rock veins on southern aspects. Temperature moderate to high in summer but mild to warm in winter (frost absent). The average daily maximum temperature is about 22–24°C and the average daily minimum for the region 10–12°C. Rainfall mainly in winter and autumn, ranging from 100–250 mm per annum (mainly cyclonic winter rain). Occasional fog provides extra moisture.

Altitude: 400–600 m.

Associated vegetation: Namaqualand Shale Shrubland of the Succulent Karoo Biome (Mucina *et al.* 2005).

Associated cremnophytes: *Bulbine pendens*, *Colpias molle*, *Ornithogalum pendens* and *Ornithogalum* sp.

Geology: Quartzitic sandstone cliffs (Kuibus Formation) of the Nama Group.

DISTRIBUTION

Endemic to the Skaaprivierspoort northwest of Springbok.

RELATED SPECIES

Tylecodon petrophilus is related to both *T. hirtifolius* from Eselfontein at the top of Spektakel Pass and *T. ellaphieae* from cliffs along the Rosyntjieberg. It is at once distinguished by its dense leaf canopy completely covering its stems. It differs from *T. hirtifolius* mainly in its broadly obovate to subrotund leaves, grey-green phyllopodia and tubular corolla. *Tylecodon hirtifolius* is a sprawling species with distinctive black stems and obovate to oblanceolate leaves which are

grooved above and lack the purplish coloration. It occurs in the shade of small shrubs on shale soil and has large leaves not covering the stems. The corolla of *T. hirtifolius* is funnel-shaped.

ADAPTATIONS TO THE CLIFF ENVIRONMENT

Habit: Compact clusters typical of many cremnoophytes. The compact growth can be viewed as an adaptation to the cliff environment.

Size and weight: Clusters up to 400 mm in diameter, of medium weight.

Roots: Fibrous.

Stem: Succulent, grey-green, up to 8 mm in diameter, covered with grey-green phyllopodia truncate at the apices.

Leaves

Orientation: Large, spreading and crowded in a central rosette.

Colour and texture: Soft, fleshy, fragile; epidermis light green, with a glandular-pubescent surface.

Age and persistence: Plants slow-growing, long-lived perennials. Leaves becoming deciduous during the long, dry summer, an adaptation to the moist conditions in winter.

Armament and camouflage: Plants fleshy, fragile and without conspicuous armament or camouflage properties as opposed to the level-ground *Tylecodon* species, the reduction in camouflage and armament due to the undisturbed conditions on the cliff face.

Sexual reproduction

Inflorescence and flowers: Elongated inflorescence with 1 or 2 dichasia each bearing 1–3 flowers; peduncle glandular pubescent. Corolla tubular, 12–15 × 5–6 mm.

Fruit/Seed

Size: Seed minute and ideal for establishment in crevices.

Dispersal: Follicles dehiscent, with seeds spontaneously released and dispersed by wind.

Time: Seeds dispersed in autumn at onset of rainy season, maximising establishment.

Vegetative reproduction: Plants will root from branches reaching crevices or pockets of soil. Detached parts of branches will root if they fall into adjacent crevices. This is an effective vegetative backup strategy for surviving the harsh conditions on the cliff face.

CONSERVATION STATUS

Localised and rare, confined to the Skaaprivierspoort northwest of Springbok, but not threatened.

ADDITIONAL NOTES

Horticulture: Best grown in containers in dry succulent karoo gardens. Outside the habitat, it is best grown under controlled conditions in a greenhouse. Propagate from branch cuttings. Easily grown, keep dry during the summer months.

VOUCHER

Van Jaarsveld 21117 (NBG).

ILLUSTRATIONS AND MAP

Plate 157, Figures 157a–157c, Map 157.

158. *Tylecodon singularis* (R.A.Dyer) Toelken in *Bothalia* 12: 380 (1978).

Cremonophyte growth form: Solitary geophyte (of light to medium weight, cliff squatter).

Growth form formula: A:S:Lar:D (ft)

Etymology: Latin *singularis*, remarkable, reflecting its uniqueness.

DESCRIPTION AND HABITAT

Dwarf-sized, perennial geophyte with subterranean tuberous base. Branch solitary or rarely branched, short, glabrous. Roots succulent, fusiform. Leaves usually single (up to 4 in cultivation), produced every season; blade orbicular, 80–150 mm in diameter, concave, cordate at base, shortly petiolate, glandular hairy, purplish below; petiole channelled. Inflorescence an erect, spreading thyrse 80–60 mm high consisting of 2–4 monochasia each bearing 5–10 flowers. Corolla tubular, up to 13 mm long, slightly widening towards throat, pale yellowish green, with short hairs on inside; lobes 6–7 mm long, recurved. Squamae square, about 1×1 mm, entire or emarginate, yellowish.

Phenology: Flowering in late spring (October–November).

Pollinators: Insects.

Habitat and aspect: Dolomite cliffs southeast of Namuskluft (Dolomite of the Port Nolloth Zone, Gariep Supergroup). Plants occur in crevices and on ledges on southern and eastern aspects. Temperature moderate to high in summer and mild to warm in winter (frost absent), but regularly lowered by fog from the Atlantic Ocean. Average daily maximum temperature about 24°C and average daily minimum for the region 10°C. Rainfall mainly in winter, about 50–75 mm per annum (mainly cyclonic winter rain). Regular fog provides extra moisture.

Altitude: 800–1100 m.

Associated vegetation: Succulent Karoo.

Associated cremnophytes: At Konsertinaberg (type locality), *Tylecodon singularis* has been recorded with *Crassula sladenii*, *C. tomentosa* var. *tomentosa*, *Drosanthemum inornatum*, *Hartmanthus* sp. and *T. buchholzianus*.

Geology: Dolomite cliffs of the Port Nolloth Zone (Gariiep Supergroup).

DISTRIBUTION

Southern Namibia, east of Rosh Pinah.

RELATED SPECIES

Related to *Tylecodon atropurpureus*, a non-cremnophilous geophyte from the Northern Cape. The latter with rosettes of smaller leaves and large subterranean tubers.

ADAPTATIONS TO THE CLIFF ENVIRONMENT

Habit: The conspicuous nature reflects its habitat, the undisturbed cliff face.

Size and weight: Plants small to medium-sized, up to 80 mm in diameter, of light to medium weight.

Roots: Rootstock tuberous; roots succulent, fusiform.

Stem: Solitary or rarely branched, short, glabrous. Squamae square, about 1 × 1 mm, entire or emarginate, yellowish.

Leaves

Orientation: Solitary, large, spreading, blade orbicular, 50–80 mm in diameter, concave, cordate at the base and shortly petiolate.

Colour and texture: Green, glandular hairy, purplish below; petiole channelled. The leaf indumentum, concave shape and somewhat channelled petiole clearly form a ‘fog trap’, an adaptation to the regular fog from the Atlantic Ocean. The fragile nature of the leaf points to a lack of disturbance by larger herbivores in the habitat.

Age and persistence: Plants slow-growing, long-lived perennials, typical of cremnophilous succulent plants. The summer-deciduous nature is an adaptation to the long, dry summers.

Armament and camouflage: Plants conspicuous, fleshy, fragile and lacking in armament or camouflage properties, reflecting the disturbance-free cliff face.

Sexual reproduction

Inflorescence and flowers: Rich flowering. Inflorescence an erect, spreading thyrse, 80–60 mm high, consisting of 2–4 monochasia each bearing 5–10 flowers. Corolla tubular, up to 13 mm long, slightly widening towards throat, pale yellowish green, with short hairs on inside; lobes 6–7 mm long, recurved.

Fruit/Seed

Size: Seed minute and ideal for establishment in crevices.

Dispersal: Follicles dehiscent, with seeds spontaneously released and dispersed by wind.

Time: Seeds dispersed in summer and autumn at onset of rainy season, maximising establishment.

Vegetative reproduction: Absent.

CONSERVATION STATUS

Classified as rare (Loots 2005), confined to dolomite cliffs within the confines of a national park where it is well protected.

ADDITIONAL NOTES

Horticulture: Best grown under controlled greenhouse conditions, in an alkaline soil. Keep dry in summer. Cultivated plants tend to grow very large leaves. Propagate from seed. Seldom grown.

VOUCHER

Van Jaarsveld 21074 (NBG).

ILLUSTRATIONS AND MAP

Figures 158a–158e, Map 158.

159. *Tylecodon sulphureus* (Toelken) Toelken var. *armianus* Van Jaarsv. in *The Flowering Plants of Africa* 50,2: t. 1984 (1989b).

Crempnophyte growth form: Dwarf-sized stem cluster (of light weight, cliff squatter).

Growth form formula: E:F:As:S/H:Ca:D (vb)

Etymology: After A.R. Mitchell, an Englishman from the Isle of Wight who discovered the species.

DESCRIPTION AND HABITAT

Dwarf-sized, cluster-forming succulents up to 100 mm in diameter; base tuberous, tubers up to 30 mm in diameter. Branches ascending, spreading to pendulous, covered with rounded phyllopodia. Leaves oblanceolate, elliptic to linear, 10–25 × 3–8 mm, glabrous; surface minutely papillate, upper surface grooved, lower surface convex; apex obtuse. Inflorescence an erect, flat-topped thyrse 35–60 mm high consisting of 1–3 monochasia; peduncle glandular pubescent, up to 20 mm high; bracts 6 × 1 mm, linear-subulate, glandular pubescent. Calyx lobes linear-lanceolate, up to 2 mm long, purplish green. Corolla tubular, 8–14 × 3–4 mm, glandular pubescent, white to pink; lobes recurved. Anthers yellow. Squamae oblong, 1 × 0.3 mm, truncate to emarginate, green.

Phenology: Flowering in midsummer (January–February).

Pollinators: Insects.

Habitat and aspect: Confined to south-facing metaquartzitic gneiss cliffs. The plants grow in shady crevices up to about 900 m (mainly southern aspects) in association with other succulent plants. Summers are hot and dry. The average daily maximum temperature is about 28°C and average daily minimum about 13°C, with frost absent from the habitat. Rainfall in spring, autumn and winter (cyclonic cold fronts and thunder showers in late summer and autumn), ranging from 50–100 mm per annum.

Altitude: 700–1110 m.

Associated vegetation: Eastern Gariiep Rocky Desert of the Desert Biome (Mucina *et al.* 2005).

Associated cremnohytes: Other succulents observed at its habitat at Groot Pellaberg include *Adromischus trigynus*, *Aloe dabenorisana*, *Bowiea gariepensis*, *Conophytum fulleri*, *Crassula exilis* subsp. *sedifolia* and *C. garibina*.

Geology: Metaquartzitic gneiss of the Hom Formation (Bushmanland Group).

DISTRIBUTION

Known only from northern Bushmanland on cliffs of similar geological formations (Northern Cape). It appears to be confined to Dabenorisberg and Pellaberg (northwest of Pofadder).

RELATED SPECIES

Tylecodon sulphureus var. *armianus* is closely related to *T. sulphureus* var. *sulphureus*, a quartz flats species from the northern Bushmanland region. The latter differs in being a much smaller and less branched geophyte (yellow flowers) that is difficult to detect as it is so well camouflaged. Only the stem apices are exposed, bearing a few leaves. The conspicuous white tubular flowers are thought to be pollinated by insects and the very tiny, light seeds are wind-dispersed. *Tylecodon reticulatus* is a conspicuous, robust stem succulent growing in exposed sites, but well armed with persistent dry inflorescences, protecting its softer growth points and leaves.

ADAPTATIONS TO THE CLIFF ENVIRONMENT

Habit: Small, compact to loose clusters, sometimes with fragile, drooping branches. The habit is typical of related cremnohytes and the fragile nature reflects the undisturbed cliff habitat.

Size and weight: Clusters small, up to 100 mm in diameter, of light weight.

Roots: The fleshy roots can be viewed as an adaptation to the xeric conditions on the cliff face.

Stem: Succulent, grey-green, up to 3–5 mm in diameter, covered with rounded phyllopodia. Branches ascending, spreading to pendulous.

Leaves

Orientation: Ascending-spreading.

Colour and texture: Light green, epidermis minutely papillate; upper surface grooved; lower surface convex.

Age and persistence: Plants slow-growing, long-lived perennials. Leaves becoming deciduous during the long, dry summer, suggesting adaptation to moist conditions in winter.

Armament and camouflage: Plants fleshy, fragile and without conspicuous armament or camouflage properties as opposed to the level-ground *Tylecodon* species, the reduction in camouflage and armament due to the undisturbed conditions on the cliff face.

Sexual reproduction

Inflorescence and flowers: Inflorescence an erect, flat-topped thyrse, 35–60 mm high, consisting of 1–3 monochasia; peduncle glandular pubescent, up to 20 mm high; bracts linear-subulate, 6 × 1 mm, glandular-pubescent. Calyx lobes linear-lanceolate, up to 2 mm long, purplish green. Corolla tubular, 8–14 × 3–4 mm, glandular pubescent, white to pink, with recurved lobes. Anthers yellow.

Fruit/Seed

Size: Seed minute and ideal for establishment in crevices.

Dispersal: Follicles dehiscent, with seeds spontaneously released and dispersed by wind.

Time: Seeds dispersed in autumn at onset of rainy season, maximising establishment.

Vegetative reproduction: Branches spreading and will fill new crevices by active growth, forming loose to tight mats (vegetative spread), an efficient vegetative backup strategy for continued existence in the harsh cliff-face environment.

CONSERVATION STATUS

Classified as rare (Raimondo *et al.* 2009) but well protected owing to the cliff habitat.

ADDITIONAL NOTES

Horticulture: Best grown in succulent karoo gardens, in rockeries or containers. Outside its habitat, it is best suited to a greenhouse, grown under controlled conditions. Propagate from stem cuttings. Easily cultivated, its vigour viewed as maximising survival.

VOUCHERS

Van Jaarsveld 19153, Van Jaarsveld & Patterson 6639 (NBG).

ILLUSTRATIONS AND MAP

Plate 159, Figures 159a–159e, Map 159.

160. *Tylecodon torulosus* Toelken in *Bothalia* 12: 381 (1978).

Cremonophyte growth form: Loose stem clusters (of medium weight, cliff squatter).

Growth form formula: E:F:As:S/H:Ca:D (vb)

Etymology: Latin *torulosus*, cylindrical with swollen portions at intervals, referring to the cylindrical stems with characteristic contractions.

DESCRIPTION AND HABITAT

Small, sparsely branched, ascending, thickset, succulent shrublet up to 250 mm tall, 250 mm wide, with tuberous base, sometimes with pendulous branches from rock face up to 300 mm long. Branches grey-white, up to 30 mm in diameter at base, tapering to 5 mm in diameter at apices; nodes characteristically swollen (torulose); bark grey, smooth; older branches flaking. Leaves ovate to spatulate, occasionally 3-lobed, 25–40 × 13–22 mm, spreading, crowded at apex, grey to yellowish green, flat; apex obtuse or acute, often becoming recurved; base cuneate. Inflorescence a short, rounded, almost sessile thyrse of 2–5 monochasia each bearing 1–3 tubular flowers; peduncle 2–3 mm long; pedicels 3–5 mm long. Calyx lobes triangular-ovate, 3 × 2 mm, green, fleshy. Corolla tubular, 14–23 × 4–5 mm, slightly expanding distally, yellowish green, glandular pubescent on outside, with purplish striations on ridges; lobes 5 × 3 mm, inside white, outside with maroon striations towards centre, lobate, spreading, becoming recurved. Squamae 1.5 × 1 mm, deeply emarginate (lobes acute), white, slightly translucent.

Phenology: Flowering in midsummer (end January–February).

Pollinators: Insects.

Habitat and aspect: Quartzitic sandstone cliffs, the plants occurring in crevices and on ledges on eastern and southern aspects. Temperature moderate to high in summer and mild to warm in winter (frost absent), but regularly lowered by fog from the Atlantic Ocean. The average daily maximum temperature is about 18°C and the average daily minimum for the region 10°C. Rainfall mainly in winter, about 50–75 mm per annum (mainly cyclonic winter rain). Regular fog provides extra moisture.

Altitude: 300–500 m.

Associated vegetation: Lekkersing Succulent Shrubland of the Succulent Karoo Biome (Mucina *et al.* 2005).

Associated cremonophytes: *Adromischus caryophyllaceus*, *Conophytum* sp., *Crassula brevifolia*, *C. macowanii*, *C. muscosa* var. *polypodacea*, *Haemanthus coccineus*, *Haworthia arachnoidea*, *Mitrophyllum clivorum*, *Tylecodon buchholzianus* and *T. racemosus*.

Geology: Quartzitic sandstone of the Stinkfontein Formation (Gariiep Supergroup).

DISTRIBUTION

Karrachab Poort near Lekkersing (Northern Cape).

RELATED SPECIES

Related to *Tylecodon decipiens*, another cremnophyte, but at once distinguished by its thicker, torulose and longer branches with much larger leaves.

ADAPTATIONS TO THE CLIFF ENVIRONMENT

Habit: Conspicuous, loose clusters.

Size and weight: Clusters medium-sized, up to 250 mm in diameter, of medium weight.

Roots: Tuberous.

Stem: Branches grey-white, up to 30 mm in diameter at the base, tapering to 5 mm at the apices, the nodes characteristically swollen (torulose); bark grey, smooth, older branches flaking.

Leaves

Orientation: Ascending-spreading, crowded at apex.

Colour and texture: Grey to yellowish green, epidermis smooth. The fragile texture is an adaptation to the absence of disturbances by larger herbivores.

Age and persistence: Plants slow-growing, long-lived perennials, typical of cremnophilous succulent plants. The summer-deciduous nature is an adaptation to the long, dry summers.

Armament and camouflage: Plants conspicuous, fleshy, fragile, lacking in armament or camouflage properties, reflecting the disturbance-free cliff face. By comparison, the related *Tylecodon schaeferianus* of level ground is smaller, inconspicuous and a master of camouflage.

Sexual reproduction

Inflorescence and flowers: Rich flowering. Inflorescence a short, rounded, almost sessile thyrses of 2–5 monochasia each bearing 1–3 tubular flowers; peduncle 2–3 mm long; pedicels 3–5 mm long. Calyx lobes triangular-ovate, 3 × 2 mm, green, fleshy. Corolla tubular, 14–23 × 4–5 mm, slightly expanding upwards, yellowish green, glandular pubescent on outside with purplish striations on ridges; lobes lobate, 5 × 3 mm, inside white, outside with maroon striations towards centre, spreading, becoming recurved.

Fruit/Seed

Size: Seed minute and ideal for establishment in crevices.

Dispersal: Follicles dehiscent, with seeds spontaneously released and dispersed by wind.

Time: Seeds dispersed in autumn at the onset of the rainy season, maximising establishment.

Vegetative reproduction: Branches spreading and will root where they touch the soil, forming loose mats (vegetative spread), an efficient vegetative backup strategy for surviving the harsh cliff-face environment.

CONSERVATION STATUS

Classified as vulnerable (Raimondo *et al.* 2009). Although rare, it is well protected owing to the cliff habitat.

ADDITIONAL NOTES

Horticulture: Best grown in succulent karoo gardens in rockeries or containers. Outside its habitat, it is best suited to a greenhouse, grown under controlled conditions. Propagate from stem cuttings. Easily cultivated, its vigour viewed as maximising survival.

VOUCHER

Toeken 5317 (PRE).

ILLUSTRATIONS AND MAP

Figures 160a–160c, Map 160.

161. *Tylecodon viridiflorus* (Toelken) Toelken in *Bothalia* 12: 382 (1978).

Crempnophyte growth form. Ascending compact shrublet (of medium weight, cliff squatter).

Growth form formula: E:F:As:S/H:Ca:D (vb)

Etymology: Latin *viridiflorus*, (*viridis*, green, *flos*, flower), pertaining to the green corolla of the plant.

DESCRIPTION AND HABITAT

Erect, sparsely branched, succulent shrub up to 350 mm high, 200 mm in diameter; base slightly tuberous, up to 15 mm in diameter, with a single to few main branches up to 10 mm in diameter; bark grey, peeling; young branches brown at first, becoming paler with age. Leaves crowded, ascending to spreading, elliptic, oblanceolate, to broadly ovate, dorsiventrally flattened, 20–55 × 8–30 mm, occasional 3-lobed; surface glandular hairy, adaxial surface often channelled; apex obtuse to acute; base cuneate. Inflorescence a thyse up to 45 mm high, of 1–3 monochasia each bearing 1 or 2 flowers; pedicels up to 12 mm long. Corolla tubular, 14–20 × 5 mm long, greenish; lobes triangular-lanceolate, up to 7 mm long, spreading, becoming recurved, distinctly yellowish green. Calyx lobes linear-lanceolate, up to 9 mm long. Squamae oblong, 1.5 mm long, slightly tapering, cream. Seed winged, a unique character in the Crassulaceae in South Africa.

Phenology: Flowering in midsummer (January).

Pollinators: Insects.

Habitat and aspect: Shady quartzitic sandstone cliffs, the plants occurring in crevices and on ledges on eastern and southern aspects. Temperature moderate to high in summer and mild to warm in winter (frost absent), but regularly lowered by fog from the Atlantic Ocean. The average daily maximum temperature is about 22°C and the average daily minimum for the region 11°C. Rainfall mainly in winter, about 50–100 mm per annum (mainly cyclonic winter rain). Regular fog provides extra moisture.

Altitude: 600–900 m.

Associated vegetation: Central Richtersveld Mountain Shrubland of the Succulent Karoo Biome (Mucina *et al.* 2005).

Associated cremnophytes: Near Eksteenfontein the following plants were observed in its habitat: *Adromischus caryophyllaceus*, *Conophytum* spp., *Crassula brevifolia*, *C. macowanii*, *C. muscosa* var. *muscosa*, *Cyrtanthus herrei*, *Haemanthus coccineus*, *Haworthia arachnoidea*, *Mitrophyllum clivorum*, *Tylecodon buchholzianus* and *T. racemosus*.

Geology: Quartzitic sandstone of the Stinkfontein Formation (Gariep Supergroup).

DISTRIBUTION

Central Richtersveld mountains, from Eksteenfontein to Kuboes in the north (Northern Cape).

RELATED SPECIES

Related to *Tylecodon fragilis*, another widespread species of level ground. *Tylecodon viridiflorus* is at once distinguished by its dorsiventrally flattened, hairy leaves and grey bark, which is not striate, and by the winged seed.

ADAPTATIONS TO THE CLIFF ENVIRONMENT

Habit: Erect shrublets.

Size and weight: Clusters medium-sized, up to 30 mm high, of medium weight.

Roots: Tuberous.

Stem: Base slightly tuberous, up to 15 mm in diameter, with a single to a few main branches up to 10 mm in diameter, with grey bark peeling vertically. Young branches brown at first, becoming paler with age.

Leaves

Orientation: Ascending to spreading, crowded.

Colour and texture: Dull green, surface glandular hairy; adaxial surface often channelled.

Age and persistence: Plants slow-growing, long-lived perennials, typical of cremnophilous succulent plants.

Armament and camouflage: Plants conspicuous, fleshy, fragile and lacking in armament or camouflage properties, reflecting the disturbance-free cliff face. By comparison, the closely related *Tylecodon fragilis* of level ground is smaller, inconspicuous and a master of camouflage among the shrublets of its habitat.

Sexual reproduction

Inflorescence and flowers: Rich flowering. Inflorescence a thyrses, up to 45 mm high, of 1–3 monochasia each bearing 1 or 2 flowers; pedicels to 12 mm long. Corolla tubular, 14–20 × 5 mm long, greenish; lobes triangular-lanceolate, up to 7 mm long, distinctly yellowish green, spreading, becoming recurved. Calyx lobes linear-lanceolate, up to 9 mm long. Squamae oblong, 1.5 mm long, cream, slightly tapering.

Fruit/Seed

Size: Seed winged and much larger and different from that of all other *Tylecodon* species.

Dispersal: Follicles dehiscent, with seeds spontaneously released and dispersed by wind. The winged seeds are a clear adaptation to wind dispersal, very effective on the cliff face.

Time: Seeds dispersed in autumn at the onset of the rainy season, maximising establishment.

Vegetative reproduction: Detached branches will root if they fall into a new crevice (vegetative spread), an efficient vegetative backup strategy for surviving the harsh cliff-face environment.

CONSERVATION STATUS

Classified as rare (Raimondo *et al.* 2009) but well protected owing to the cliff habitat.

ADDITIONAL NOTES

Horticulture: Best grown in succulent karoo gardens, in rockeries or containers. Outside its habitat, it is best suited to a greenhouse, grown under controlled conditions. Propagate from stem cuttings. Easily cultivated, its vigour viewed as maximising survival.

VOUCHER

Van Jaarsveld 22285 (NBG).

ILLUSTRATIONS AND MAP

Figures 161a–161f, Map 161.

GERANIACEAE

Pelargonium L'Hér.

162. *P. mutans* Vorster

163. *P. vanderwaltii* Van Jaarsv.

PELARGONIUM L'Hér.

162. *Pelargonium mutans* Vorster in The Flowering Plants of Africa 52,1: t. 2060 (1992).

Cremonophyte growth form: Dwarf-sized, compact to spreading shrublet (of medium weight to heavy, cliff squatter).

Growth form formula: E:F:As:S/H:Es (vb)

Etymology: The epithet *mutans*, changeable, pertains to the changeable number of petals (varying between 4 and 5).

DESCRIPTION AND HABITAT

Spreading, trailing, succulent shrub with stems up to 2 m long, moderately branched. Roots fibrous. Stems spreading, erect or decumbent, succulent, 8–10 mm in diameter, terete, green at first, characteristically articulated, swollen at nodes; surface covered with gland-tipped and non-gland-tipped hairs, becoming brownish green and glabrescent with age and bearing remnants of persistent stipules. Leaves simple, crowded at apices, ascending; indumentum membranaceous as in young stems; lamina 40–70 × 45–80 mm, with or without purplish zonal markings, shallowly to deeply 5-lobed; margin with shallow dentations; apex obtuse; base cordate; petiole 20–45 mm long. Inflorescence terminal, producing a solitary 6–8-flowered pseudo-umbel on peduncles 45–250 mm long; pseudo-umbels up to 80 mm in diameter; pedicels 5–10 mm long, pilose. Sepals linear-lanceolate, 5 × 2 mm, acute, pilose. Petals 5, linear-obovate, apices rounded to slightly retuse, white; posterior two 15 × 5 mm, reflexed; anterior three 15 × 3.4 mm. Stamens 6, fertile. Mericarps 7 mm long, tail 30–34 mm long.

Phenology: Flowering throughout the year, but with a peak in spring. Seeds with typical *Pelargonium* seed dispersal strategy.

Pollinators: Insects.

Habitat and aspect: *Pelargonium mutans* grows on cliffs and cliff tops where the plants occur in sandstone rock crevices. Summers are very hot, with temperatures frequently above 30°C. Winters are mild and frost is absent or very light. The average daily maximum temperature is about 27°C and the average daily minimum about 14°C. Average annual rainfall varies from 800–1000 mm and occurs mainly in the summer months (mainly thunder showers).

Altitude: 400–1000 m.

Associated vegetation: Eastern Valley Bushveld of the Savanna Biome (Mucina *et al.* 2005).

Associated cremnophytes: Near Kranskop in KwaZulu-Natal *Pelargonium mutans* grows with the following cliff-dwelling plants: *Crassula expansa* subsp. *fragilis*, *C. perfoliata*, *Delosperma lebomboensis* and *Gasteria batesiana*.

Geology: Mainly sandstone of Natal Group (Cape Supergroup).

DISTRIBUTION

Pelargonium mutans grows in river valleys of KwaZulu-Natal, from the Pongola River in the north to near Durban in the south.

RELATED SPECIES

Pelargonium mutans is related to *P. multibracteatum*, an East African species differing from it in its much thicker, articulated, succulent stems and much thinner petals.

ADAPTATIONS TO THE CLIFF ENVIRONMENT

Habit: Small spreading shrublets, stems rooting where they enter crevices, plants becoming deciduous during the dry season.

Size and weight: Clusters small, of medium weight.

Stems: Terete, succulent, articulated at intervals, the nodes swollen where moisture is stored on the elongated stems.

Leaves

Orientation: Ascending-spreading, crowded at apices.

Colour: Green, sometimes with purplish zonal markings.

Age and persistence: Deciduous during the dry season.

Armament: Plants unarmed.

Sexual reproduction

Inflorescence and flowers: Inflorescence terminal, producing a solitary pseudo-umbel. Petals 5, white, pollinated by insects.

Fruit/Seed

Size: Mericarps 7 mm long, tail 30 mm long.

Dispersal: Mericarps spontaneously released and dispersed by wind.

Time: Mainly in summer and autumn.

Vegetative reproduction: *Pelargonium mutans* is a vigorous grower with spreading stems, rooting where they come into contact with adjacent ledges or crevices and forming new colonies. This vegetative regeneration is a vegetative backup, aiding long-term survival.

CONSERVATION STATUS

Localised on the cliffs of dry river valleys where it is not threatened owing to the safe inaccessible habitat.

ADDITIONAL NOTES

Horticulture: *Pelargonium mutans* is best for dry subtropical, coastal and bushveld gardens (Van Jaarsveld 2010). It can be grown on steep embankments, window sills or balconies, also doing well in containers, in full sun or partial shade. Propagate from cuttings from spring to autumn. Outside its native habitat, it should be grown under controlled conditions in a greenhouse. At Kirstenbosch, it has quickly spread to other containers in the cremnophyte nursery, the seed dispersed by wind.

VOUCHER

Van Jaarsveld 18042 (NBG).

ILLUSTRATIONS AND MAP

Figures 162a–162d, Map 162.

163. *Pelargonium vanderwaltii* Van Jaarsv., in Van Jaarsveld & Van Wyk in *Aloe* 43,2 & 3: 32–34 (2006c).

Cremonophyte growth form: Dwarf-sized, compact shrublet (of medium weight to heavy, cliff squatter).

Growth form formula: E:F:As:S/H:Es (vb)

Etymology: Commemorates Johannes Jacobus Adriaan (Adri) van der Walt (1938–2004), botanist and *Pelargonium* specialist.

DESCRIPTION AND HABITAT

Succulent shrublet up to 180 mm tall, 300 mm in diameter, much and irregularly branched, compact, winter-deciduous, slightly aromatic. Roots fibrous. Stems erect or decumbent, succulent, (5–)8–10 mm in diameter, terete, green at first becoming reddish brown, dark brown and smooth with age; surface of young branches sericeous (densely covered with soft white hairs) becoming glabrescent with age. Leaves simple, crowded at apices, ascending; lamina broadly ovate-cordate to almost subrotund, 15–30(–50) × 25–38(–65) mm; margin dentate, sinuate, minutely ciliate; adaxial surface pilose, veins prominent, abaxial surface pilose (sparsely covered with multicellular translucent hairs); apex rounded; base cordately incised, shortly cuneate; petiole (20–)40–100(–175) mm long, persistent, drying to grey-white;

stipules persistent, triangular, 2×3 mm, minutely velutinous, margin ciliate. Inflorescence terminal, producing a solitary 3-flowered pseudo-umbel, 50–70 mm in diameter; peduncle short, 5–10 mm long, pilose; pedicels 20 mm long, pilose. Sepals linear-lanceolate, 5×1.5 –2.5 mm, acute, pilose. Hypanthium 3 mm long, pilose. Petals 5, spatulate, apices rounded to slightly retuse, varying from dark to pale mauve (Purple Group 76a–d, RHS Colour Chart); posterior two 12×6 mm, reflexed at 90° ; anterior three 9×4 mm, reflexed at more than 90° . Stamens 6, fertile, 2 shorter; pollen white. Mericarps 5 mm long, tail 12 mm long.

Phenology: Flowering throughout the year, but with a peak in December. Seeds with typical *Pelargonium* seed dispersal strategy.

Pollinators: Insects.

Habitat and aspect: Grows on south-facing cliffs and cliff tops, on the Otjihipa Mountains just east of Otjinhungwa, where the plants occur in granite rock crevices. The habitat preference of *P. vanderwaltii* in the Kaokoveld reflects an afromontane affinity rather than adaptation to the arid semidesert conditions prevailing in the region. The average annual rainfall in the Kaokoveld varies from less than 50 mm along the coast to about 350 mm on the highlands (Mendelsohn *et al.* 2002). Precipitation is erratic and occurs mainly in the form of thunder showers in summer. At Otjihipa the average annual rainfall is estimated at 150–250 mm.

Altitude: 1800–1900 m.

Associated vegetation: Mainly arid savanna.

Associated cremnophytes: *Pelargonium vanderwaltii* occurs sympatrically with other cliff-dwelling succulents such as *Aeollanthus haumannii*, *Kalanchoe lanceolata* and *Tetradenia kaokoensis*.

Geology: Granite (Fransfontein Granite Suite, Simplified Geological Map of Namibia, 1980).

DISTRIBUTION

Known only from the Otjihipa Mountains in northwestern Namibia.

RELATED SPECIES

Pelargonium vanderwaltii is a member of section *Cortusina* and is closely related to three other species in the same section, *P. cortusifolium*, *P. echinatum* and *P. crassicaule*. It is at once distinguished from these species by being winter-deciduous, by its long, (20–)40–100(–175) mm, persistent petioles, and broadly cordate-ovate to almost subrotund leaves of which the surface is only sparsely pilose. It further differs in its solitary pseudo-umbel of 3 or 4 flowers and mericarps of which the tails are only 12 mm long.

ADAPTATIONS TO THE CLIFF ENVIRONMENT

Habit: Small, compact shrublets, becoming deciduous during the dry season.

Size and weight: Clusters small.

Stems: Terete, succulent where moisture is stored.

Leaves

Orientation: Ascending, crowded at apices.

Colour and texture: Green, both surfaces pilose.

Age and persistence: Becoming deciduous during the dry season.

Armament: The persistent petioles can be viewed as a form of armament.

Sexual reproduction

Inflorescence and flowers: Inflorescence terminal, producing a solitary 3-flowered pseudo-umbel, 50–70 mm in diameter; peduncle short, 5–10 mm long. Petals 5, spatulate, apices rounded to slightly retuse, varying from dark to pale mauve (Purple Group 76a–d, RHS Colour Chart).

Fruit/Seed

Size: Mericarps 5 mm long, tail 12 mm long.

Dispersal: Mericarps spontaneously released and dispersed by wind.

Time: Summer and autumn (rainy season in its habitat).

Vegetative reproduction: The succulent stems will root where they come into contact with adjacent ledges or crevices, forming new colonies. This vegetative regeneration is a vegetative backup, aiding long-term survival.

CONSERVATION STATUS

Localised and confined to the Otjhipa Mountains where it is not threatened owing to the safe inaccessible habitat.

ADDITIONAL NOTES

Horticulture: *Pelargonium vanderwaltii* is best for dry semidesert, warm-temperate gardens (Van Jaarsveld 2010). It can be grown on steep embankments, window sills and balconies, also doing well in containers, in full sun or partial shade. Propagate from cuttings from spring to autumn. Outside its native habitat, it should be grown under controlled greenhouse conditions.

VOUCHER

Van Jaarsveld 18873 (NBG).

ILLUSTRATIONS AND MAP

Figures 163a & 163b, Map 163.

GESNERIACEAE

Streptocarpus Lindl.

164. *S. kentaniensis* L.L.Britten & Story

STREPTOCARPUS Lindl.

164. *Streptocarpus kentaniensis* L.L.Britten & Story in *Bothalia* 6,2: 433 (1954).

Cremnophyte growth form: Clusters with drooping foliage (of light to medium weight, cliff squatter).

Growth form formula: A:S:Lper:Lc:Ca (vb)

Etymology: After Kentani near the Kei River in the Transkei, Eastern Cape.

DESCRIPTION AND HABITAT

Perennial, stemless, rosulate, succulent plants up to 300 mm in diameter. Roots fibrous. Leaves linear-lanceolate, 100–190 × 15–30 mm, thick, fleshy, ascending-spreading, becoming drooping on cliff; surface rugose, covered with short non-glandular hairs, lower surface densely and prominently veined, veins succulent; margin crenate, undulating, slightly revolute; apex acute; petiole distinct, purplish, up to 10–30 mm long, 6–7 mm in diameter, fleshy, succulent, continuing along lower leaf surface. Peduncle hairy, 90–120 mm long, arising from distal end of petiole in series of 3–5 and extending shortly on lamina, 2-flowered. Calyx 3 mm long; segments hairy. Corolla 25–29 mm long, tubular, cylindrical, slightly curved, hairy, light violet, spotted; limb 17–20 mm across; lobes 5–6 mm long. Stamens with twisted filaments, 4 mm long; anthers connivent, explosive; pollen powdery. Gynoecium 13 mm long; ovary and style hairy, style about twice as long as ovary. Capsule slender, about 50 mm long, scabrous. (Description partly based on Story 1955.)

Phenology: Flowering in midwinter. Seed wind-dispersed.

Pollinators: Insects.

Habitat and aspect: Shale cliffs and mainly on shady southern aspects. Plants are rooted in crevices and on rock ledges. Winters are cool but frost is a rarity or absent. The average daily maximum temperature is 22°C and the average daily minimum 14°C. Rainfall occurs from spring to autumn but occasionally also in winter and ranges from 1000–1250 mm per annum.

Altitude: 100–200 m.

Associated vegetation: Buffels Thicket, Albany Thicket Biome (Mucina *et al.* 2005).

Associated cremnophytes: Near Kei Mouth, the plants grow with the following cliff dwellers: *Crassula cordata*, *C. foveata*, *C. lactea*, *C. spathulata*, *Cyrtanthus sanguineus*, *Delosperma*

sp., *Haworthia cymbiformis* var. *setulifera*, *Kalanchoe crenata*, *Peperomia blanda*, *Petopentia natalensis*, *Plectranthus strigosus*, *Rhipsalis baccifera* and *Stenoglottis fimbriata*.

Geology: Mainly Beaufort shale (Karoo Supergroup).

DISTRIBUTION

Streptocarpus kentaniensis is confined to cliff faces of the lower Kei River and its tributaries.

RELATED SPECIES

Streptocarpus kentaniensis with its markedly succulent leaves with a thick midrib is a distinct species not confused with any other southern African species. It is in fact the most succulent of all *Streptocarpus* species and has been taken up in the succulent lexicon of Egli (2002: 304).

ADAPTATIONS TO THE CLIFF ENVIRONMENT

Habit: Compact, rosulate growth, the thick succulent leaves (especially the midrib) enabling plants to survive periods of drought on the sheer cliff face. The plants sometimes become desiccated during dry periods but soon regain turgidity after sufficient rain, ensuring their survival on the cliff face. When the thick petiole is damaged or falls into a crevice, it will simply root, a valuable vegetative backup system.

Size and weight: Clusters small.

Leaves

Orientation: Spreading-ascending to drooping.

Colour: Green.

Sexual reproduction

Inflorescence and flowers: Peduncle 90–120 mm long, 2-flowered. Corolla 25–29 mm long. Conspicuous, light violet coloured, spotted.

Fruit/Seed

Size: Very fine dust diaspores.

Dispersal: Seeds explosively released and dispersed by wind.

Time: Flowering in midwinter ensures that seeds ripen by spring, in time for spring rains.

Vegetative reproduction: *Streptocarpus kentaniensis* regenerates from leaves (midrib) that come into contact with soil or land in crevices, establishing new colonies. Detached leaves that fall into adjacent crevices will root and establish new plants. This vegetative regeneration is a vegetative backup, aiding long-term survival.

CONSERVATION STATUS

Classified as vulnerable (Raimondo *et al.* 2009). However, it is localised and confined to cliffs where it is not threatened owing to the inaccessible habitat.

ADDITIONAL NOTES

Horticulture: *Streptocarpus kentaniensis* is an ornamental species, best for dry subtropical, coastal and thicket gardens. It can be grown as a house plant or on steep embankments, window sills or balconies, also doing well in containers in partial shade (Van Jaarsveld 2010). Propagate from leaf cuttings in a sand-peat mixture from spring to summer. Outside its native habitat, it should be grown under controlled conditions in a greenhouse.

VOUCHER

Van Jaarsveld 17923 (NBG).

ILLUSTRATIONS AND MAP

Plate 164, Figures 164a & 164b, Map 164.

LAMIACEAE

Aeollanthus Mart. ex Spreng.

- 165. *A. haumannii* Van Jaarsv.
- 166. *A. rydingianus* Van Jaarsv. & A.E.van Wyk

Plectranthus L'Hér.

- 167. *P. dolomiticus* Codd
- 168. *P. ernstii* Codd
- 169. *P. mutabilis* Codd
- 170. *P. mzimvubuensis* Van Jaarsv.
- 171. *P. purpuratus* Harv. subsp. *purpuratus*
- 172. *P. saccatus* Benth. subsp. *pondoensis* Van Jaarsv. & Milstein

Tetradenia Benth.

- 173. *T. kaokoensis* Van Jaarsv. & A.E.van Wyk

AEOLLANTHUS Mart. ex Spreng.

165. *Aeollanthus haumannii* Van Jaarsv., in Van Jaarsveld & Van Wyk in *Aloe* 43,4: 72–73 (2006d).

Cremonophyte growth form: Dwarf-sized, ascending, succulent shrublet (of medium weight, cliff squatter).

Growth form formula: E:F:As:S/H:Es (vb)

Etymology: After Mr Tielman Haumann and his son, Dr Carl Haumann, farmers and lovers of African plants.

DESCRIPTION AND HABITAT

Soft, semisucculent, herbaceous, single to multistemmed (branched from base, rarely dichotomously branched) perennial up to 160 mm tall, most parts beset with minute glandular hairs, aromatic (smell of *leberwurst*), becoming glabrescent with age. Roots fibrous. Branches 4-angled to subterete, at first pale to almost whitish green, becoming grey-brown, eventually black; main branches up to 8 mm in diameter (9 mm at swollen nodes), often articulated and becoming ribbed; nodes distinctly swollen, internodes (10–)20(–30) mm long; main branches often distinctly grooved (above each leaf axil); younger branches 4 mm in diameter, sparsely covered with translucent glandular hairs shorter than 0.1 mm. Leaves fleshy, decussate, petiolate, broadly ovate to broadly triangular-ovate to ovate, 35–55(–60) × 28–35(–45) mm; adaxial surface pale glaucous green; margin serrate (bearing 4–8 pairs of teeth), sometimes slightly wavy, often decurrent on petiole; apex obtuse, subacute to subrotund; base truncate, rarely cuneate to attenuate; petiole subterete, 15–25(–30) mm long, spreading. Inflorescence a lax, terminal, candelabra-shaped panicle up to 150 mm high and about 220 mm wide at base; peduncle 3 mm in diameter at base, gradually narrowing distally; axis of main spike 25–30 mm long, with opposite flowers (not secund), becoming gradually smaller towards tip; other

spikes bearing 1 or 2 flowers at each node (secundly arranged, and 1–4 flowers opening at the same time on each spike); basal spikes up to 80 mm long (with stalks up to 35 mm long), bearing leaf-like bracts at base, each bearing short side branches from base. Corolla white or light mauve, laterally compressed; tube 5–6 mm long, 0.7–1.0 mm in diameter, expanding to 2.5 mm at throat (angle of expansion about 35–45°). Stamens in 2 pairs, upper two longer, exposed for 4–6 mm, lower two shorter, with slightly larger anthers, exposed for about 2–3 mm; anthers of lower pair reniform, 0.7 mm long; pollen pale orange. Disc circular, about 1 mm in diameter (bearing a prominent lobe in fruiting stage). Style at first 8–10 mm long, exposed for 3–4 mm from throat, bifid, lengthening up to 13 mm when ripe. Nutlets roundish, 0.8 × 0.6 mm, smooth, black, shiny.

Phenology: Flowering in autumn (March–April).

Pollinators: Insects.

Habitat and aspect: *Aeollanthus haumannii* grows on south-facing cliffs on both peaks of the Otjihipa Mountains just east of Otjinhungwa where the plants occur in granite rock crevices. The habitat preference of *A. haumannii* in the Kaokoveld reflects an afromontane affinity rather than adaptation to the arid semidesert conditions prevailing in the region. Average annual rainfall is estimated at 150–250 mm.

Altitude: 1500–1900 m.

Associated vegetation: Mainly arid savanna.

Associated cremnophytes: Occurs sympatrically with other cliff-dwelling succulents such as *Kalanchoe lanceolata*, *Pelargonium vanderwaltii* and *Tetradenia kaokoensis*.

Geology: Granite (Fransfontein Granite Suite, Simplified Geological Map of Namibia, 1980).

DISTRIBUTION

Known only from the Otjihipa Mountains in northwestern Namibia.

RELATED SPECIES

Aeollanthus haumannii is most closely related to *A. candelabrum* (not a cremnophyte), from which it differs by being a much smaller and fragile perennial with 4-angled or subterete branches which turn distinctly black and ribbed with age (often articulated at nodes). *Aeollanthus candelabrum* is a larger, rigid subshrub up to 1 m high. It sometimes also has thickened nodes, but that is where the resemblance ends. The small size and fragile nature of *A. haumannii* can be seen as an adaptation to the undisturbed cliff-face habitat.

ADAPTATIONS TO THE CLIFF ENVIRONMENT

Habit: Small, brittle shrublets at first with whitish green, succulent stems. During the dry season the leaves become deciduous.

Size and weight: Shrublet small, of medium weight.

Leaves

Orientation: Ascending-spreading.

Colour: Pale green, turning purplish (production of anthocyanins) during drought stress, a character that can be related to the vertical cliff habitat. This change of colour reduces the penetration of light, thus also reducing the photosynthesis process, and is typical of succulent plants.

Age and persistence: Plants deciduous. The fleshy leaves become turgid after rain, but are often in a semi-desiccated state during dry periods. The fact that the leaves are aromatic can perhaps be interpreted as a chemical defence mechanism against predation by phytophagous insects. Plants re-sprout from the rootstock if damaged.

Armament and camouflage: The plants are mechanically unarmed, with conspicuous succulent stems.

Sexual reproduction

Inflorescence and flowers: Inflorescence ascending, short racemes. The white to pink flowers attract insects in the bee family.

Fruit/Seed

Size: Seed (nutlet) rounded, small, 0.6–0.8 mm in diameter.

Dispersal: Nutlets released once calyx breaks free at the abscission layer and then locally dispersed. A habitat specialist, with plants well adapted to remain in the cliff-face sites.

Time: Germination after about 21 days.

Vegetative reproduction: Stems will root when reaching a crevice.

CONSERVATION STATUS

Localised and not threatened owing to the inaccessible habitat.

ADDITIONAL NOTES

Horticulture: Best suited to dry bushveld (savanna) gardens. Outside the habitat, it is best suited to a greenhouse where conditions can be controlled. Propagate from stem cuttings in spring or summer after plants have sprouted, in sandy, well-drained soil. Keep in dappled shade and feed in spring and summer.

VOUCHER

Van Jaarsveld 18874 (NBG).

ILLUSTRATIONS AND MAP

Figures 165a–165c, Map 165.

166. *Aeollanthus rydingianus* Van Jaarsv. & A.E.van Wyk in *Bothalia* 35,2: 157–160 (2005f).

Cremonophyte growth form: Ascending, succulent shrublet (of medium weight, cliff squatter).

Growth form formula: E:F:As:S/H:D (vb)

Etymology: After Olof Ryding of Sweden, specialist on the genus *Aeollanthus*.

DESCRIPTION AND HABITAT

Softly semisucculent, herbaceous, branched, erect subshrubs up to 600 mm tall, most parts covered with glandular hairs and sharply aromatic. Roots fibrous. Branches terete, main branch up to 20 mm in diameter, with brown peeling bark at base; younger branches 7–8 mm in diameter, green, sparsely covered with translucent glandular hairs up to 2 mm long; nodes 20–30 mm long, internodes covered in short, axillary, crowded, leafy branches, each with 3 pairs of leaves overtopped by normal leaves. Leaves decussate; those on axillary branches 20–40 × 15–20 mm (occasionally much shorter), very shortly petiolate; normal leaves spreading, long-petiolate, 70–140(–200) × 40–80(–100) mm, becoming drooping, often exposing suppressed, axillary branches; lamina broadly ovate to broadly triangular-ovate, fleshy, tomentose, slightly viscous owing to glandular translucent hairs; adaxial surface channelled, slightly rugose, densely covered in soft translucent glandular hairs 0.5–2.0 mm long, abaxial surface reticulate; veins prominent, densely beset with glandular hairs, elsewhere hairy; margin dentate with 7–10 pairs of teeth 5–7 mm long and each with secondary tooth at base, decurrent on petiole; apex acute to subacute; base cuneate to attenuate; petiole 15–40 mm long, 5 mm in diameter, subterete. Inflorescence a terminal, lax pyramid-shaped panicle, 100–125(–200) mm high, 60 mm wide at base; spikes becoming gradually smaller towards tip, those of main axis with opposite flowers, other spikes bearing 1 or 2 flowers at each node; basal spikes up to 30 mm long, shortly stalked, each with a pair of short side branches at base; peduncle 4 mm in diameter at base, gradually becoming thinner distally; bracts concave, broadly ovate, densely imbricate, 5.5–8.0 × 4.0–5.5 mm, surface with 3 obscure veins, covered with short glandular hairs, apex acute, sterile bracts slightly smaller. Calyx green, 1.75–2.5 mm long, bell-shaped, basal part circular, 1 mm in diameter, widening towards apex; upper lip 3-lobed; lower lip infolded. Corolla white (Angola) or mauve (Namibia), (12–)18–19 mm long, 2-lipped; tube 1 mm in diameter at base, widening to 3.5 mm at throat; upper lip erect, 4-lobed, 8 mm high, bearing dark purple dots; lower lip 8–9 mm long, horizontal, cymbiform, obtuse at apex. Stamens 8–9 mm long, mauve; anthers 1 mm in diameter; pollen yellow. Style (9–)15–16 mm long, lengthening to up to (11–)17–18 mm when ripe. Nutlets 1.3 × 1 mm, smooth, black.

Phenology: Flowering in late autumn and winter (May–August). Seeds with local non-specialist dispersal strategy.

Habitat and aspect: In the Kaokoveld (northwestern corner of Namibia) this taxon is confined to the upper sandstone cliffs of the southeastern part of the Baynes Mountains. This rugged range consists of a flat-topped sandstone massive that rises to about 2000 m and is bordered by sheer cliffs. Plants of *Aeollanthus rydingianus* occur in a restricted area on a narrow south-facing ledge. Although the plants grow in the shade of the cliffs in winter, they receive some sunlight for part of the day in summer. The average annual rainfall in the Kaokoveld varies from less than 50 mm along the coast to 350 mm on the highlands (Mendelsohn *et al.* 2002). Precipitation is erratic and occurs mainly in the form of thunder showers in the summer months. At Omavanda, where the average annual rainfall is an

estimated 250–300 mm, *A. rydingianus* receives substantial additional moisture in the form of water that seeps from the porous sandstone rock. Its habitat clearly represents a restricted relatively moist refuge in a generally arid area.

Altitude: 1600 m.

Associated vegetation: Mainly arid savanna. However, the occurrence of *Aeollanthus rydingianus* in the Kaokoveld reflects an afro-montane affinity rather than an adaptation to the arid semidesert conditions prevailing in the region. Its presence in the Kaokoveld may be an outlier occurrence and this would also support its treatment as a taxon conspecific with *Aeollanthus* sp. A of the Huila Plateau. It is likely that more records of the new species would come from the wetter and botanically still poorly explored Serra da Chella mountain range, which extends from the Huila Plateau southwards towards the Kaokoveld.

Associated cremno-phytes: Associated species include the trees *Cussonia angolensis*, *Ficus bubu*, *F. glumosa*, *F. ilicina* and *Nuxia congesta*, as well as the pendent *Aloe omavandae*.

Geology: Sandstone of the Damara Sequence (Simplified Geological Map of Namibia, Geological Survey of Namibia, 1980).

DISTRIBUTION

Aeollanthus rydingianus is known only from two localities, one in Kaokoveld, northwestern Namibia, the other in southern Angola (Lubango), a disjunction.

RELATED SPECIES

Aeollanthus rydingianus belongs to section *Rotundobasis*, a group that also includes *A. elsholzioides* (Angola), *A. rehmannii* (Namibia and South Africa) and *A. parvifolius* (South Africa). It is most closely related to the annual *A. elsholzioides*, from which it differs in being a perennial, semisucculent subshrub up to 600 mm high. It furthermore differs from *A. elsholzioides* in having an indumentum that is more densely glandular, long-petioled, triangular-ovate leaves that are larger, 70–140(–200) × 40–80(–100) mm, an inflorescence that is a lax, pyramidal, terminal panicle up to 125 × 60 mm, shortly stalked, dense spikes, larger and broader, subacute, imbricate fertile bracts, 5.5–8.0 × 4.0–5.5 mm, and a larger corolla (12–)18–19 mm long.

ADAPTATIONS TO THE CLIFF ENVIRONMENT

Habit: Herbaceous semisucculent plants.

Size and weight: Shrubs of medium weight.

Leaves

Orientation: Ascending-spreading.

Colour and texture: Green, sticky.

Age and persistence: Plants are evergreen. The fleshy leaves become turgid after rain, but are often in a semi-desiccated state during dry periods. The fact that the leaves are aromatic can perhaps be interpreted as a chemical defence mechanism against predation by phytophagous insects. Plants re-sprout from the rootstock if damaged.

Armament and camouflage: The plants are mechanically unarmed, with conspicuous succulent stems.

Sexual reproduction

Inflorescence and flowers: Inflorescence ascending, short racemes. The white to pink flowers attract insects in the bee family.

Fruit/Seed

Size: Seed (nutlet) rounded, small, 1.3 mm in diameter.

Dispersal: Black nutlets released once calyx breaks free at the abscission layer and then locally dispersed. Plants thus well adapted, releasing nutlets close to the mother plant and remaining in the cliff-face sites.

Time: Late winter and spring.

Vegetative reproduction: At and after flowering, the inflorescence develops vegetative branchlets, a vegetative dispersal method that can be viewed as a backup strategy. Fallen branchlets will root under suitable conditions, ensuring long-term survival.

CONSERVATION STATUS

Localised and not threatened owing to the inaccessible habitat.

ADDITIONAL NOTES

Horticulture: Best grown in highveld or dry bushveld gardens, on embankments or in containers, in dappled shade. Outside its habitat, it is best suited to a greenhouse where the conditions can be controlled. *Aeollanthus rydingianus* is an attractive perennial and is floriferous in cultivation. Propagate it from cuttings or from branchlets formed on the inflorescence.

VOUCHER

Van Jaarsveld 17481 (NBG).

ILLUSTRATIONS AND MAP

Plate 166, Figures 166a–166d, Map 166.

PLECTRANTHUS L'Hér.

167. *Plectranthus dolomiticus* Codd in Bothalia 15: 142 (1984).

Cremonophyte growth form: Pendent cluster (of medium weight, cliff hanger).

Growth form formula: E:F:P:Els (vb)

Etymology: The epithet *dolomiticus* refers to its dolomitic, rocky substrate.

DESCRIPTION AND HABITAT

Decumbent, semisucculent herb, up to 300 mm tall. Rootstock tuberous. Branches square to subterete. Leaves fleshy, broadly ovate, 20–30 × 18–30 mm; surface almost glabrous; margin crenate-dentate with 5–7 pairs of teeth; apex acute or obtuse; base truncate; petiole up to 35 mm long. Inflorescence a terminal raceme up to 130 mm long, occasionally with a pair of basal branches. Calyx 2.5 mm long, enlarging to 6 mm after flowering. Corolla up to 10 mm long, violet-purple, deflexed and widening towards throat. Nutlets 1.75 mm long, brown.

Phenology: Flowering in autumn (March–April), but also in spring and summer.

Pollinators: Insects.

Habitat and aspect: *Plectranthus dolomiticus* is confined to dolomitic cliffs and steep slopes, growing in dry bushveld (savanna). Plants trail from rock crevices, fissures and ledges in dappled shade or full sun. In Zimbabwe it has been collected on granites. Extreme temperatures as high of 40°C have been recorded. Winters are cooler but frost is a rarity or absent. The average daily maximum temperature is 26°C and the average daily minimum about 16°C. Rainfall is low, 400–500 mm per annum, and occurs mainly from spring to autumn.

Altitude: 800–1000 m.

Associated vegetation: Mainly Bushveld and recorded from Pong Dolomite Mountain Bushveld (Mucina *et al.* 2005).

Associated cremonophytes: *Crassula expansa* subsp. *fragilis*, *Gasteria batesiana* var. *dolomitica* and *Orbea hardyi*.

Geology: Dolomite of the Malmani Subgroup, Chuniespoort Group (Transvaal Subgroup).

DISTRIBUTION

Plectranthus dolomiticus appears to be endemic to the Olifants River in Mpumalanga and Limpopo Provinces.

RELATED SPECIES

Recognised by its Dutchman's pipe violet-purple flowers, small semisucculent, broadly ovate leaves and tuberous roots. This species is closely related to *Plectranthus petiolaris*, which has

larger leaves and fibrous roots, occurring in river valleys. The small size and tuberous roots of *P. dolomiticus* can be seen as adaptations to the xeric conditions of the dolomite cliff face.

ADAPTATIONS TO THE CLIFF ENVIRONMENT

Habit: Spreading, pendent nature, forming loose clusters up to 500 mm in diameter. Stems becoming drooping, often rooting where in contact with soil. During the dry season the leaves become purplish green to purplish. The succulent roots help with conservation of water in the extreme vertical environment. It grows more slowly than the non-cremnohyte *Plectranthus petiolaris*. The slow growth rate is retained in cultivation.

Size and weight: Clusters small, of medium weight.

Leaves

Orientation: Ascending-spreading, small.

Colour: Green, turning purplish under drought stress, a character that can be related to its vertical cliff habitat. This change of colour reduces unnecessary penetration of light, thus also reducing photosynthesis, and is typical of succulent plants.

Age and persistence: Evergreen, but with leaves withering from the base. The fleshy leaves become turgid after rain, but are often in a semi-desiccated state during dry periods. The fact that the leaves are aromatic can perhaps be interpreted as a chemical defence mechanism against predation by phytophagous insects. Plants re-sprout from the rootstock if damaged.

Armament and camouflage: The plants are mechanically unarmed, with conspicuous succulent stems.

Sexual reproduction

Inflorescence and flowers: Inflorescence ascending, short racemes. The conspicuous violet-purple flowers attract insects in the bee family.

Fruit/Seed

Size: Seed (nutlet) rounded, 1.75 mm in diameter.

Dispersal: Nutlets shaken from the fruiting calyx and locally dispersed.

Time: Nutlets ripening in summer and autumn, coinciding with the rainfall. Germination after about 21 days.

Vegetative reproduction: The pendent to spreading branches root where they touch the soil. This is an efficient vegetative backup strategy for surviving the harsh, xeric cliff-face conditions.

CONSERVATION STATUS

Classified as critically rare (Raimondo *et al.* 2009). However, although localised to the dolomite formations of the Olifants River gorge, it is not threatened owing to the inaccessible habitat.

ADDITIONAL NOTES

Horticulture: Best for dry subtropical and bushveld (savanna) gardens, grown on embankments, rockeries or in containers, also a useful drought-tolerant groundcover (Van Jaarsveld 2010). Outside its habitat, it is best grown under controlled conditions in a greenhouse. Propagate from stem cuttings in spring or summer. Flowering throughout summer and autumn.

VOUCHER

Van Jaarsveld 7052 (NBG).

ILLUSTRATIONS AND MAP

Figures 167a–167c, Map 167.

168. *Plectranthus ernstii* Codd in The Flowering Plants of Africa 47: t. 1855 (1982).

Cremonophyte growth form: Dwarf-sized cluster (of medium weight, cliff squatter).

Growth form formula: E:F:As:S/H:Ca:Ev (vb)

Etymology: After Ernst van Jaarsveld (1953–), horticulturist at Kirstenbosch National Botanical Garden.

DESCRIPTION AND HABITAT

Decumbent to erect, cluster-forming, succulent herb up to 120 mm high. Roots fibrous to somewhat succulent, up to 4 mm in diameter. Branches compact, articulated at nodes, short, somewhat moniliform, occasionally globose, brownish striated, becoming grey, up to 50 mm in diameter, succulent, younger stems square. Leaves succulent, broadly ovate to deltoid, 12–30 × 10–25 mm, dentate, with 3 pairs of teeth; both surfaces green, purplish tinged, glabrescent to puberulous, undersurface with reddish brown to pale gland dots, pleasantly aromatic; apex acute to obtuse; base obtuse to truncate. Inflorescence 50–170 mm long, often with a pair of side branches, racemose; verticillasters 6-flowered, 5–12 mm apart; bracts ovate, 3 mm long, persistent beyond flowering stage; pedicel 4–5 mm long. Corolla 7–12 mm long, white to mauve; tube 6–8 mm long, ventricose at base, constricted at throat. Fruiting calyx 3–5 mm long. Nutlets rounded, 2 mm long, brown.

Phenology: Flowering in autumn (March–April), but also in spring.

Pollinators: Insects.

Habitat and aspect: South-facing sandstone cliffs. Plants are rooted in crevices and on rock ledges. Extreme temperatures as high of 40°C have been recorded. Winters are cooler but frost is a rarity or absent. The average daily maximum temperature is about 24°C and the average daily minimum 16°C. Rainfall mainly from spring to autumn but occasionally also in winter, ranging from 1000–1250 mm per annum.

Altitude: 200–350 m.

Associated vegetation: Pondoland-Ugu Sandstone Coastal Sourveld of the Indian Ocean Coastal Belt (Mucina *et al.* 2005).

Associated cremnophytes: *Aloe arborescens*, *Aptenia cordifolia*, *Cotyledon orbiculata* var. *oblonga*, *Crassula flanaganii*, *C. multicava*, *C. perfoliata* var. *perfoliata*, *Delosperma repens*, *D. tradescantioides*, *Gasteria croucheri*, *Petopentia natalensis*, *Portulacaria afra*, *Rhipsalis baccifera* and *Sarcostemma viminale*.

Geology: Quartzitic sandstone of the Natal Group (Cape Supergroup).

DISTRIBUTION

Plectranthus ernstii is endemic to the sandstone gorges between the Msikaba River (Eastern Cape) and Oribi Gorge (southern KwaZulu-Natal).

RELATED SPECIES

Plectranthus ernstii is related to both *P. saccatus* and *P. strigosus* (section *Plectranthus*) of the same region. *Plectranthus saccatus* is a much larger forest and forest margin shrub up to 1 m tall with much larger flowers. *Plectranthus strigosus* is a procumbent coastal forest species without the succulent stems, with white flowers.

ADAPTATIONS TO THE CLIFF ENVIRONMENT

Habit: Compact, cluster-forming, 80–150 mm in diameter, stems often rooting where in contact with soil. During the dry season the leaves become purplish green to purplish. The compact cluster-forming growth and slow growth rate, compared to that of other non-cremnophilous *Plectranthus* species, can be seen as an adaptation to the cliff face. The slow growth rate is retained in cultivation and plants can take up to five years or longer to reach maturity, differing from most other level-ground species. Forms from the Msikaba River at the southern end of its distribution tend to be more trailing, with longer elongated branches. *Plectranthus saccatus* subsp. *saccatus* is a related non-cremnophilous, rapid-growing shrubby species.

Size and weight: Clusters small, of medium weight.

Stem: Branches succulent, often moniliform and articulated at nodes. Forms from Sikuba and Msikaba with spreading, subpendent stems rooting where they touch the ground.

Leaves

Orientation: Small, spreading, maximising absorption of light.

Colour: Green, turning purplish under drought stress (production of anthocyanins), a character that can be related to the vertical cliff habitat. This change of colour reduces penetration of light, thus also reducing photosynthesis, and is typical of succulent plants.

Age and persistence: Plants evergreen, but with leaves withering from the base. The fleshy leaves become turgid after rain, but are often in a semi-desiccated state during dry

periods. The fact that the leaves are aromatic can perhaps be interpreted as a chemical defence mechanism against predation by phytophagous insects.

Armament and camouflage: The plants are mechanically unarmed and the conspicuous succulent stems are vulnerable, suggesting a reduction in armament in response to the undisturbed cliff habitat in contrast to the often thorny but grazed surrounding subtropical and thicket vegetation.

Sexual reproduction

Inflorescence and flowers: Inflorescence ascending, short racemes. The conspicuous light mauve to mauve flowers attract insects in the bee family.

Fruit/Seed

Size: Seed (nutlet) rounded, 2 mm in diameter.

Dispersal: Nutlets shaken from the fruiting calyx and locally dispersed.

Time: Nutlets ripening in autumn, coinciding with autumn rainfall. Germination after about 21 days.

Vegetative reproduction: The moniliform, articulated branches root where they touch the soil. The southern forms of *Plectranthus ernstii* have elongated branches rooting at the nodes or where they touch the soil or crevice, establishing new populations. This is a vegetative backup strategy for surviving the harsh cliff-face conditions.

CONSERVATION STATUS

Classified as critically rare (Raimondo *et al.* 2009). Localised and confined to dissected east-flowing river gorges of KwaZulu-Natal Sandstone (Cape Supergroup) where it is not threatened owing to the inaccessible habitat.

ADDITIONAL NOTES

Horticulture: Best for subtropical coastal gardens, on embankments or rockeries, in dappled shade (Van Jaarsveld 2010). Outside the habitat, it is best grown in sandy, slightly acidic soil, under controlled conditions in a greenhouse. Seeds have been distributed to growers in Europe and Japan and owing to its small, tree-like habit and ornamental appeal (Oribi Gorge form) it is now popular under the name 'Bonsai Mint'. Propagate from cuttings or seed, trim regularly to keep a neat, compact growth (see Van Jaarsveld 2006a).

VOUCHER

Van Jaarsveld 2196 (NBG).

ILLUSTRATIONS AND MAP

Plate 168, Figures 168a–168e, Map 168.

169. *Plectranthus mutabilis* Codd in Bothalia 11: 404 (1975).

Cremonophyte growth form: Pendent mats (of medium weight, cliff hanger).

Growth form formula: E:F:P:Els (vb)

Etymology: Latin *mutabilis*, changeable, pertaining to its variability.

DESCRIPTION AND HABITAT

Prostrate, semisucculent herb. Branches often hanging from cliffs. Leaves ovate to broadly ovate, 15–50 × 15–50 mm, tomentose to glabrescent, glands orange; margin crenate or crenate-dentate with 4–6 pairs of teeth; apex acute or obtuse; base truncate. Inflorescence terminal, racemose, 100–250 mm long, occasionally with a pair of side branches; verticillasters 6–14-flowered. Calyx 2 mm long, elongating to 4 mm after flowering. Corolla 8–15 mm long, purple-blue; tube centrally deflexed, widening towards throat. Nutlets 1 mm long, dark brown.

Phenology: Flowering in autumn (March–April), but also in spring.

Pollinators: Insects.

Habitat and aspect: Cliffs along mountains and river valleys. Plants grow in dry savanna or the fringes of afro-montane forest. *Plectranthus mutabilis* grows in light shade in well-drained, humus-rich soils. The average daily maximum temperature is about 25°C and the average daily minimum about 10°C. Rainfall ranges from 600–1250 mm per annum.

Altitude: 1000–2230 m.

Associated vegetation: Wolkberg Dolomite Grassland, Soutpansberg Summit Sourveld, Mamabolo Mountain Bushveld and Moot Plains Bushveld of the Savanna Biome (Mucina *et al.* 2005).

Associated cremonophytes: At Chuniespoort it grows with *Adromischus umbraticola* subsp. *ramosa*, *Aeollanthus buchnerianus*, *Aloe mutabilis* and *Crassula expansa* subsp. *fragilis*.

Geology: Sandstone or dolomite (Sandstone of the Wyllies Poort Formation, Soutpansberg Group) and dolomite of the Malmani Subgroup (Transvaal Supergroup).

DISTRIBUTION

Plectranthus mutabilis is widespread in the Mpumalanga and Gauteng Provinces.

RELATED SPECIES

Characterised by prostrate, free-rooting stems and purple-blue flowers. Related to *Plectranthus aliciae*, *P. madagascariensis*, *P. grandidentatus* and *P. woodii*, all with white flowers.

ADAPTATIONS TO THE CLIFF ENVIRONMENT

Habit: Spreading, pendent, forming mat-like clusters up to 500 mm in diameter and drooping from the cliff faces. Stems becoming drooping and rooting where in contact with soil.

Size and weight: Clusters small.

Leaves

Orientation: Ascending-spreading, small.

Colour and texture: Green, turning purplish under drought stress (owing to the production of anthocyanins), a character that can be related to the vertical cliff habitat. This change of colour reduces penetration of light, thus also reducing photosynthesis, and is typical of succulent plants. The sometimes hairy nature also helps the plants to deal with drought stress.

Age and persistence: Plants evergreen, but with leaves withering from the base. The fleshy leaves become turgid after rain, but are often in a semi-desiccated state during dry periods. The fact that the leaves are aromatic can perhaps be interpreted as a chemical defence mechanism against predation by phytophagous insects.

Armament and camouflage: The plants are mechanically unarmed, with conspicuous succulent stems.

Sexual reproduction

Inflorescence and flowers: Inflorescence ascending, short racemes. The conspicuous violet-purple flowers attract insects in the bee family.

Fruit/Seed

Size: Seed (nutlet) rounded, 1 mm in diameter.

Dispersal: Dark brown nutlets shaken from the fruiting calyx and locally dispersed.

Time: Nutlets ripening in summer and autumn, coinciding with the rainfall. Germination after about 21 days.

Vegetative reproduction: The pendent to spreading branches root where they touch the soil, establishing new populations. This is an efficient vegetative backup strategy for continued existence despite the harsh, xeric cliff-face conditions.

CONSERVATION STATUS

Localised and confined to gorges where it is not threatened owing to the inaccessible habitat.

ADDITIONAL NOTES

Horticulture: *Plectranthus mutabilis* is best for dry bushveld or highveld gardens and ideal for steep embankments, grown in partial shade. Outside its habitat, it is best grown under controlled conditions in a greenhouse. Propagate from stem cuttings. Effective as a groundcover (Van Jaarsveld 2006a, 2010).

VOUCHERS

Van Jaarsveld 17207, 19777 (NBG).

ILLUSTRATIONS AND MAP

Plate 169, Figures 169a–169d, Map 169.

170. *Plectranthus mzimvubuensis* Van Jaarsv., in Van Jaarsveld & Van Wyk in *Bothalia* 34: 30–32 (2004c).

Cremonphyte growth form: Pendent cluster (of medium weight to heavy, cliff squatter).

Growth form formula: E:F:As:S/H:Es (vb)

Etymology: After the Mzimvubu River where it was first collected. The Xhosa name *Mzimvubu* means ‘the home of the hippo’ (*Hippopotamus amphibius*), but the animals were wiped out in the area more than a century ago.

DESCRIPTION AND HABITAT

Perennial, aromatic shrub up to 1 m tall, 3 m in diameter, scandent, pendent from cliffs. Roots fibrous to slightly fleshy, bearing distinct oblong to rounded, grey tubers 25–50 × 14–20 mm. Stems herbaceous, semisucculent, 4-angled, terete in older branches and with a succulent basal caudex, 100 mm in diameter. Bark smooth, grey. Leaves broadly ovate-deltoid to subrotund, 25–50 × 28–50 mm; surface covered with slightly sunken translucent gland dots (becoming yellowish brown in dried specimens); margin serrate-dentate with 6–10 pairs of teeth; apex acuminate, with short drip-tip; base truncate to subcordate, occasionally slightly decurrent on petiole, thin-textured; petiole 10–20(–30 mm) long, reddish purple. Inflorescence a short terminal raceme (30–)70–90(–120) mm long, sometimes with a pair of side branches at base; rachis sparsely strigose, bearing scattered, sessile glands, yellowish brown. Flowers in sessile, 1–3-flowered cymes forming 2–6-flowered verticillasters, the latter 6–12(–18) mm apart. Calyx up to 4 mm long, accrescent, lengthening to 10–11 mm in fruit, 2-lipped. Corolla pink; tube straight, 9–10 mm long, laterally compressed, 3 mm deep, slightly deflexed forming a swollen saccate base, 2-lipped; upper lip 4-lobed, 8 mm high, becoming reflexed when stigma matures, upper lobes bent forward and forming an ascending-spreading 2-spurred hood; lower lip boat-shaped, 6 mm long, soon becoming reflexed. Style 14 mm long, extending up to 20 mm when mature, exposed for 8 mm. Nutlets rounded, 1.3–1.5 mm long, smooth, dark brown.

Phenology: Flowering in late autumn (April–June). Seeds with local non-specialist dispersal strategy.

Pollinators: Insects.

Habitat and aspect: Grows on shady south-facing shale cliffs, where the plants scramble among shrubs. The vegetation consists of Eastern Valley Bushveld (Mucina *et al.* 2005). The climate is subtropical, with hot summers and dry, sunny, frost-free winters, and cool evenings. The average daily maximum temperature is about 24°C and the average daily minimum about 14°C. Rainfall occurs mainly from spring to autumn, 1000–1250 mm per annum.

Altitude: 300–800 m.

Associated vegetation: Eastern Valley Bushveld (Mucina *et al.* 2005).

Associated cremnophytes: *Plectranthus mzimvubuensis* shares its habitat with other succulent plants such as *Adromischus cristatus* subsp. *mzimvubuensis*, *Bulbine natalensis*, *Crassula cordata*, *C. cultrata*, *C. multicava* subsp. *floribunda*, *C. orbicularis*, *Cyanotis speciosus*, *Delosperma tradescantioides* and *Peperomia blanda*. Trees and shrubs in the area include *Bauhinia bowkeri*, *Celtis africana*, *Ficus burkei* and *Euphorbia tirucalli*.

Geology: Beaufort shale, Emakwezeni Subgroup (Karoo Supergroup).

DISTRIBUTION

Plectranthus mzimvubuensis appears to be endemic to the Mzimvubu River in the Eastern Cape.

RELATED SPECIES

Plectranthus mzimvubuensis is distinguished by its scandent growth and short, parallel-sided corolla tube 10 mm long. It appears to be closest to *P. reflexus*, an erect shrub (non-cremnophyte) with a corolla tube of 25 mm long, constricted at the mouth. A further distinction of *P. mzimvubuensis* are the distinct root tubers. *Plectranthus reflexus* has fleshy roots.

ADAPTATIONS TO THE CLIFF ENVIRONMENT

Habit: Spreading, scandent to pendent nature, forming shrubs up to 2 m tall. Stems becoming drooping. During the dry season the leaves become purplish green. The succulent roots help to conserve water on the dry cliffs. The root tubers are potato-like and 60 mm in diameter, also aiding water conservation. Stems become terete and are longer lived and less herbaceous than in other *Plectranthus* species.

Size and weight: Shrubs 2–3 m high, heavy.

Leaves

Orientation: Ascending-spreading.

Colour: Green, without any obvious adaptation to drought stress.

Age and persistence: Evergreen, but leaves withering from the base. The semisucculent leaves become turgid after rain, but often in a semi-desiccated state during dry periods. The fact that the leaves are aromatic can perhaps be interpreted as a chemical defence mechanism against predation by phytophagous insects. Damaged plants re-sprout from the rootstock.

Armament: Plants unarmed.

Sexual reproduction

Inflorescence and flowers: Inflorescence ascending, short racemes. The conspicuous pink flowers attract insects in the bee family.

Fruit/Seed

Size: Seeds (nutlets) rounded, 1.3–1.5 mm in diameter.

Dispersal: Nutlets shaken from the fruiting calyx and locally dispersed.

Time: Nutlets ripening in late autumn, coinciding with the rainfall. Germination after about 21 days.

Vegetative reproduction: Absent.

CONSERVATION STATUS

Classified as rare (Raimondo *et al.* 2009). Localised and confined to gorges where it is not threatened owing to the inaccessible habitat.

ADDITIONAL NOTES

Horticulture: Best for subtropical coastal gardens, in dappled shade on embankments. Outside its habitat, it is best grown under controlled conditions in a greenhouse. Propagate from cuttings in spring or summer (Van Jaarsveld 2006a, 2010).

VOUCHER

Van Jaarsveld, Xaba & Harrower 92e (NBG).

ILLUSTRATIONS AND MAP

Plates 170 & 170a, Figures 170a–170d, Map 170.

171. *Plectranthus purpuratus* Harv. subsp. *purpuratus*, Harvey, Thesaurus capensis 1: 53, t. 83 (1859).

Cremonophyte growth form: Compact, mat-forming leaf succulent (of light weight, cliff hugger).

Growth form formula: E:F:As:S/H:Es (vb)

Etymology: The epithet *purpuratus* refers to the dark purplish green leaves.

DESCRIPTION AND HABITAT

Erect to decumbent, spreading, succulent herbs. Stems 30–100 mm long. Leaves often densely packed or imbricate in an almost pseudostem, ovate to broadly ovate, 15–35 × 15–35 mm, succulent, purplish below, densely to sparsely strigose; glands red; margin shallowly crenate; apex rounded or acute; base truncate to cuneate. Inflorescence terminal, racemose, 30–120 mm long, often with a pair of side branches; verticillasters up to 8-flowered. Calyx 3

mm long, enlarging to 5–6 mm after flowering. Corolla 10–11 mm long, white to bluish; tube saccate at base, constricted near middle. Nutlets 1 mm long, light to dark brown.

Phenology: Flowering from spring to autumn but with a peak in autumn (March–April). Seeds with local non-specialist dispersal strategy, dispersed in autumn.

Habitat and aspect: Plants occur mainly on upper south-facing cliffs. The climate is subtropical, with hot summers and dry, sunny, frost-free winters, and cool evenings. The average daily maximum temperature is 25–26°C and the average daily minimum 8–16°C. Rainfall occurs mainly from spring to autumn, ranging from 1000–1250 mm per annum.

Altitude: 460–795 m.

Associated vegetation: Eastern Valley Bushveld (Mucina *et al.* 2005).

Associated cremnophytes: *Aeollanthus parvifolius*, *Aloe arborescens*, *Bulbine natalensis*, *Crassula pellucida* subsp. *brachypetala*, *C. perforata*, *Cyanotis speciosus*, *Scilla natalensis*, *Stenoglottis woodii* and *Tridactyle bicaudata*.

Geology: Quartzitic sandstone of the Natal Group (Cape Supergroup).

DISTRIBUTION

Plectranthus purpuratus subsp. *purpuratus* is endemic to the Pietermaritzburg-Durban region of KwaZulu-Natal, confined to south-facing cliffs (river valleys and mountainous terrain).

RELATED SPECIES

Plectranthus purpuratus subsp. *purpuratus* is immediately distinguished from its two non-cremnophilous relatives (*P. purpuratus* subsp. *montanus* and *P. purpuratus* subsp. *tongaensis*) by its compact growth, with decumbent stems and subimbricate leaves. It is related to *P. strigosus* but distinguished by the corolla tube which is constricted in the centre. The leaves of *P. strigosus* are usually rusty strigose and the corolla tube is constricted at the throat.

ADAPTATIONS TO THE CLIFF ENVIRONMENT

Habit: Plants are compact, the leaves subimbricate, very succulent and purplish green, an adaptation the dry vertical habitat. A purplish pigment (anthocyanins) is produced during dry periods, blocking out excessive light.

Size and weight: Dwarf-sized, of light weight.

Leaves

Orientation: Ascending-spreading, subimbricate, can adjust according to the light source and moisture regime.

Colour: Purplish green, an adaptation to dry conditions.

Age and persistence: Evergreen, but leaves withering from the base. The very succulent leaves become turgid after rain, but are often in a semi-desiccated state during dry periods. The fact that the leaves are aromatic suggests a chemical defence mechanism against predation by phytophagous insects.

Armament: Plants unarmed.

Sexual reproduction

Inflorescence and flowers: Inflorescence ascending, consisting of short racemes. The conspicuous white flowers attract insects of the bee family.

Fruit/Seed

Size: Seed (nutlet) rounded, 1 mm in diameter,.

Dispersal: Dark brown nutlets shaken from the fruiting calyx and locally dispersed.

Time: Nutlets ripening in late autumn, coinciding with the rainfall. Germination after about 21 days.

Vegetative reproduction: The spreading, mat-forming branches root where they touch the soil, establishing new populations. This is an efficient vegetative backup strategy enabling the plants to survive under the harsh, xeric cliff-face conditions.

CONSERVATION STATUS

Localised and confined to south-facing cliffs and river gorges where it is not threatened owing to the inaccessible habitat.

ADDITIONAL NOTES

Horticulture: *Plectranthus purpuratus* subsp. *purpuratus* is easy to grow. Best for subtropical coastal gardens, grown in rockeries or as a pot plant in light shade. Outside its native habitat, it is best grown under controlled conditions in a greenhouse. Propagate from stem cuttings (Van Jaarsveld 2006a, 2010).

VOUCHER

Van Jaarsveld 17042 (NBG).

ILLUSTRATIONS AND MAP

Figures 171a–171e, Map 171.

172. *Plectranthus saccatus* Benth. subsp. *pondoensis* Van Jaarsv. & Milstein, in Van Jaarsveld & Edwards in *Bothalia* 27,1: 4 (1997).

Cremonophyte growth form: Pendent shrub (heavy, cliff hanger).

Growth form formula: E:F:P:Els (vb)

Etymology: After Pondoland in the Eastern Cape, its habitat.

DESCRIPTION AND HABITAT

Trailing glutinous succulent herb, becoming pendent on ledges, aromatic, much-branched, succulent shrub with spreading to pendent branches up to 2 m long. Stems obscurely 4-angled; young stems 2–5 mm in diameter, purplish, minutely glandular pubescent, becoming glabrous; older stems striate; internodes 6–40 mm long. Leaves ovate to broadly trullate, minutely glandular pubescent, 12–27 × 10–28 mm; petiole 5–25 mm long. Racemes secund, 30–50 mm long. Calyx 3–6 mm long, enlarging to 8 mm in fruit; upper lip ascending, ovate, 1 mm long; lower lobes 4, linear-lanceolate, 1 mm long. Corolla saccate; tube 6–20 × 3–7 mm; upper lip 2-lobed, 9–13 × 7–12 mm, erect, lobes folded back; lower lip 8 mm long, horizontal or slightly drooping, blue to pale mauve-pink, inner surface speckled with purple. Stamens 14 mm long, declinate in lower lip, free for 8 mm; anthers purple, bent upwards. Style 11–12 mm long. Nutlets 2 mm long, dark brown.

Phenology: Flowering from spring to autumn but with a peak in autumn (March–April).

Pollinators: Insects.

Habitat and aspect: Mainly south-facing quartzitic sandstone cliffs. Plants are rooted in crevices and on rock ledges. Winters are cool but frost is a rarity or absent. The average daily maximum temperature is 24°C and the average daily minimum 16°C. Rainfall occurs from spring to autumn but occasionally also in winter, ranging from 1000–1250 mm per annum.

Altitude: 300–600 m.

Associated vegetation: Pondoland-Ugu Sandstone Coastal Sourveld of the Indian Ocean Coastal Belt Biome (Mucina *et al.* 2005).

Associated cremnoophytes: *Aloe arborescens*, *Aptenia cordifolia*, *Cotyledon orbiculata* var. *oblonga*, *Crassula flanaganii*, *C. multicava*, *C. perfoliata* var. *perfoliata*, *Delosperma repens*, *D. tradescantioides*, *Gasteria croucheri*, *Petopentia natalensis*, *Portulacaria afra*, *Rhipsalis baccifera* and *Sarcostemma viminale*.

Geology: Quartzitic sandstone of the Natal Group (Cape Supergroup).

DISTRIBUTION

Plectranthus saccatus subsp. *pondoensis* is endemic to the sandstone gorges between the Msikaba River (Eastern Cape) and Oribi Gorge (southern KwaZulu-Natal) in the north.

RELATED SPECIES

Plectranthus saccatus subsp. *pondoensis* is distinguished from the typical subspecies by its distinctly succulent leaves and decumbent to procumbent pendent habit, with flexible (flaccid) stems up to 4 m long. The secondary growth of the species is anomalous, with many broad

collenchymatous rays which impart flexibility (Van Jaarsveld & Edwards 1997). The two subspecies maintain their vegetative characters under uniform cultivation.

ADAPTATIONS TO THE CLIFF ENVIRONMENT

Habit: Its succulent nature and long, flexible stems suggest an adaptation to the cliff-face environment, ensuring long-term survival in the sheer habitat. During the dry season the leaves become purplish green to purplish. The succulent nature, compared to that of the forest non-cremnohyte (subsp. *saccatus*), can be seen as a adaptation to the cliff environment.

Size and weight: Shrubs of medium weight to heavy.

Leaves

Orientation: Small, spreading, maximising absorption of light.

Colour: Green, turning purplish under drought stress, a character that can be related to the vertical cliff habitat. This change of colour reduces penetration of light, thus also reducing photosynthesis, and is typical of succulent plants.

Age and persistence: Plants evergreen, but with leaves withering from the base. The fleshy leaves become turgid after rain, but are often in a semi-desiccated state during dry periods. The fact that the leaves are strongly aromatic can perhaps be interpreted as a chemical defence strategy against predation by phytophagous insects.

Armament and camouflage: The plants are mechanically unarmed and the conspicuous succulent leaves and stems are vulnerable to larger herbivores.

Sexual reproduction

Inflorescence and flowers: Inflorescence ascending, short racemes. The conspicuous mauve-pinkish flowers attract insects.

Fruit/Seed

Size: Seed (nutlet) rounded, 2 mm in diameter.

Dispersal: Nutlets shaken from the fruiting calyx and locally dispersed.

Time: Nutlets ripening in summer and autumn, coinciding with the rainfall. Germination after about 21 days.

Vegetative reproduction: The spreading, mat-forming branches root where they touch the soil, establishing new populations. This is an efficient vegetative backup strategy for surviving the harsh, xeric cliff-face conditions.

CONSERVATION STATUS

Localised and confined to gorges where it is not threatened owing to the inaccessible habitat.

ADDITIONAL NOTES

Horticulture: Best for subtropical coastal gardens, grown on steep embankments, balconies, gabions and rockeries in partial shade. Can be used as an effective groundcover on slopes, preventing soil erosion. Outside its native habitat, it is best grown under controlled conditions in a greenhouse. Propagate from stem cuttings (Van Jaarsveld 2006a, 2010).

VOUCHER

Van Jaarsveld 2201 (NBG).

ILLUSTRATIONS AND MAP

Plate 172, Figures 172a & 172b, Map 172.

TETRADENIA Benth.

173. *Tetradenia kaokoensis* Van Jaarsv., in Van Jaarsveld & Van Wyk in *Bothalia* 33,1: 107 (2003c).

Cremonophyte growth form: Erect shrublet (of medium weight, cliff squatter).

Growth form formula: E:F:As:W:D (r)

Etymology: After Kaokoveld, its native habitat in northwestern Namibia.

DESCRIPTION AND HABITAT

Erect, semisucculent, deciduous shrub up to 600 mm tall. Roots succulent, up to 10 mm in diameter, tapering. Stem terete, 12–20 mm in diameter, succulent, brittle, grey-brown, sparsely longitudinally fissured; young branches densely velvety tomentose, white-green. Leaves crowded, shortly petiolate (base persistent, 2–4 mm long becoming woody with a characteristic cordate abscission scar); blade ovate-lanceolate, ovate to ovate-triangular, 65–140 × 45–115 mm, densely white tomentose on abaxial surface, less so on upper surface; margin crenate-dentate (± 20 pairs of teeth); apex acute to rounded; base cordate; petiole 10–20 mm long, with basal subpetiolar purplish glands (swelling). Inflorescence in lateral or terminal, oblong to pyramidal panicles up to 200 mm long and 120 mm in diameter, appearing with leaves; bracts ovate to triangular, 6–9 mm long, with petiole 1.5–2 mm long; male flower spikes dense, 20–25 mm long; floral bracts broadly triangular-ovate, 0.5 × 1.5 mm, translucent. Flowers in 3-flowered cymes, forming 6-flowered verticillasters. Calyx 1 mm long, 5-lobed, densely hairy; lobes ovate, 0.7–0.5 × 0.3 mm. Corolla white, bilobed, 5-lipped, 3–4 mm in diameter when open, 3 mm long, glabrous on inside, tomentose on outside; lower lip oblong-oval, 1.5 × 0.7 mm, upper lobes ovate, 1 × 0.7 mm. Stamens 5.3 mm long, translucent. Ovary oblong-ovate; disc 2-lobed, bright red, lobes exceeding ovary; stigma 1 mm long, bifid, purplish. Female flowers: gynoecium 2.3 mm long; stigma bifid, 0.8 mm long. Male flowers: anthers white. Seed 0.7–0.8 mm long, oblong-ovoid, brown.

Phenology: Flowering mainly from November–February. Flowers sweetly scented. Seeds wind-dispersed, in summer and autumn.

Pollinators: Insects.

Habitat and aspect: Dolomite, sandstone and granite cliffs, the plants growing mainly on southern aspects (also eastern). Plants are firmly rooted in crevices and size often depends on the growing space allowed by the crevice. Temperature high in summer (up to about 40°C). Winters are cooler and frost is absent. Rainfall is about 200–250 mm per annum and occurs in summer, with a peak in February.

Altitude: 1600–2000 m.

Associated vegetation: Arid savanna.

Associated cremnoophytes: At Otjihipa it has been recorded with the following cliff dwellers: *Aeollanthus haumannii*, *Kalanchoe laciniata*, *Pelargonium vanderwaltii* and *Plectranthus hereroensis*.

Geology: Dolomite (Otavi Group), dark-coloured and rough-textured, also sandstone (Omavanda) and granite (Otihipa).

DISTRIBUTION

Mainly Baynes and Otjihipa Mountains in the Kaokoveld (northwestern Namibia) as well as Iona Peak in Angola.

RELATED SPECIES

Tetradenia kaokoensis is related to the widespread *T. riparia*, which is highly aromatic, has glandular hairs, flowers from late autumn to midwinter, lacks the conspicuous dense white vestiture and the leaves are deciduous at the time of flowering. *Tetradenia kaokoensis* is a smaller, robust species with succulent roots, thick branches, larger leaves and it flowers in summer. The persistent, raised, woody leaf bases (phyllodia) are unique in the genus. *Tetradenia* is endemic to Africa and Madagascar and contains eight species (five in Africa, three in Madagascar).

ADAPTATIONS TO THE CLIFF ENVIRONMENT

Habit: Long-lived, erect, compact, sturdy, deciduous shrublets.

Size and weight: Shrubs of medium weight to heavy.

Roots: Fleshy, tapering roots suggest an adaptation to the xeric conditions found on the vertical cliffs.

Stem: Branches terete, succulent; young branches grey-white (indumentums) and can be viewed as an adaptation to the xeric cliff-face conditions.

Leaves

Orientation: Ascending-spreading, making the most of the available light in the shady kloof environment.

Colour and texture: Green, soft and fleshy, covered with a dense indumentum, an adaptation to the hot, dry environment. Leaves with flexibility in size (phenotypic plasticity) and can adapt to the availability of light (larger leaves in shade, smaller in exposed areas).

Age and persistence: Becoming deciduous during the dry winter.

Armament: Lacking the very strong aroma of the related *Tetradenia riparia*, suggesting a reduction in chemical defence. The sharp, woody petiole scars perhaps a mechanical defence against predators such as the chacma baboon (*Papio ursinus*) and Kaokoveld rock dassie (*Procavia capensis welwitschii*).

Sexual reproduction

Inflorescence and flowers: Flowering during the rainy season when in leaf (November to February). Dense, conspicuous, white-flowered, lateral or terminal, oblong to pyramidal panicles. The species is dioecious, with male and female flowers on separate plants.

Fruit/Seed

Size: Nutlets of two types: normal type more common, larger, 0.7 mm long, oblong-ovoid; smaller type 0.5 mm long, oblong, longitudinally ridged with 4–7 dark brown ridges.

Dispersal: Mainly by wind. The function of the two types of seed not clearly understood. The smaller type is perhaps more aerodynamic, enabling long-distance dispersal.

Time: Mainly autumn (during the rainy season).

Vegetative reproduction: Absent.

CONSERVATION STATUS

A local endemic, not threatened.

ADDITIONAL NOTES

Horticulture: For dry bushveld (savanna) gardens, in full sun or dappled shade on embankments. Grow under controlled greenhouse conditions outside the habitat. Propagate from stem cuttings in summer. Its very easy growing nature maximises survival rate (Van Jaarsveld 2010).

VOUCHER

Van Jaarsveld 16617 (NBG).

ILLUSTRATIONS AND MAP

Figures 173a–173c, Map 173.



MESEMBRYANTHEMACAEAE

Carruanthus (Schwantes) Schwantes

174. *C. peersii* L.Bolus

Conophytum N.E.Br.

175. *C. auriflorum* Tischer subsp. *turbiniforme* (Rawe) S.A.Hammer
176. *C. bolusiae* Schwantes subsp. *bolusiae*
177. *C. carpianum* L.Bolus
178. *C. danielii* Pavelka
179. *C. ernstii* S.A.Hammer subsp. *ernstii*
180. *C. francoiseae* (S.A.Hammer) S.A.Hammer
181. *C. fulleri* L.Bolus (Pella form)
182. *C. hanae* Pavelka
183. *C. luckhoffii* Lavis
184. *C. marginatum* Lavis subsp. *haramoepense* (L.Bolus) S.A.Hammer
185. *C. marginatum* Lavis subsp. *littlewoodii* (L.Bolus) S.A.Hammer
186. *C. obscurum* N.E.Br. subsp. *sponsaliorum* (S.A.Hammer) S.A.Hammer
187. *C. quaesitum* (N.E.Br.) N.E.Br. subsp. *densipunctum* (L.Bolus) S.A.Hammer
188. *C. quaesitum* (N.E.Br.) N.E.Br. subsp. *quaesitum* var. *rostratum* (Tischer) S.A.Hammer
189. *C. ricardianum* Loesch & Tischer subsp. *ricardianum*
190. *C. stephanii* Schwantes subsp. *stephanii*
191. *C. tantillum* N.E.Br. subsp. *amicorum* S.A.Hammer & Barnhill
192. *C. taylorianum* (Dinter & Schwantes) N.E.Br. subsp. *ernianum* (Loesch & Tischer) de Boer ex S.A.Hammer
193. *C. taylorianum* subsp. *rosynense* S.A.Hammer

Delosperma N.E.Br. emend Lavis

194. *Delosperma* sp. A
195. *Delosperma* sp. B
196. *D. esterhuyseniae* L.Bolus
197. *D. knox-daviesii* Lavis
198. *D. laxipetalum* L.Bolus
199. *D. nubigenum* (Schltr.) L.Bolus
200. *D. saxicola* Lavis
201. *D. subpetiolatum* L.Bolus
202. *D. tradescantioides* (A.Berger). L.Bolus
203. *D. velutinum* L.Bolus
204. *D. waterbergense* L.Bolus
205. *D. zoutpansbergense* L.Bolus

Drosanthemum Schwantes

206. *D. anemophilum* Van Jaarsv. & S.A.Hammer
207. *D. expersum* (N.E.Br.) Schwantes
208. *D. inornatum* (L.Bolus) L.Bolus

Erepsia N.E.Br.

209. *E. heteropetala* (Haw.) Schwantes

Esterhuysenia L.Bolus

210. *E. stokoei* (L.Bolus) H.E.K.Hartmann

Jensenobotrya A.G.J.Herre

211. *J. lossowiana* A.G.J.Herre

Lampranthus N.E.Br.

212. *L. affinis* L.Bolus

Machairophyllum Schwantes

213. *M. brevifolium* L.Bolus

Oscularia Schwantes

214. *O. cremnophila* Van Jaarsv., Desmet & A.E.van Wyk

Ruschia Schwantes

215. *R. knysnana* (L.Bolus) L.Bolus

216. *R. promontorii* L.Bolus

Scopelogenia L.Bolus

217. *S. bruynsii* Klak

218. *S. verruculata* (L.) L.Bolus

CARRUANTHUS (Schwantes) Schwantes

174. *Carruanthus peersii* L.Bolus, Notes on Mesembryanthemum and allied genera 3: 4 (1936).

Cremonophyte growth form: Pendent clusters (of medium weight, cliff hugger).

Growth form formula: E:F:P:Els (vb) (r)

Etymology: After its collector, V.S. Peers (1874–1940), Australian collector of plants who settled in South Africa, just after the Anglo-Boer War (Gunn & Codd 1981).

DESCRIPTION AND HABITAT

Plants with heads dividing and forming small, dense, mat-like clusters up to 300 mm in diameter, becoming pendent, with stems up to 500 mm long, with about 10–25 heads, each head with 6–8 functional green leaves withering and becoming deciduous basally. Roots fibrous. Branches up to 5 mm in diameter, greyish brown, with remnants of old dried leaf bases; older branches up to 10 mm in diameter. Leaves crowded or with short internodes up to 10 mm long, decussate and slightly connate at base, oblong trigonous-clavate (linear-oblongate viewed from the top), 30–60 × 15 mm (lateral compression at apex 10 mm in diameter), somewhat dorsiventrally compressed, keeled below; surface grey-green, smooth, becoming wrinkled and purplish green during drought; apex obtuse to acute, somewhat laterally compressed. Flowers in dichotomous cymes, only opening in late afternoon, pedicellate, yellow, 25–50 mm in diameter; axillary flower often suppressed in autumn;

pedicels terete, 2 mm in diameter, thickened to 4 mm (10–)20–30(–42) mm long, with 1 or 2 pairs of small leaf sheaths; bracts trigonous, 5–6 mm long, keel decurrent on pedicel. Petals numerous in 2 series, linear-lanceolate, 10–22 × 1–1.5 mm, radiate and incurved. Stamens erect, 7–9 mm long, white at base, numerous and crowded at first in a column. Ovary inferior, with raised, ridged, conical centre up to 2 mm high, glands 5, linear, 1.3 × 0.5 mm, separate, greenish yellow; stigmas 5 mm long, filiform, apices becoming coiled outward. Fruiting capsule 10 × 10 mm, opening hygrochastically, bowl-shaped, covering membranes rudimentary (0.5 mm ledge) and almost absent. Seed oval, 0.5 × 0.9 mm, light brown.

Phenology: Main flowering season in spring (August–October) and can be flowering sporadically throughout the year.

Pollinators: Insects (generalist).

Habitat and aspect: Plants are confined to east- and west-facing cliffs, growing in crevices and on ledges of the lower and upper slopes, in ample soil. The climate is hot and dry, with rainfall in summer and winter. The average daily maximum temperature is about 25°C and average daily minimum about 10°C, with frost absent from the habitat. Rainfall occurs in winter and summer (cyclonic cold fronts and thunder showers), 200–300 mm per annum.

Altitude: 800–1200 m.

Associated vegetation: Gamka Thicket of the Albany Thicket Biome (Mucina *et al.* 2005).

Associated cremnophytes: Other cremnophytes observed at Toorwaterspoort include *Adromischus subdistichus*, *Albuca tortuosa*, *Bulbine* sp., *Cotyledon woodii*, *Crassula capitella* subsp. *thyrsiflora*, *C. cotyledonis*, *C. muscosa* var. *muscosa*, *C. pellucida* subsp. *marginalis*, *C. perfoliata* var. *minor*, *C. pubescens* var. *radicans*, *C. rupestris*, *C. velutina*, *Cyrtanthus montanus*, *Drimia uniflora*, *Haemanthus albiflos*, *Haworthia decipiens* var. *decipiens*, *H. viscosa*, *Lampranthus affinis* and *Senecio talinoides*.

Geology: Witteberg Quartz (Cape Supergroup).

DISTRIBUTION

Toorwaterspoort (between the Slypsteenbergrivier to the west and Groot Swartberg to the east, Eastern Cape).

RELATED SPECIES

Related to *Carruanthus ringens* and *Bijlia tugwelliae*. *Carruanthus peersii* is immediately distinguished from *C. ringens* by its toothless (or almost toothless), oblong, trigonous-clavate leaves and pendent, mat-forming clusters. It is confined to conglomerate and quartz (quartzitic sandstone) and grows on level or hilly terrain, the leaves with numerous pairs of teeth and clustered growth.

ADAPTATIONS TO THE CLIFF ENVIRONMENT

Habit: Conspicuous pendent clusters up to 300 mm in diameter and up to 500 mm long.

Size and weight: Clusters medium-sized.

Stem: Up to 500 mm long.

Leaves

Orientation: Ascending-spreading. The leaves have no teeth, suggesting a moisture strategy that differs from that of other species of *Carruanthus*. In the related *C. ringens*, the leaves have teeth, possibly a ‘dew trap’ or ‘fog trap’ on flat areas. Leaf margins in *C. peersii* are smooth (or with only faint remnants of teeth), suggesting a different strategy and the subsequent loss of teeth.

Colour: Glaucous, green to dirty green, plants becoming purplish green (production of anthocyanins) during drought, thus reducing penetration of light from the sun.

Age and persistence: Plants slow-growing, long-lived perennials.

Armament and camouflage: Plants without armament or camouflage properties.

Sexual reproduction

Flowers: Melittophilous (Hartmann 1991).

Fruit/Seed

Size: Seed 0.5×0.75 mm, light brown, ovoid, the small seeds easily becoming wedged in crevices, ideal for establishment of seedlings.

Dispersal: Hydrochory (ombrohydrochory). Hygrochastic capsules opening with rain but seeds dispersed by ‘wash-out dispersal’ (Hartmann 1988). The capsules have no covering membranes. Rain fills the bowl-like cavity of the capsule and the seeds are washed or splashed out. This dispersal strategy would ensure local dispersal on the cliff, the seeds becoming wedged in crevices, ideal for establishment.

Time: Seeds released in autumn and winter, coinciding with autumn or winter rains, thus during the cool season, maximising establishment.

Vegetative reproduction: Plants increase vegetatively, forming small, dense mats or clusters, with active vegetative growth and rooting where they come into contact with soil, an efficient vegetative dispersal backup and adaptation to the cliff face.

CONSERVATION STATUS

Little-known species, not threatened owing to the remote, safe habitat.

ADDITIONAL NOTES

Horticulture: Best for thicket and succulent karoo gardens, grown on rockeries, embankments or containers. Very easily cultivated. Propagate from cuttings, division or seed. Grow in full sun or light shade. Water sparingly in winter and summer.

VOUCHER

Van Jaarsveld 17412 (NBG).

ILLUSTRATIONS AND MAP

Plate 174, Figures 174a–174c, Map 174.

CONOPHYTUM N.E.Br.

175. *Conophytum auriflorum* Tischer subsp. *turbiniforme* (Rawe) S.A.Hammer in *Cactus and Succulent Journal* (U.S.) 52: 231 (1993).

Cremonophyte growth form: Clustered, mat-forming growth (of light weight, cliff hugger).

Growth form formula: A:S:Lar:Lf (vb) (r)

Etymology: The specific epithet *auriflorum* pertains to the yellow flowers.

DESCRIPTION AND HABITAT

Plants forming compact, mat-like, globose clusters. Roots fibrous. Leaves fused into turbiniform, obconical bodies, each body 10–18 × 38 × 3–8 mm, truncate or convex; epidermis glabrous, pale whitish green to reddish green, spotted, translucent at fissure; fissure 1–3 mm long; summer sheath white to pale brown. Flowers yellow, up to 20 mm in diameter. Petals numerous, in 2 or 3 series, spatulate, 8–10 × 2 mm. Fruiting capsule very fragile, 4-locular, 3 × 4 mm, opening hygrochastically. Seed 0.55–0.70 × 0.45–0.55 × 0.25–30 mm, tuberculate, dark brown. (Description based on Hammer 1993, 2002.)

Phenology: Flowering in autumn. Flowers diurnal, scentless, conspicuous, in profusion.

Pollinators: Insects.

Habitat and aspect: Confined to cliffs of the western escarpment margin, growing in crevices, fissures and on ledges, on various aspects, but more in sheltered, shady spots. This region is subject to occasional fog. The average daily maximum temperature is about 19°C and average daily minimum about 10°C, with frost absent from the habitat. Rainfall mainly in winter (cyclonic cold fronts), 100–200 mm per annum.

Altitude: 540–860 m.

Associated vegetation: Namaqualand Klipkoppe Shrubland of the Succulent Karoo (Mucina *et al.* 2005).

Associated cremonophytes: Associated cremonophytes include *Adromischus* sp. and *Ficus ilicina*.

Geology: Quartz of the Bushmanland Group, Khurisberg Subgroup.

DISTRIBUTION

Confined to the escarpment mountains in the Spektakel Pass region, southwest of Springbok (Northern Cape).

RELATED SPECIES

Distinguished from related species by its small turbiniform bodies, translucent fissure and yellow flowers.

ADAPTATIONS TO THE CLIFF ENVIRONMENT

Habit: Inconspicuous globose to mat-forming clusters in fissures along ledges and crevices.

Size and weight: Clusters small (of light weight).

Stem: Short to medium length, branched and usually unexposed.

Leaves

Orientation: Fused into obconical to turbinate bodies, truncate, with a smooth epidermis and translucent fissure, maximising exposure to light.

Colour: Green to reddish green.

Age and persistence: Plants slow-growing, long-lived perennials, becoming dormant in spring, remaining older leaves recycled and forming a protective sheath for successive newly formed leaves.

Armament and camouflage: Plants without conspicuous armament or camouflage properties.

Sexual reproduction

Flowers: Yellow, up to 20 mm in diameter, diurnal. The rich flowering and floriferous nature can be seen as an adaptation to the cliff environment, maximising visibility.

Fruit/Seed

Size: Seed $0.55\text{--}0.70 \times 0.45\text{--}0.55 \times 0.25\text{--}30$ mm.

Dispersal: Hydrochory as in other *Conophytum* species. Tuberculate surface of seed ideal for establishment in crevices.

Time: Hygrochastic capsules releasing seeds only during the rainy season, maximising establishment.

Vegetative reproduction: Plants increase vegetatively, forming small, dense mats or clusters, with active vegetative growth and rooting where they come into contact with soil, an efficient vegetative dispersal backup and adaptation to the cliff face.

CONSERVATION STATUS

Classified as rare (Raimondo *et al.* 2009). However, not threatened owing to the cliff habitat.

ADDITIONAL NOTES

Horticulture: Best for greenhouses, grown under controlled conditions. Propagated from seed or by division (Hammer 1993). Resting in summer, active in winter. Grow in partial shade, in small containers, in a sandy, well-drained mixture. Plants grow rapidly, forming dense clusters.

VOUCHER

Van Jaarsveld 21125 (NBG).

ILLUSTRATIONS AND MAP

Figures 175a & 175b, Map 175.

176. *Conophytum bolusiae* Schwantes subsp. *bolusiae*, Schwantes in Die Gartenwelt 33: 25 (1929).

Cremnophyte growth form: Clustered, mat-forming growth (of light to medium weight, cliff hugger).

Growth form formula: A:S:Lar:Lf (vb) (r)

Etymology: After Louisa Bolus (1877–1970) of the University of Cape Town, well-known authority on mesembs.

DESCRIPTION AND HABITAT

Plants forming globose to mat-like clusters of 10 to 200, sometimes with long trailing stems and forming groups of up to 600 mm in diameter. Roots fibrous. Leaves fused into turbiniform obconical bodies, each body 10–25 × 8–12 × 8–12 mm, truncate at top to slightly convex; epidermis densely papillate, glaucous; summer sheath white to yellowish white. Flowers magenta, up to 25 mm in diameter. Petals numerous, in 2 or 3 series, up to 10 × 2 mm. Fruiting capsule 4–6-locular, 2 × 4 mm, opening hygrochastically, very fragile. Seed 0.7 × 0.55 × 0.45 mm, densely tuberculate. (Description based on Hammer 2002.)

Phenology: Flowering in spring or early summer. Flowers diurnal, scentless, conspicuous, in profusion.

Pollinators: Insects.

Habitat and aspect: Plants are confined to sheer east-facing shady cliffs, growing in crevices and on ledges of the upper slopes in ample soil, on southern aspects in the fog belt. Summers are hot and dry but plants are ‘misted’ by regular fog from the Atlantic Ocean (some 30 km from the coast). Average daily maximum temperature is about 19°C and average daily minimum about 10°C, with frost absent from the habitat. Rainfall occurs mainly in winter (cyclonic cold fronts), 50–100 mm per annum.

Altitude: 500–750 m.

Associated vegetation: Vyftienmyl se Berge Succulent Shrubland of the Succulent Karoo Biome (Mucina *et al.* 2005).

Associated cremnophytes: Other cremnophytes observed at Vyftienmyl se Berge include *Bulbine vitrea*, *Adromischus montium-klinghardtii*, *Conophytum stephanii*, *Crassula muscosa* var. *muscosa*, *C. velutina*, *Haworthia arachnoidea*, *Kleinia cephalophora*, *Tylecodon bodleyae*, *T. buchholzianus*, *T. rubrovenosus* and *T. similis*.

Geology: Rough quartz of the De Hoop Subgroup (Gariiep Supergroup).

DISTRIBUTION

Confined to the Vyftienmyl se Berge (Oograbies Mountains).

RELATED SPECIES

Distinguished from related level-ground *Conophytum* species by its large, conspicuous, globose clusters. Related species from non-cliff habitats usually smaller and less conspicuous (camouflage), often with a sunken growth.

ADAPTATIONS TO THE CLIFF ENVIRONMENT

Habit: Conspicuous globose to mat-forming clusters up to 600 mm in diameter, rooting along ledges and crevices.

Size and weight: Clusters of medium weight.

Stem: Short to medium length, branched and usually unexposed.

Leaves

Orientation: Fused into obconical to turbinate bodies, truncate at the top to slightly convex, with a white to yellowish white summer sheath.

Colour and texture: Green to glaucous green. Densely papillate epidermis, an adaptation trapping fog, often associated with fog belt mesembs such as *Conophytum stephanii*.

Age and persistence: Plants slow-growing, long-lived perennials, becoming dormant in spring, remaining older leaves recycled and forming a protective sheath for successive newly formed leaves.

Armament and camouflage: Plants without conspicuous armament or camouflage properties.

Sexual reproduction

Flowers: Conspicuous, magenta, up to 25 mm in diameter (same diameter as leaf body), opening towards late afternoon; petals numerous in 2 or 3 series, up to 8–10 mm long, when in flower bodies hardly visible. The rich flowering and floriferous nature can be seen as an adaptation to the cliff environment, maximising visibility.

Fruit/Seed

Size: Seed $0.7 \times 0.55 \times 0.45$ mm, densely tuberculate.

Dispersal: Hydrochory. Hydrochastic capsules, 2×4 mm, opening with rain but seeds dispersed by ‘wash-out dispersal’ (Hartmann 1988), indicating local dispersal. Remaining on the cliff is vital to survival. The capsules have broad rectangular valve wings, no covering membranes. Rain fills the saucer-like cavity of the capsule and the seeds are washed out and down the cliffs, succumbing to gravity until they become wedged in a crevice. The large, tuberculate seeds indicate adaptation to the cliff habitat and this method of dispersal, providing good anchorage for seedlings in the quartz crevices (compared to other *Conophytum* species). *Conophytum bachelorum*, a non-cremnohyte of section *Wettsteinia* with solitary bodies (well-camouflaged) and smaller dark pink flowers, has finely tuberculate seeds. Most other facultative cremnohytes have finely tuberculate seed.

Time: Hydrochastic capsules releasing seeds only during the rainy season, maximising establishment.

Vegetative reproduction: Plants increase vegetatively, forming small, dense mats or clusters, with active vegetative growth and rooting where they come into contact with soil, an efficient vegetative dispersal backup and adaptation to the cliff face.

CONSERVATION STATUS

Although classified as rare (Raimondo *et al.* 2009), it is not threatened owing to the cliff habitat.

ADDITIONAL NOTES

Horticulture: Very easily cultivated compared to other level-ground species, its adaptability in cultivation and growth vigour viewed as maximising survival. Hammer (1993) reports clusters becoming so large that they fall to the ground. Easily propagated from seed or by division (Hammer 1993). Resting in summer, active in winter. Best grown in partial shade, in small containers. Dividing annually and rapidly forming dense clusters.

VOUCHERS

Hall 23032, Van Jaarsveld 23062 (NBG).

ILLUSTRATIONS AND MAP

Figures 176a–176d, Map 176.

177. *Conophytum carpianum* L.Bolus, Notes on Mesembryanthemum and allied genera 3: 264–265 (1954).

Cremnophyte growth form: Clustered, mat-forming growth (of light to medium weight, cliff hugger).

Growth form formula: A:S:Lar:Lf (vb) (r)

Etymology: After Bernard Carp of Cape Town, lover of succulent plants who sponsored many of Harry Hall's expeditions.

DESCRIPTION AND HABITAT

Plants forming dense cushions of many bodies. Roots fibrous. Leaves fused into subcylindrical bodies, each body 6–15 × 4–8 × 3–4 mm, leaf tips free, keeled; epidermis minutely papillate (velvety surface), greyish green; fissure, spotted, gaping; sheath greyish brown to whitish. Flowers white. Petals in 2 series, 2–6 × 1 mm. Fruiting capsule 4-locular, 2 × 2 mm. Seed 0.85 × 0.55 × 0.40 mm, tuberculate. (Description based on Hammer 2002.)

Phenology: Flowering in autumn. Flowers nocturnally scented.

Pollinators: Night-flying insects.

Habitat and aspect: Confined to exposed granite domes, among lichens. Plants are subject to regular fog from the Atlantic Ocean. The average daily maximum temperature is about 25°C and average daily minimum about 10°C. Rainfall mainly in winter (cyclonic cold fronts), 50–100 mm per annum.

Altitude: 900–1160 m.

Associated vegetation: Goarieb Mountain Shrubland of the Succulent Karoo Biome (Mucina *et al.* 2005).

Associated cremnophytes: *Crassula garibina* and *C. macowanii*.

Geology: Granite of the Kuboos-Bremen Suite (Kuboos Pluton Subgroup, Gariiep Supergroup).

DISTRIBUTION

Confined to the upper slopes of the Ploegberg near Kuboes (Richtersveld, Northern Cape).

RELATED SPECIES

Related to *Conophytum quaesitum* and *C. hians*.

ADAPTATIONS TO THE CLIFF ENVIRONMENT

Habit: Globose clusters rooting in narrow crevices among lichens and moss.

Size and weight: Clusters small to medium weight.

Stem: Short, branched and unexposed.

Leaves

Orientation: Fused into subcylindrical bodies.

Colour: Greyish green.

Age and persistence: Plants slow-growing, long-lived perennials, becoming dormant in late spring, remaining older leaves recycled and forming a protective sheath for the successive newly formed leaves.

Armament and camouflage: Plants without conspicuous armament.

Sexual reproduction

Flowers: White, nocturnal.

Fruit/Seed

Size: Seed up to 0.85 mm in diameter, tuberculate.

Dispersal: Hydrochory. Hydrochastic capsules opening with rain but seeds dispersed by ‘wash-out dispersal’ (Hartmann 1988), thus also a strategy for local dispersal.

Time: Hydrochastic capsules releasing seeds only during the rainy season, maximising establishment.

Vegetative reproduction: Plants increase vegetatively, forming dense, tight mats or clusters, the active vegetative growth an efficient vegetative dispersal backup and adaptation to the cliff face.

CONSERVATION STATUS

Classified as rare (Raimondo *et al.* 2009), but well protected in the habitat, not threatened.

ADDITIONAL NOTES

Horticulture: *Conophytum carpianum* is easily cultivated compared to other level-ground species, according to Hammer (pers. comm.) a ‘great drinker’, rapidly swelling with moisture and making the most of the dry cliff terrain. Its adaptability in cultivation and growth vigour can be viewed as maximising survival. Best grown in partial shade, in small containers.

VOUCHER

Van Jaarsveld 22302 (NBG).

ILLUSTRATIONS AND MAP

Figures 177a–177c, Map 177.

178. *Conophytum danielii* Pavelka in *Kaktusy* 35,1: 1–32 (1999).

Cremonophyte growth form: Clustered, mat-forming growth (of light weight, cliff hugger).

Growth form formula: A:S:Lar:Lf (vb) (ft) (r)

Etymology: After Daniel Pavelka, father of Petr Pavelka.

DESCRIPTION AND HABITAT

Plants forming tight, dome-shaped cushions. Roots fibrous. Leaves fused into cylindrical, shortly bilobed bodies, up to 20 mm long; epidermis papillate, pale green to yellowish green; sheath sometimes spotted with brown dots. Flowers diurnal (initially nocturnal), pink, white or cream, in 2 or 3 series, up to 7×1.52 mm. Fruiting capsule 4- or 5-locular, whitish, opening hydrochastically. Seed up to 0.86 in diameter, with rounded papillae.

Phenology: Flowering in late autumn. Flowers initially nocturnal, scented.

Pollinators: Insects.

Habitat and aspect: Confined to low, shady cliffs. Summers are hot and dry but plants may benefit from occasional thunder showers in spring and autumn. The average daily maximum temperature is about 26–27°C and average daily minimum about 10–11°C, with frost absent or light. Rainfall is mainly in winter, spring and autumn (cyclonic cold fronts and thunder showers), ranging from 100–200 mm per annum.

Altitude: 1000–1150 m.

Associated vegetation: Kamiesberg Mountains Shrubland of the Succulent Karoo Biome (Mucina *et al.* 2005).

Associated cremonophytes: Associated plants include species of *Crassula* and mesembs.

Geology: Banke granidiorite (Spektakel Suite).

DISTRIBUTION

Confined to a single formation.

RELATED SPECIES

Related to the mat-forming *Conophytum marginatum*.

ADAPTATIONS TO THE CLIFF ENVIRONMENT

Habit: Conspicuous small, dome-shaped clusters.

Size and weight: Clusters small.

Stem: Short, usually unexposed.

Leaves

Orientation: Fused into cylindrical, shortly lobed bodies.

Colour and texture: Epidermis pale green, papillate.

Age and persistence: Plants long-lived perennials.

Armament and camouflage: Plants fragile, without conspicuous armament or camouflage properties, an adaptation to the largely undisturbed habitat.

Sexual reproduction

Flowers: Pink, white or cream, diurnal.

Fruit/Seed

Size: Seed up to 0.86 mm in diameter, densely tuberculate.

Dispersal: Hydrochory. Hydrochastic fruiting capsules 4- or 5-locular, white, opening hydrochastically and seed locally dispersed ('wash-out dispersal', Hartmann 1988). The fairly large tuberculate seeds indicate adaptation to the cliff habitat where they become wedged in crevices, providing anchorage for seedlings in the quartz crevices.

Time: Hydrochastic capsules releasing seeds only in the rainy season, maximising establishment.

Vegetative reproduction: Plants increase vegetatively, forming small, dense, tight mats or clusters, the active vegetative growth an efficient vegetative dispersal backup and adaptation to the cliff face.

CONSERVATION STATUS

Threatened owing to its unique fragile habit. Little-known species.

ADDITIONAL NOTES

Horticulture: Best under controlled conditions in a greenhouse. Easily cultivated but should be given ample shade. Its adaptability in cultivation and growth vigour can be viewed as maximising survival. Best grown in sandy soil in small containers and, as for most other species of *Conophytum*, allow for a summer resting period.

VOUCHER

Pavelka 962 (PRC).

ILLUSTRATIONS AND MAP

Map 178.

179. *Conophytum ernstii* S.A.Hammer subsp. *ernstii*, Hammer in Cactus and Succulent Journal (U.S.) 60,6: 262–263 (1988).

Cremnophyte growth form: Clustered, mat-forming (of light to medium weight, cliff hugger).

Growth form formula: A:S:Lar:Lf (vb) (r) (ft)

Etymology: After Ernst van Jaarsveld (1953–), horticulturist at Kirstenbosch National Botanical Garden.

DESCRIPTION AND HABITAT

Plants forming globose clusters of 10 to 60 bodies and up to 120 mm in diameter. Roots fibrous. Leaves fused into turbiniform bodies, each body 12–15 × 10–18 × 10–18 mm, truncate at top to slightly concave; epidermis densely papillate, glaucous; summer sheath greyish brown, well-spotted, elevated at margins. Flowers pale pink to pink, up to 34 mm in diameter. Petals numerous, in 2 or 3 series, up to 15 × 3 mm. Fruiting capsule 2 × 2 mm, opening hygrochastically. Seed 0.7 × 0.45 × 0.35 mm, densely papillate.

Phenology: Flowering in late autumn. Flowers conspicuous, in profusion, diurnal.

Pollinators: Insects.

Habitat and aspect: Confined to south-facing cliffs (Violsdrif Suite) of hills overlooking the Orange (Gariep) River, growing in crevices and on ledges of the upper slopes in ample soil in the fog belt. Summers are hot and dry but plants are ‘misted’ by regular fog from the Atlantic Ocean (some 80 km from the coast). The average daily maximum temperature is about 20°C and average daily minimum about 10°C, with frost absent from the habitat. Rainfall mainly in winter (cyclonic cold fronts), 50–100 mm per annum.

Altitude: 400–1200 m.

Associated vegetation: Richtersveld Sheet Wash Desert, Desert Biome (Mucina *et al.* 2005).

Associated cremnophytes: Other cremnophytes observed at Sandberg include *Adromischus alstonii*, *Conophytum rostratum*, *Crassula garibina*, *C. muscosa* var. *muscosa*, *C. velutina* and *Haworthia tessellata*.

Geology: Rough quartz of the Rosyntjieberg Formation (Orange River Group).

DISTRIBUTION

Confined to the Sandberg region of the Richtersveld Transfrontier National Park (Northern Cape) and adjacent hills in Namibia, and within the fog zone.

RELATED SPECIES

Distinguished from related level-ground *Conophytum* species by its large, conspicuous, globose clusters. The other level-ground *Conophytum* species usually well camouflaged and often with sunken growth. *Conophytum ernstii* subsp. *cerebellum* is slightly smaller (clusters and leaves).

ADAPTATIONS TO THE CLIFF ENVIRONMENT

Habit: Conspicuous globose clusters up to 120 mm in diameter, rooting in narrow crevices.

Size and weight: Clusters of light to medium weight.

Stem: Short, branched and unexposed.

Leaves

Orientation: Fused into turbiniform bodies, truncate at the top to slightly concave;

Colour and texture: Glaucous; epidermis densely papillate; summer sheath greyish brown, well-spotted, elevated at margins. Densely papillate epidermis, an adaptation trapping fog, often found in fog belt with mesembs such as *Conophytum stephanii*.

Age and persistence: Plants slow-growing, long-lived perennials, becoming dormant in spring, remaining older leaves recycled and forming a protective sheath for the successive newly formed leaves.

Armament and camouflage: Plants without conspicuous armament or camouflage properties.

Sexual reproduction

Flowers: Pale pink to pink, up to 34 mm in diameter (same diameter as leaf body), opening towards late afternoon; petals numerous, in 2 or 3 series, up to 15×3 mm, when in flower, bodies hardly visible. The rich flowering and floriferous nature can be seen as an adaptation to the cliff environment, maximising visibility.

Fruit/Seed

Size: Seed $0.7 \times 0.45 \times 0.35$ mm, densely papillate.

Dispersal: Hydrochory. Hygrochastic capsules 2×2 mm, opening with rain but seeds dispersed by 'wash-out dispersal' (Hartmann 1988), thus also a strategy for local dispersal.

Time: Seeds released during the rainy season in winter, maximising establishment.

Vegetative reproduction: Plants increase vegetatively, forming small, dense, tight mats or clusters, the active vegetative growth an efficient vegetative dispersal backup and adaptation to the cliff face.

CONSERVATION STATUS

Classified as rare (Raimondo *et al.* 2009) but well-protected within the Richtersveld Transfrontier National Park and also by the cliff-face habitat. A little-known species, not threatened.

ADDITIONAL NOTES

Horticulture: *Conophytum ernstii* is best grown under controlled conditions in a greenhouse. Very easily cultivated compared to other level-ground species, the growth vigour viewed as maximising survival. Propagate from seed, cuttings or by division. Allow for a summer rest. Best grown in partial shade, in small containers. Dividing annually and rapidly forming dense clusters. Cultivated by mesemb enthusiasts.

VOUCHER

Van Jaarsveld 8512 (NBG).

ILLUSTRATIONS AND MAP

Figures 179a–179e, Map 179.

180. *Conophytum francoiseae* (S.A.Hammer) S.A.Hammer, Dumpling and his wife: new views of the genus *Conophytum*: 133 (2002).

Cremonophyte growth form: Clustered, mat-forming growth (of light to medium weight, cliff hugger).

Growth form formula: A:S:Lar:Lf (vb) (r)

Etymology: After Françoise Williamson, wife of Graham Williamson, botanist and expert on the Richtersveld.

DESCRIPTION AND HABITAT

Plants forming rounded clusters up to 60 mm in diameter (15–25 bodies). Roots fibrous. Leaves fused into turbiniform, obconical bodies, concave at apices, each body 8–15 × 9–15 × 8–13 mm; epidermis smooth, glaucous, faintly green-spotted; summer sheath pale to dark brown. Calyx tube 8 mm long, bearing 4–6 green sepals. Flowers magenta, up to 30 mm in diameter. Petals numerous, in 1 or 2 series, up to 15 × 1.5 mm. Fruiting capsule obovate, soft, 4–6-locular, 2 × 4 mm, opening hygrochastically. Seed 0.60 mm in diameter, pustulate. (Description based on Hammer 2002.)

Phenology: Flowering in early spring. Flowers diurnal, scentless.

Pollinators: Insects.

Habitat and aspect: Confined to sheer, shady, south-facing cliffs, in crevices and on ledges of the upper slopes in ample soil, in the fog belt. Summers are hot and dry but plants are ‘misted’ by regular fog from the Atlantic Ocean (some 30 km from the coast). Average daily maximum temperature is about 19°C and average daily minimum about 10°C, with frost absent from the habitat. Rainfall mainly in winter (cyclonic cold fronts), 50–100 mm per annum.

Altitude: 250–350 m.

Associated vegetation: Vyftienmyl se Berge Succulent Shrubland of the Succulent Karoo Biome (Mucina *et al.* 2005).

Associated cremnophytes: *Conophytum meyeri*, *C. obscurum*, *Crassula pseudohemisphaerica*, *Mitrophyllum grande*, *Tylecodon bodleyae*, *T. buchholzianus* and *T. similis*.

Geology: Quartz of the De Hoop Subgroup (Gariiep Supergroup).

DISTRIBUTION

Confined to northern portion of Vyftienmyl se Berge (northeast of Port Nolloth).

RELATED SPECIES

Distinguished from *Conophytum wettsteinii* by its greyish blue clusters.

ADAPTATIONS TO THE CLIFF ENVIRONMENT

Habit: Conspicuous rounded clusters up to 60 mm in diameter, rooting along ledges and crevices.

Size and weight: Clusters of medium weight.

Stem: Short to medium length, branched and usually unexposed.

Leaves

Orientation: Fused into turbiniform, obconical bodies, concave at the apices.

Colour: Glauous; epidermis smooth, glauous, faintly green-spotted.

Age and persistence: Plants slow-growing, long-lived perennials, becoming dormant in spring, remaining older leaves recycled and forming a protective sheath for the successive newly formed leaves.

Armament and camouflage: Plants without conspicuous armament or camouflage properties.

Sexual reproduction

Flowers: Conspicuous, rich magenta, up to 30 mm in diameter (same diameter as leaf body), opening towards late afternoon; petals numerous, in 1 or 2 series, up to 15 mm long, when in flower bodies hardly visible. The rich flowering and floriferous nature can be seen as an adaptation to the cliff environment, maximising visibility.

Fruit/Seed

Size: Seed 0.6 mm long, densely tuberculate.

Dispersal: Hydrochory, as in other *Conophytum* species.

Time: Hygrochastic capsules releasing the seeds only during the rainy season, maximising establishment.

Vegetative reproduction: Plants increase vegetatively, rooting and forming dense mats or clusters, the active vegetative growth an efficient vegetative dispersal backup and adaptation to the cliff face.

CONSERVATION STATUS

Not threatened owing to the cliff habitat.

ADDITIONAL NOTES

Horticulture: Very easily cultivated compared to other level-ground species. Its adaptability in cultivation and growth vigour can be viewed as maximising survival. Best grown in partial shade, in small containers. Dividing annually and rapidly forming dense clusters.

VOUCHER

Van Jaarsveld 23076 (NBG).

ILLUSTRATIONS AND MAP

Figures 180a–180d, Map 180.

181. *Conophytum fulleri* L.Bolus, Notes on Mesembryanthemum and allied genera 2: 62 (1929).

Cremonophyte growth form: Clustered, mat-forming growth (of light to medium weight, cliff hugger).

Growth form formula: A:S:Lar:Lf (vb) (r)

Etymology: After E.R. Fuller, succulent plant enthusiast and postmaster at Kakamas and Pofadder.

DESCRIPTION AND HABITAT

Plants forming small, rounded mats of interlocking, very fragile bodies. Roots fibrous. Leaves fused into obconical bodies, each body 6–20 × 5–18 × 5 mm, truncate to convex at top; epidermis yellowish green to green, papillate, shiny, spotted with translucent dots; summer sheath whitish to pale yellowish; fissure small, up to 2 mm long. Flowers pink, up to 35 mm in diameter. Petals numerous, in 2–4 series, up to 15 × 2 mm. Fruiting capsule 4- or 5-locular, 2 × 4 mm, opening hygrochastically. Seed 0.6 × 0.5 × 0.35 mm, papillate.

Phenology: Flowering in late autumn. Flowers diurnal, conspicuous.

Pollinators: Insects.

Habitat and aspect: Confined to shady south- or east-facing cliffs. Summers are hot and dry. The average daily maximum temperature is about 27°C and the average daily minimum about 14°C. Rainfall occurs mainly in spring, winter and autumn (thunder showers and cyclonic cold fronts), 50–100 mm per annum.

Altitude: 980–1150 m.

Associated vegetation: Eastern Gariiep Rocky Desert of the Desert Biome (Mucina *et al.* 2005).

Associated cremnophytes: Associated plants include *Adromischus diabolicus*, *Aloe dabenorisana* and *Bowiea gariiepensis*.

Geology: Quartz of the Hom Formation (Bushmanland Group).

DISTRIBUTION

Confined to the mountains of the Orange River (Pellaberg), Pofadder region.

RELATED SPECIES

Distinguished from the related level-ground *Conophytum ectypum* by its large, conspicuous, translucent spots.

ADAPTATIONS TO THE CLIFF ENVIRONMENT

Habit: Conspicuous clusters of interlocking bodies.

Size and weight: Clusters small.

Stem: Short to medium length, branched and usually unexposed.

Leaves

Orientation: Fused into obconical bodies, truncate or convex at the top.

Colour: Green; epidermis very fragile, green, with large, translucent, darker dots; summer sheath yellowish brown.

Age and persistence: Plants slow-growing, long-lived perennials, becoming dormant in late spring, remaining older leaves recycled and forming a protective sheath for the successive newly formed leaves.

Armament and camouflage: Plants fragile, without conspicuous armament or camouflage properties, an adaptation to the largely undisturbed habitat.

Sexual reproduction

Flowers: Conspicuous, up to 35 mm in diameter, pink, attractive. Hammer (2002) describes it as honey-scented.

Fruit/Seed

Size: Seed up to 0.6 mm long, papillate.

Dispersal: Hydrochory. Hydrochastic capsules opening with rain, seeds locally dispersed by ‘wash-out dispersal’ (Hartmann 1988).

Time: Hydrochastic capsules releasing seeds only during the rainy season, maximising establishment.

Vegetative reproduction: Plants increase vegetatively, forming small, dense, tight mats or clusters, the active vegetative growth an efficient vegetative dispersal backup and adaptation to the cliff face.

CONSERVATION STATUS

Not threatened and within the limits of a national park.

ADDITIONAL NOTES

Horticulture: *Conophytum fulleri* is best grown under controlled conditions in a greenhouse. Very easily cultivated and its growth vigour can be viewed as maximising survival. Propagate from seed, cuttings or by division. Keep dry from late spring to summer. Best grown in partial shade or full sun, in sandy soil in small containers.

VOUCHER

Van Jaarsveld 1452/28 (BOL).

ILLUSTRATIONS AND MAP

Figures 181a–181c, Map 181.

182. *Conophytum hanae* Pavelka in *Kaktusy* 35,1: 1–32 (1999).

Cremonophyte growth form: Clustered, mat-forming growth (of medium weight, cliff hugger).

Growth form formula: A:S:Lar:Lf (vb) (r)

Etymology: After Hanna, wife of Petr Pavelka, author of this taxon.

DESCRIPTION AND HABITAT

Plants forming small, dome-shaped clusters up to 80 mm in diameter, consisting of many heads. Roots fibrous. Leaves fused into soft, compressed, obconical body; apices 2-lobed; lobes rounded, 10–16 × 8–10 × 3–4 mm; epidermis glabrous, green; margins reddish. Flowers slightly scented, about 30 mm in diameter, magenta. Petals in 1 or 2 series, up to 15 × 2 mm. Fruiting capsule 5- or 6-locular, 3–4 × 4–5 mm, truncate to pointed at apex. Seed 0.7 × 0.5 × 0.3 mm, tuberculate.

Phenology: Flowering in early autumn. Flowers scentless, diurnal.

Pollinators: The architecture of the large bright flowers suggests a diurnal flying insect.

Habitat and aspect: Confined to south-facing cliffs. The plants grow in shady crevices (all aspects) in association with other succulent plants. Summers are hot and dry and the average daily maximum temperature is about 26°C and average daily minimum about 7°C, with occasional frost. Rainfall occurs in spring, autumn and winter (cyclonic cold fronts and thunder showers in late summer and autumn), 100–200 mm per annum.

Altitude: 1000–1300 m.

Associated vegetation: Kamiesberg Mountains Shrubland of the Succulent Karoo Biome (Mucina *et al.* 2005).

Associated cremnoophytes: Other succulents observed at its habitat at Ramkop include *Adromischus filicaulis* var. *filicaulis*, *Crassula garibina* and *Othonna cakilifolia*.

Geology: Gneiss of the Bitterfontein Subgroup (Bushmanland Group).

DISTRIBUTION

Known only from the eastern Kamiesberg, on cliffs of similar geological formations.

RELATED SPECIES

Distinguished from related level-ground species by its more conspicuous, rounded clusters of softer bodied leaves (with reddish margins). The related level-ground species are usually well camouflaged among the quartz gravel flats or outcrops.

ADAPTATIONS TO THE CLIFF ENVIRONMENT

Habit: Conspicuous dome-shaped clusters.

Size and weight: Clusters of medium weight.

Stem: Short, usually unexposed.

Leaves

Orientation: Fused into soft, compressed obconical body, the apices 2-lobed; lobes rounded.

Colour: Epidermis glabrous, green, margins reddish; summer sheath yellowish brown, papery.

Age and persistence: Long-lived perennials.

Armament and camouflage: Conspicuous mounds of soft-leaved bodies and compared to level-ground species that are well camouflaged (*Conophytum marginatum* var. *marginatum*, *C. marginatum* var. *littlewoodii* and *C. herreanthus*), this reduction in camouflage can be seen as an adaptation to the largely undisturbed cliff-face habitat.

Sexual reproduction

Flowers: Magenta, about 30 mm in diameter, slightly scented, diurnal; petals in 2 series, up to 15×2 mm.

Fruit/Seed

Size: Seed $0.7 \times 0.5 \times 0.3$ mm, tuberculate.

Dispersal: Hydrochory. Fruiting capsules 5- or 6-locular, $3\text{--}4 \times 4\text{--}5$ mm, truncate to pointed at the top, fragile, opening hygrochastically with rain but seeds dispersed by 'wash-out dispersal' (Hartmann 1988). The capsules broad rectangular valve wings, no covering membranes. Rain fills the saucer-like cavity of the capsule and the seeds are washed out and down the cliffs, succumbing to gravity until they become wedged in a crevice. The papillate seeds indicate adaptation to the cliff habitat and this method of dispersal, providing good anchorage for seedlings in the quartz crevices.

Time: Hygrochastic capsules releasing the seeds only during the rainy season, maximising establishment.

Vegetative reproduction: Plants increase vegetatively, forming small, dense, tight mats or clusters, the active vegetative growth an efficient vegetative dispersal backup and adaptation to the cliff face.

CONSERVATION STATUS

Common in the habitat, not threatened.

ADDITIONAL NOTES

Horticulture: *Conophytum hanae* is best grown under controlled conditions in a greenhouse. Very easily cultivated and its growth vigour can be viewed as maximising survival. Propagate from seed, cuttings or by division. Keep dry from late spring to summer. Best grown in partial shade or full sun, in sandy soil in small containers.

VOUCHER

Pavelka 1369 (PRC).

ILLUSTRATIONS AND MAP

Figures 182a–182d, Map 182.

183. *Conophytum luckhoffii* Lavis, in Bolus, Notes on Mesembryanthemum and allied genera 2: 291–292 (1931). (*Conophytum edwardsiae* variant.)

Cremnophyte growth form: Clustered, mat-forming growth (of light weight, cliff hugger).

Growth form formula: A:S:Lar:Lf (vb) (r)

Etymology: After Dr James Luckhoff, succulent plant enthusiast.

DESCRIPTION AND HABITAT

Plants forming small to large, dome-shaped clusters up to 150 mm in diameter. Roots fibrous. Leaves fused into elongate-cordiform bodies; apices with sharply keeled, ornamented lobes, each body 8–15 × 4–8 × 2–5 mm; epidermis greyish green to purplish green, glabrous. Flowers diurnal, strongly scented, about 35 mm in diameter, magenta to carmine. Petals in 2–4 series, up to 15 × 2 mm. Fruiting capsule 4- or 5-locular, 2 × 4 mm, angular, fragile. Seed 0.9 × 0.5 × 0.4 mm, tuberculate-wrinkled.

Phenology: Flowering in early autumn. Flowers scentless, suggesting a night-flying pollinating insect.

Pollinators: The architecture of the large bright flowers suggests a diurnal flying insect.

Habitat and aspect: Confined to the Cape Fold Belt mountains where it grows on west-facing cliffs, occasionally also on other accessible sandstone pockets. The plants occur in crevices in association with other succulents. Summers are hot and dry but plants are occasionally ‘misted’ by fog from the Atlantic Ocean. Average daily maximum temperature about 23°C and average daily minimum about 12°C, with frost absent. Rainfall mainly in winter (cyclonic cold fronts), late summer and autumn (thunder showers), 400–500 mm per annum.

Altitude: 100–980 m.

Associated vegetation: Piketberg Sandstone Fynbos of the Fynbos Biome (Mucina *et al.* 2005).

Associated cremnohytes: Other succulents observed at Piekenierskloof Pass include *Adromischus hemisphaericus*, *Crassula montana* subsp. *montana*, *C. atropurpurea* var. *watermeyeri*, *C. rupestris* and *Tylecodon paniculatus*.

Geology: Quartzitic sandstone of the Graafwater Subgroup (Table Mountain Group, Cape Supergroup).

DISTRIBUTION

Piketberg, Citrusdal and northwards to Clanwilliam.

RELATED SPECIES

Distinguished from related level-ground species in the section *Minuscula* by its slightly larger bodies, but not much different. The related level-ground species are usually well camouflaged among the lichen and moss-filled stone pockets.

ADAPTATIONS TO THE CLIFF ENVIRONMENT

Habit: Conspicuous dome-shaped clusters.

Size and weight: Clusters small to medium weight.

Stem: Short, usually unexposed.

Leaves

Orientation: Fused into elongate-cordiform bodies, apices with sharply keeled and ornamented lobes.

Colour: Epidermis glabrous, greyish green to purplish green; summer sheath papery, whitish.

Age and persistence: Plants long-lived perennials.

Armament and camouflage: The fused, soft-leaved bodies are without conspicuous armament or camouflage properties and in comparison to level-ground species that are well camouflaged (*Conophytum phoeniceum* and *C. depressum*), this reduction in camouflage can be seen as an adaptation to the largely undisturbed cliff-face habitat.

Sexual reproduction

Flowers: Magenta to carmine, about 35 mm in diameter, strongly scented, diurnal, flowering in early autumn; petals in 2–4 series, up to 15 × 2 mm.

Fruit/Seed

Size: Seed 0.9 × 0.5 × 0.4 mm, tuberculate-wrinkled.

Dispersal: Hydrochory. Fruiting capsules 4- or 5-locular, 2 × 4 mm, angular, fragile, opening hygrochastically with rain but seeds dispersed by ‘wash-out dispersal’ (Hartmann 1988). Capsules have broad rectangular valve wings, no covering membranes. Rain fills the saucer-like cavity of the capsule and the seeds are washed out and down the cliffs, succumbing to gravity until they become wedged in a crevice. The large, tuberculate seeds indicate adaptation to the cliff habitat and this method of dispersal, providing good anchorage for seedlings.

Time: Hygrochastic capsules releasing the seeds only during the rainy season, maximising establishment.

Vegetative reproduction: Plants increase vegetatively, forming small, dense, tight mats or clusters, the active vegetative growth an efficient vegetative dispersal backup and adaptation to the cliff face.

CONSERVATION STATUS

Common in the habitat, not threatened.

ADDITIONAL NOTES

General: *Conophytum luckhoffii* is not an obligate cremnophyte when its distribution as a whole is taken into account. However, the form from Piekenierskloof was described as *C. edwardsiae*, an obligate cremnophyte.

Horticulture: Plants of *Conophytum luckhoffii* are best grown under controlled conditions in a greenhouse. Very easily cultivated, their growth vigour viewed as maximising survival. Propagate from seed, cuttings or by division. Keep dry from late spring to summer. Best grown in partial shade or full sun, in sandy soil in small containers.

VOUCHER

Van Jaarsveld 22794, Luckhoff 2488/30 (BOL).

ILLUSTRATIONS AND MAP

Figures 183a–183e, Map 183.

184. *Conophytum marginatum* Lavis subsp. *haramoepense* (L.Bolus) S.A.Hammer, Dumpling and his wife: new views of the genus *Conophytum*: 181 (2002).

Cremonophyte growth form: Clustered, mat-forming growth (of light to medium weight, cliff hugger).

Growth form formula: A:S:Lar:Lf (vb) (r)

Etymology: The specific epithet *marginatum* refers to its reddish margin and the subspecific epithet to a farm, Haramoep, in Bushmanland, Northern Cape.

DESCRIPTION AND HABITAT

Plants forming small, dome-shaped clusters to large mats 200 mm in diameter, consisting of many heads (20–200). Roots fibrous. Leaves fused into soft, oblong to obconical body; apices compressed, with purplish, ornamented lobes or fused; lobes rounded, 10–16 × 4–8 × 4 mm; epidermis glabrous, yellowish green to pinkish green; fissure papillate; sheath pale grey to opaque. Flowers diurnal, slightly scented, about 35 mm in diameter, magenta to pale rose. Petals in 1–3 series, 15 × 2 mm. Fruiting capsule 5- or 6-locular, 2 × 4 mm, obtrullate, pointed. Seed 0.65 × 0.4 × 0.3 mm, distinctly tuberculate.

Phenology: Flowering in early autumn. Flowers faintly scented.

Pollinators: The architecture of the large bright flowers suggests a diurnal flying insect.

Habitat and aspect: Confined to south-facing cliffs. Plants grow in sheltered crevices (all aspects) in association with other succulent plants. Summers are hot and dry and the average daily maximum temperature is about 28°C and average daily minimum about 13°C, with frost absent from the habitat. Rainfall occurs in spring, autumn and winter (cyclonic cold fronts and thunder showers in late summer and autumn), 50–100 mm per annum.

Altitude: 940–1200 m.

Associated vegetation: Eastern Gariiep Rocky Desert of the Desert Biome (Mucina *et al.* 2005).

Associated cremnophytes: Other succulents observed at its habitat at Groot Pellaberg include *Adromischus trigynus*, *Aloe dabenorisana*, *Bowiea gariepensis*, *Crassula exilis* subsp. *sedifolia*, *C. garibina* and *Tylecodon sulphureus* var. *armianus*.

Geology: Metaquartzitic gneiss of the Hom Formation (Bushmanland Group).

DISTRIBUTION

Known only from northern Bushmanland, on cliffs of similar geological formations (Naip se Berg to Pofadder).

RELATED SPECIES

Distinguished from related level-ground species by its more conspicuous, rounded clusters of softer bodied leaves (with purple apices). The related level-ground species are usually well camouflaged among the quartz gravel flats or outcrops.

ADAPTATIONS TO THE CLIFF ENVIRONMENT

Habit: Conspicuous dome-shaped clusters.

Size and weight: Clusters of light to medium weight.

Stem: Short, usually unexposed.

Leaves

Orientation: Fused into soft, oblong to obconical body, the apices compressed, with purplish ornamented lobes or fused; lobes rounded.

Colour: Epidermis glabrous, yellowish green to pinkish green; fissure papillate; summer sheath whitish, papery.

Age and persistence: Plants long-lived perennials.

Armament and camouflage: Plants growing in conspicuous mounds of soft-leaved bodies and in comparison to level-ground species that are well camouflaged (*Conophytum marginatum* var. *marginatum*, *C. herreanthus* and *C. regale*), this reduction in camouflage can be seen as an adaptation to the largely undisturbed cliff-face habitat.

Sexual reproduction

Flowers: Magenta to pale rose, about 35 mm in diameter, slightly scented, diurnal; petals in 1–3 series, up to 15 × 2 mm.

Fruit/Seed

Size: Seed $0.7 \times 0.4 \times 0.3$ mm, papillate.

Dispersal: Hydrochory. Fruiting capsules 5- or 6-locular, 2×4 mm, angular, fragile, opening hygrochastically with rain but seeds dispersed by ‘wash-out dispersal’ (Hartmann 1988). The capsules have broad rectangular valve wings, no covering membranes. Rain fills the saucer-like cavity of the capsule and the seeds are washed out and down the cliffs, succumbing to gravity until they become wedged in a crevice. The papillate seeds indicate adaptation to the cliff habitat and this method of dispersal, providing good anchorage for seedlings in the quartz crevices.

Time: Hygrochastic capsules releasing the seeds only during the rainy season, maximising establishment.

Vegetative reproduction: Plants increase vegetatively, forming small, dense, tight mats or clusters, the active vegetative growth an efficient vegetative dispersal backup and adaptation to the cliff face.

CONSERVATION STATUS

Common in the undisturbed habitat, not threatened.

ADDITIONAL NOTES

Horticulture: *Conophytum marginatum* subsp. *haramoepense* is best grown under controlled conditions in a greenhouse. Very easily cultivated and its growth vigour can be viewed as maximising survival. Propagate from seed, cuttings or by division. Keep dry from late spring to summer. Best grown in partial shade, in sandy soil in small containers. Under moist conditions the reddish colour of the leaves is lost (see Figure 184b).

VOUCHER

P. van Heerde 10774 (BOL).

ILLUSTRATIONS AND MAP

Figures 184a–184d, Map 184.

185. *Conophytum marginatum* Lavis subsp. *littlewoodii* (L.Bolus) S.A.Hammer, Dumpling and his wife: new views of the genus *Conophytum*: 181 (2002).

Cremonophyte growth form: Clustered, mat-forming growth (of light to medium weight, cliff hugger).

Growth form formula: A:S:Lar:Lf (vb) (r)

Etymology: After Roy Littlewood (1924–1967), collector of succulent plants.

DESCRIPTION AND HABITAT

Plants forming small, dome-shaped clusters to large mats 200 mm in diameter, consisting of many heads (20–50). Roots fibrous. Leaves fused into soft, elongated, heart-shaped bodies; apices lobed, somewhat diverging, grey- to olive-green, with purplish, ornamented lobes, 10–15 × 5–9 × 4–7 mm; epidermis glabrous, dotted with large green idioblasts; fissure papillate; sheath pale grey to opaque. Flowers diurnal, slightly scented, about 35 mm in diameter, magenta to carmine. Petals in 1–3 series, 22 × 2 mm. Fruiting capsule 5- or 6-locular, 2 × 4 mm, obtrullate, pointed. Seed 0.60 × 0.4 × 0.3 mm, distinctly tuberculate.

Phenology: Flowering in early autumn. Flowers faintly scented.

Pollinators: The architecture of the large bright flowers suggests a diurnal flying insect.

Habitat and aspect: Mainly confined to south-facing cliffs, in sheltered crevices in association with other succulents. Summers are hot and dry, the average daily maximum temperature about 28°C and average daily minimum about 13°C, with frost absent from the habitat. Rainfall occurs mainly in spring, autumn and winter (cyclonic cold fronts and thunder showers in late summer and autumn), 50–100 mm per annum.

Altitude: 750–1200 m.

Associated vegetation: Eastern Gariiep Rocky Desert of the Desert Biome (Mucina *et al.* 2005).

Associated cremnophytes: Habitat not seen.

Geology: Metaquartzitic gneiss of the Hom Formation (Bushmanland Group).

DISTRIBUTION

Known only from Naroep in northern Bushmanland, on cliffs (Northern Cape).

RELATED SPECIES

Distinguished from related level-ground species in its more conspicuous, rounded clusters of softer bodied leaves (with purple apices). The related level-ground species are usually well camouflaged among the quartz gravel flats or outcrops.

ADAPTATIONS TO THE CLIFF ENVIRONMENT

Habit: Conspicuous dome-shaped clusters.

Size and weight: Clusters of light to medium weight.

Stem: Short, usually unexposed.

Leaves

Orientation: Fused into soft, elongated, heart-shaped bodies, the apices lobed, somewhat diverging.

Colour: Epidermis glabrous, greyish green, dotted with large green idioblasts; fissure papillate; lobes purplish ornamented; summer sheath whitish, papery.

Age and persistence: Plants long-lived perennials.

Armament and camouflage: Plants growing in conspicuous mounds of soft-leaved bodies and in comparison to level-ground species that are well camouflaged (*Conophytum marginatum* var. *marginatum*, *C. herreanthus* and *C. regale*), this reduction in camouflage can be seen as an adaptation to the largely undisturbed cliff-face habitat.

Sexual reproduction

Flowers: Magenta to carmine, about 35 mm in diameter, slightly scented, diurnal; petals in 1–3 series, up to 22 × 2 mm.

Fruit/Seed

Size: Seed 0.65 × 0.4 × 0.3 mm, distinctly tuberculate.

Dispersal: Hydrochory. Fruiting capsules 5- or 6-locular, 2 × 4 mm, angular, fragile, opening hygrochastically with rain but seeds dispersed by ‘wash-out dispersal’ (Hartmann 1988). The capsules have broad rectangular valve wings, no covering membranes. Rain fills the saucer-like cavity of the capsule and the seeds are washed out and down the cliffs, succumbing to gravity until they become wedged in a crevice. The distinctly tuberculate seeds indicate adaptation to the cliff habitat and this method of dispersal, providing good anchorage for seedlings in the quartz crevices.

Time: Hygrochastic capsules release the seeds only in the rainy season, maximising establishment.

Vegetative reproduction: Plants increase vegetatively, forming small, dense, tight mats or clusters, the active vegetative growth an efficient vegetative dispersal backup and adaptation to the cliff face.

CONSERVATION STATUS

Common in the habitat, not threatened.

ADDITIONAL NOTES

Horticulture: Best grown under controlled greenhouse conditions. Very easily cultivated, its growth vigour possibly maximising survival. Propagate from seed, cuttings or by division. Keep dry from late spring to summer. Best grown in partial shade, in sandy soil in small containers.

VOUCHER

Van Jaarsveld 711/59 (BOL).

ILLUSTRATIONS AND MAP

Map 185.

186. *Conophytum obscurum* N.E.Br. subsp. *sponsaliorum* (S.A.Hammer) S.A.Hammer, Dumpling and his wife: new views of the genus *Conophytum*: 212 (2002).

Cremonophyte growth form: Clustered, mat-forming (of light to medium weight, cliff hugger).

Growth form formula: A:S:Lar:Lf (vb) (r)

Etymology: The epithet *sponsaliorum* refers to a betrothal, a marriage or a spouse and honours the married.

DESCRIPTION AND HABITAT

Plants forming small dwarf mats (2–10 bodies). Roots fibrous. Leaves fused into obconical bodies, each body 4–12 × 3–8 × 3–8 mm, truncate at top; epidermis glabrous, shining, pale bluish green to dark green, spotted; fissure short, inconspicuous; summer sheath white, foveate. Flowers pinkish, up to 18 mm in diameter. Petals numerous, in 1 or 2 series, up to 8 × 1 mm. Fruiting capsule 4-locular, 1.5–2.0 × 2.0–2.5 mm, opening hygrochastically. Seed 0.65–0.42 × 0.32 mm, dark brown, covered with small ring- or crescent-shaped bumps. (Description based on Hammer 2002.)

Phenology: Flowering in autumn. Flowers diurnal, scentless, conspicuous.

Pollinators: Insects.

Habitat and aspect: Confined to quartz cliffs where the plants grow in sheltered crevices and on ledges (various aspects), often in shade and subject to occasional fog. The average daily maximum temperature is about 19°C and average daily minimum about 10°C, with frost absent from the habitat. Rainfall mainly in winter (cyclonic cold fronts), 50–100 mm per annum.

Altitude: 680 m.

Associated vegetation: Kahams Mountain Desert of the Desert Biome (Mucina *et al.* 2005).

Associated cremonophytes: Species of *Adromischus*, *Crassula* and *Tylecodon*.

Geology: Quartz of the Stinkfontein Subgroup (Gariiep Supergroup).

DISTRIBUTION

Known only from the type locality at Skimmelberg, Richtersveld (Northern Cape).

RELATED SPECIES

Distinguished from related subspecies by its bright green bodies and very dwarf-sized, depauperate stature.

ADAPTATIONS TO THE CLIFF ENVIRONMENT

Habit: Inconspicuous mat-forming dwarf-sized clusters in fissures along ledges and crevices.

Size and weight: Clusters very small, up to 20 mm in diameter.

Stem: Very short and unexposed.

Leaves

Orientation: Fused into obconical bodies, truncate at the top, with a smooth epidermis.

Colour: Bluish green to dark green.

Age and persistence: Plants slow-growing, long-lived perennials, becoming dormant in spring, remaining older leaves recycled and forming a protective sheath for the successive newly formed leaves.

Armament and camouflage: Plants without conspicuous armament or camouflage properties.

Sexual reproduction

Flowers: Light pink, up to 20 mm in diameter, diurnal.

Fruit/Seed

Size: Seed with large humps, efficient for establishment in crevices

Dispersal: Hydrochory, as in other *Conophytum* species.

Time: Hygrochastic capsules releasing the seeds only in the rainy season, maximising establishment.

Vegetative reproduction: Plants increase vegetatively, rooting and forming dense mats or clusters, the active vegetative growth an efficient vegetative dispersal backup and adaptation to the cliff face.

CONSERVATION STATUS

Not threatened owing to the cliff habitat.

ADDITIONAL NOTES

Horticulture: Best grown under controlled conditions in a greenhouse, in a sandy, well-drained soil mixture. Keep in dappled shade and dry in summer. Propagated from seed or by division. Introduced into ornamental horticulture by S.A. Hammer in 1995.

VOUCHER

S. Hammer 1437 (BOL).

ILLUSTRATIONS AND MAP

Map 186.

187. *Conophytum quaesitum* (N.E.Br.) N.E.Br. subsp. *densipunctum* (L.Bolus) S.A.Hammer, The genus *Conophytum*: a conograph: 238 (1993).

Cremnophyte growth form: Clustered, mat-forming growth (of light weight, cliff hugger).

Growth form formula: A:S:Lar:Lf (vb)

Etymology: The epithet *densipunctum* pertains to the densely spotted leaves.

DESCRIPTION AND HABITAT

Plants forming dense cushions or mats. Roots fibrous. Leaves fused into a laterally compressed, obovate body, bilobed, lobes keeled, 15–25 × 12–15 × 8–10 mm; epidermis finely papillate, pale yellowish green, densely spotted; sheath white, densely spotted. Flowers milky white, 15 × 2 mm. Fruiting capsule 5-locular, 2 × 5 mm, opening hygrochastically. Seed 0.70 × 0.5 × 0.3 mm, densely tuberculate. (Description based on Hammer 2002.)

Phenology: Flowering in autumn. Flowers initially nocturnally scented.

Pollinators: Insects.

Habitat and aspect: Confined to the higher mountains of the Sperrgebiet (Lower Orange River Valley) in southwestern Namibia, the plants growing on shady cliffs in the fog belt. Summers are hot and dry but plants are ‘misted’ by fog from the Atlantic Ocean. The average daily maximum temperature is about 20–22°C and average daily minimum about 10–12°C, with frost absent from the habitat. Rainfall occurs mainly in winter (cyclonic cold fronts), 25–50 mm per annum.

Altitude: 1050–1200 m.

Associated vegetation: Succulent Karoo Biome.

Associated cremnophytes: Habitat not seen.

Geology: Quartzitic sandstone, gneiss.

DISTRIBUTION

Widespread in the higher mountains of the Sperrgebiet (southern Namibia).

RELATED SPECIES

Distinguished from related level-ground species by its conspicuous dome-shaped, mat-forming growths and soft bodies. The other related level-ground *Conophytum* species are usually well camouflaged, often with sunken growth and mat-forming.

ADAPTATIONS TO THE CLIFF ENVIRONMENT

Habit: Conspicuous dome-shaped to mat-forming clusters.

Size and weight: Clusters of light to medium weight.

Stem: Short, usually unexposed.

Leaves

Orientation: Fused into a laterally compressed, obovate body, bilobed, lobes keeled.

Colour: Epidermis finely papillate, pale yellowish green, densely spotted; sheath white, densely spotted.

Age and persistence: Long-lived perennials.

Armament and camouflage: Fragile, without conspicuous armament or camouflage properties, an adaptation to the largely undisturbed habitat.

Sexual reproduction

Flowers: Scented, milky white, flowering in late autumn,

Fruit/Seed

Size: Seed $0.70 \times 0.5 \times 0.3$ mm, densely tuberculate and ideal for small establishment in crevices.

Dispersal: Hydrochory. Fruiting capsule 4–6-locular, 2×3 mm, opening hygrochastically with rain but seeds dispersed by ‘wash-out dispersal’ (Hartmann 1988). The capsules have broad rectangular valve wings, no covering membranes. Rain fills the saucer-like cavity of the capsule and the seeds are washed out and down the cliffs, succumbing to gravity until they become wedged in a crevice. The large tubercles on the seed surface indicate adaptation to the cliff habitat and this method of dispersal, providing good anchorage for seedlings in the quartz crevices.

Time: Hygrochastic capsules releasing the seeds only in the rainy season, maximising establishment.

Vegetative reproduction: Plants increase vegetatively, forming small, dense, tight mats or clusters, the active vegetative growth an efficient vegetative dispersal backup and adaptation to the cliff face.

CONSERVATION STATUS

Little-known species, not threatened.

ADDITIONAL NOTES

Horticulture: *Conophytum quaesitum* subsp. *densipunctum* is best grown under controlled conditions in a greenhouse. Very easily cultivated and its growth vigour can be viewed as maximising survival. Propagate from seed, cuttings or by division. Keep dry from late spring to summer. Best grown in partial shade, in sandy soil in small containers.

VOUCHER

Erni 2027/27 (NBG).

ILLUSTRATIONS AND MAP

Map 187.

188. *Conophytum quaesitum* (N.E. Br.) N.E. Br. subsp. *quaesitum* var. *rostratum* (Tischer) S.A.Hammer, The genus *Conophytum*: a conograph: 261 (1993).

Cremnophyte growth form: Clustered, mat-forming growth (of light weight, cliff hugger).

Growth form formula: A:S:Lar:Lf (vb)

Etymology: The epithet *quaesitum*, rare or special, pertains to the plants, although they are quite common in certain regions; *rostratum*, a beak, refers to the beaked lobes of the leaves.

DESCRIPTION AND HABITAT

Plants forming dense cushions or mats. Roots fibrous. Leaves fused into a cylindrical, lobed body; lobes keeled, 25–40 × 8–15 × 8–10 mm; epidermis finely papillate, dull to bluish green, spotted or immaculate. Flowers white, straw-coloured, yellowish. Petals 8 × 2 mm. Fruiting capsule 2 × 6 mm, opening hygrochastically. Seed 0.65 × 0.5 × 0.3 mm, densely tuberculate. (Description based on Hammer 2002.)

Phenology: Flowering in late autumn. Flowers initially nocturnally scented.

Pollinators: Insects.

Habitat and aspect: Confined to the higher mountains of the Lower Orange River Valley, the plants growing on shady cliffs in the fog belt. Summers are hot and dry but plants are 'misted' by fog from the Atlantic Ocean. The average daily maximum temperature is about 20–22°C and average daily minimum about 10–12°C, with frost absent from the habitat. Rainfall occurs mainly in winter (cyclonic cold fronts), 50–100 mm per annum.

Altitude: 700–1200 m.

Associated vegetation: Noms Mountain Desert and Richtersveld Mountain Desert of the Desert Biome (Mucina *et al.* 2005).

Associated cremnophytes: Associated plants include *Aloe meyeri*, *Crassula garibina*, *C. sericea* var. *hottentotta* and *Gasteria pillansii* var. *pillansii*.

Geology: Quartzitic sandstone, gneiss (Namaqua Metamorphic Complex) and quartz and conglomerate of the Stinkfontein Formation (Gariiep Supergroup).

DISTRIBUTION

Widespread in the higher mountains of the northern Richtersveld (Northern Cape).

RELATED SPECIES

Distinguished from related level-ground species by its conspicuous dome-shaped, mat-forming growths and soft bodies. The other related level-ground *Conophytum* species are usually well camouflaged, often with sunken growth and mat-forming.

ADAPTATIONS TO THE CLIFF ENVIRONMENT

Habit: Conspicuous dome-shaped to mat-forming clusters.

Size and weight: Clusters of light to medium weight.

Stem: Short, usually unexposed.

Leaves

Orientation: Fused into broadly obovoid to almost cylindrical, lobed bodies, acutely keeled to round at apex.

Colour and texture: Epidermis finely papillate, dull to grey-green or yellowish green, spotted or immaculate; summer sheath white to pale yellow to brown, maculate. The soft texture can be viewed as a response to the undisturbed habitat.

Age and persistence: Plants long-lived perennials.

Armament and camouflage: Plants fragile, without conspicuous armament or camouflage properties, an adaptation to the largely undisturbed habitat.

Sexual reproduction

Flowers: Scented, white, straw-coloured, yellow to rose-pink, flowering in late autumn.

Fruit/Seed

Size: Seed $0.65 \times 0.5 \times 0.3$ mm, densely tuberculate and ideal for establishment in crevices.

Dispersal: Hydrochory. Fruiting capsules 4–6-locular, 2×3 mm, opening hygrochastically with rain but seeds dispersed by ‘wash-out dispersal’ (Hartmann 1988). The capsules have broad rectangular valve wings, no covering membranes. Rain fills the saucer-like cavity of the capsule and the seeds are washed out and down the cliffs, succumbing to gravity until they become wedged in a crevice. The large tubercles on the seeds indicate adaptation to the cliff habitat and this method of dispersal, providing good anchorage for seedlings in the quartz crevices.

Time: Hygrochastic capsules releasing the seeds only during the rainy season, maximising establishment.

Vegetative reproduction: Plants increase vegetatively, forming small, dense, tight mats or clusters, the active vegetative growth an efficient vegetative dispersal backup and adaptation to the cliff face.

CONSERVATION STATUS

Little-known species, not threatened.

ADDITIONAL NOTES

Horticulture: *Conophytum quaesitum* subsp. *quaesitum* var. *rostratum* is best grown under controlled conditions in a greenhouse. Very easily cultivated and its growth vigour can be viewed as maximising survival. Propagate from seed, cuttings or by division. Keep dry from late spring to summer. Best grown in partial shade, in sandy soil in small containers.

VOUCHER

Van Jaarsveld 19944 (NBG).

ILLUSTRATIONS AND MAP

Figures 188a & 188b, Map 188.

189. *Conophytum ricardianum* Loesch & Tischer subsp. *ricardianum*, Loesch & Tischer *Monatsschrift der Deutschen Kakteen-Gesellschaft* 4: 74–76 (1932).

Cremnophyte growth form: Clustered, mat-forming growth (of light to medium weight, cliff hugger).

Growth form formula: A:S:Lar:Lf (vb) (r) (ft)

Etymology: After nurseryman Richard Graessner of Perleberg.

DESCRIPTION AND HABITAT

Plants forming dense mats of 10–60 bodies and up to 120 mm in diameter. Roots fibrous. Leaves fused into turbiniform bodies, each body 20 mm in diameter, truncate at top; epidermis pale green, glabrous, very fragile, soft; fissure very small; summer sheath vertically fluted, pale yellowish brown, well-spotted. Flowers milky white, up to 34 mm in diameter. Petals numerous, in 2 or 3 series, up to 15 × 3 mm, spatulate. Fruiting capsule 3 × 3 mm, opening hygrochastically. Seed 0.8 × 0.45 × 0.35, pale brown, pustulate. (Description based on Hammer 2002.)

Phenology: Flowering in late autumn. Flowers conspicuous, diurnal, in profusion.

Pollinators: Insects.

Habitat and aspect: Confined to south-facing cliffs (reddish sandstone) of hills overlooking the Orange (Gariep) River, the plants growing in crevices and on ledges of the upper slopes in ample soil in the fog zone. Summers are hot and dry but plants are ‘misted’ by regular fog from the Atlantic Ocean (some 80 km from the coast). The average daily maximum temperature is about 20°C and average daily minimum about 10°C, with frost absent from the habitat. Rainfall mainly in winter (cyclonic cold fronts), 50–100 mm per annum.

Altitude: 400–1200 m.

Associated vegetation: Richtersveld Sheet Wash Desert of the Desert Biome (Mucina *et al.* 2005).

Associated cremnophytes: Other cremnophytes observed at Kuamsib include *Aloe pavelkae*, *Conophytum quaesitum* var. *rostratum*, *Crassula velutina*, *Gasteria pillansii* var. *ernesti-ruschii* and *Tylecodon torulosus*.

Geology: Rough quartz of the Rosyntjieberg Formation (Orange River Group).

DISTRIBUTION

Confined to the Lorelei in the west, to the Kuamsib Mountains in the east and mountains of the Richtersveld Transfrontier National Park (Northern Cape and Namibia) and adjacent hills in Namibia, and within the fog zone.

RELATED SPECIES

Distinguished from related level-ground *Conophytum* species (*C. wettsteinii* group) by its large, conspicuous, very soft, fragile mats. The other level-ground *Conophytum* species usually have firm bodies.

ADAPTATIONS TO THE CLIFF ENVIRONMENT

Habit: Conspicuous globose clusters up to 120 mm in diameter, rooting in narrow crevices.

Size and weight: Clusters of light to medium weight.

Stem: Short, branched and unexposed.

Leaves

Orientation: Fused into turbiniform bodies, turbinate and truncate at the top.

Colour: Green. Epidermis smooth, very fragile; summer sheath vertically fluted, pale yellowish brown, well-spotted.

Age and persistence: Plants slow-growing, long-lived perennials, becoming dormant in spring, remaining older leaves recycled and becoming a protective sheath for the successive newly formed leaves.

Armament and camouflage: Plants with very fragile bodies, without conspicuous armament or camouflage properties.

Sexual reproduction

Flowers: Milky white, up to 34 mm in diameter (same diameter as leaf body), opening towards late afternoon; petals numerous, in 2 or 3 series, up to 15×3 mm, when in flower, bodies hardly visible. The rich flowering and floriferous nature can be seen as an adaptation to the cliff environment, maximising visibility.

Fruit/Seed

Size: Seed $0.8 \times 0.45 \times 0.35$ mm, densely pustulate.

Dispersal: Hydrochory. Hydrochastic capsules 3×3 mm, opening with rain but seeds dispersed by 'wash-out dispersal' (Hartmann 1988), thus also a strategy for local dispersal.

Time: Seeds released during the rainy season in winter, maximising establishment.

Vegetative reproduction: Increasing vegetatively, forming small, dense mats or clusters, the active vegetative growth an efficient vegetative dispersal backup and adaptation to the cliff face.

CONSERVATION STATUS

Well-protected within the Ai-Ais Richtersveld Transfrontier National Park and also by the cliff-face habitat. A little-known species, not threatened.

ADDITIONAL NOTES

Horticulture: *Conophytum ricardianum* is best grown under controlled conditions in a greenhouse. Very easily cultivated compared to level-ground species; the growth vigour can be viewed as maximising survival. Propagate from seed, cuttings or by division. Allow for a summer rest. Best grown in partial shade in small containers. Dividing annually and rapidly forming dense clusters. Cultivated by mesemb enthusiasts.

VOUCHER

Van Jaarsveld 21087 (NBG).

ILLUSTRATIONS AND MAP

Plate 189, Figures 189a–189c, Map 189.

190. *Conophytum stephanii* Schwantes subsp. *stephanii*, Schwantes in Die Gartenwelt 33: 25 (1929).

Cremonophyte growth form: Clustered, mat-forming growth (of light weight, cliff hugger).

Growth form formula: A:S:Lar:Lf (vb) (ft) (r)

Etymology: After Paul Stephan, who was Curator of the succulent plant collection of the Hamburg Botanical Gardens.

DESCRIPTION AND HABITAT

Plants forming many-headed, dome-shaped clusters up to 50 mm in diameter. Roots fibrous. Leaves fused into subglobose bodies, each body 7–15 × 4 – 8 × 4 mm; apices convex or somewhat truncate; epidermis olive-green to reddish brown, very hairy owing to dense, tapering, translucent white papillae up to 1.5 mm long. Flowers about 6–8 mm in diameter, reddish, reddish yellow to bronze. Fruiting capsule 3–5-locular, 3 × 4 mm, globose, fragile, hairy. Seed 0.7 × 0.5 × 0.4 mm, finely pustulate. (Description based on Hammer 2002.)

Phenology: Flowering in early autumn. Flowers nocturnal, strongly scented, suggesting a night-flying pollinator.

Pollinators: The nocturnal flowers (becoming diurnal) suggest a night-flying insect.

Habitat and aspect: Confined to quartz cliff faces, the plants growing on shady southern aspects. Summers are hot and dry but plants are occasionally ‘misted’ by fog from the Atlantic Ocean. The average daily maximum temperature is about 26°C and average daily minimum about 10–12°C, with frost absent from the habitat. Rainfall mainly in winter (cyclonic cold fronts), late summer and autumn (thunder showers), 25–50 mm per annum.

Altitude: 600–1169 m.

Associated vegetation: Rosyntjieberg Succulent Shrubland and Namaqualand Klipkoppe Shrubland of the Succulent Karoo Biome (Mucina *et al.* 2005).

Associated cremnoophytes: Associated succulents observed on the Rosyntjieberg include *Aloe meyeri*, *Crassula garibina*, *C. sericea* var. *hottentotta*, *Trachyandra aridimontana* and *Tylecodon ellaphieae*.

Geology: Quartzitic sandstone, gneiss (Namaqua Metamorphic Complex) and quartz of the Stinkfontein Formation (Gariiep Supergroup).

DISTRIBUTION

Confined to Vyftienmyl se Berge (Oograbies Mountains) near the Port Nolloth coast (Northern Cape).

RELATED SPECIES

Distinguished from related level-ground species in the section *Barbata* (*Conophytum depressum* and *C. phoeniceum*, larger sized, solitary or little branched) by its conspicuous globose clusters of densely hairy bodies. These related level-ground species are usually well camouflaged, often with sunken growth or inconspicuous dwarf-sized mats.

ADAPTATIONS TO THE CLIFF ENVIRONMENT

Habit: Conspicuous dome-shaped clusters.

Size and weight: Clusters medium-sized.

Stem: Short, usually unexposed.

Leaves

Orientation: Fused into subglobose bodies, the apices convex or somewhat truncate.

Colour and texture: Epidermis olive-green to reddish brown, very hairy owing to the dense, tapering, translucent white papillae up to 1.5 mm long. The densely hairy nature of the plant bodies and the habitat that receives regular fog indicate a moisture-trapping adaptation. Summer sheath whitish, densely papillate, perforate, an adaptation to the long, dry summers.

Age and persistence: Long-lived perennials.

Armament and camouflage: Plants bodies are soft, without conspicuous armament or camouflage properties as opposed to level-ground species that are well camouflaged (*Conophytum phoeniceum* and *C. depressum*). This reduction in camouflage can be seen as an adaptation to the largely undisturbed cliff-face habitat.

Sexual reproduction

Flowers: Reddish, reddish yellow to bronze, about 6–8 mm in diameter, strongly scented, flowering in early autumn, nocturnal, suggesting a night-flying specialist pollinator (insect).

Fruit/Seed

Size: Seed $0.7 \times 0.5 \times 0.4$ mm, finely pustulate.

Dispersal: Hydrochory. Fruiting capsules 3–5-locular, 3×4 mm, globose, fragile, hairy, opening hygrochastically with rain, but seeds dispersed by ‘wash-out dispersal’ (Hartmann 1988). The capsules have broad rectangular valve wings, no covering membranes. Rain fills the saucer-like cavity of the capsule and the seeds are washed out and down the cliffs, succumbing to gravity until they become wedged in a crevice. The large, tuberculate seeds indicate adaptation to the cliff habitat and this method of dispersal, providing good anchorage for seedlings in the quartz crevices.

Time: Hygrochastic capsules releasing the seeds only during the rainy season, maximising establishment.

Vegetative reproduction: Increasing vegetatively, forming small, dense mats or clusters, the active vegetative growth an efficient vegetative dispersal backup and adaptation to the cliff face.

CONSERVATION STATUS

A little-known species, not threatened owing to the inaccessible habitat and some of the population being within the Richtersveld Transfrontier National Park.

ADDITIONAL NOTES

Horticulture: *Conophytum stephanii* is best grown under controlled conditions in a greenhouse. Very easily cultivated and its growth vigour can be viewed as maximising survival. Propagate from seed, cuttings or by division. Keep dry from late spring to summer. Best grown in partial shade, in sandy soil in small containers.

VOUCHER

Van Jaarsveld 19130 (NBG).

ILLUSTRATIONS AND MAP

Plate 190, Figures 190a–190e, Map 190.

191. *Conophytum tantillum* N.E.Br. subsp. *amicorum* S.A.Hammer & Barnhill in *Bradleya* 15: 42–43 (1997).

Cremonophyte growth form: Clustered, mat-forming growth (of light to medium weight, cliff hugger).

Growth form formula: A:S:Lar:Lf (vb) (r)

Etymology: According to Hammer (2002), subsp. *amicorum* was named by two of the four ‘amis’ who found it simultaneously.

DESCRIPTION AND HABITAT

Plants forming dome-shaped clusters up to 80 mm in diameter. Roots fibrous. Leaves fused into narrow obcordate bodies; apices bearing blunt keels, slightly curved, ornamented, each body 15–20 × 8–10 × 5–7 mm; epidermis pale greyish green with a few scattered dots, papillate; sheath light brown, spotted. Flowers diurnal, about 20 mm in diameter, golden yellow. Petals in 1 or 2 series, up to 8 × 2 mm. Fruiting capsule 4- or 5-locular, 2 × 2 mm, angular, fragile. Seed 0.7 × 0.5 × 0.3 mm, pustulate.

Phenology: Flowering in early autumn. Flowers scentless, suggesting a night-flying pollinating insect.

Pollinators: The architecture of the bright flowers suggests a diurnal flying insect.

Habitat and aspect: Confined to the western escarpment fringe where it grows on inaccessible cliffs but occasionally also on other accessible sandstone pockets. The plants occur in association with other succulent plants on sheltered south-facing aspects. Summers are hot and dry but plants are occasionally ‘misted’ by fog from the Atlantic Ocean. The average daily maximum temperature is about 24°C and average daily minimum about 9°C, with frost absent from the habitat. Rainfall occurs mainly in winter (cyclonic cold fronts), late summer and autumn (thunder showers), 150–250 mm per annum.

Altitude: 850 m.

Associated vegetation: Umdaus Mountains Succulent Shrubland of the Succulent Karoo Biome (Mucina *et al.* 2005).

Associated cremnophytes: Other succulents in the habitat include *Adromischus alstonii*, *Crassula atropurpurea* var. *watermeyerii* and *Tylecodon paniculatus*.

Geology: Quartzitic cliffs of the Kuibis Subgroup (Nama Group).

DISTRIBUTION

South of Steinkopf, Richtersveld (Northern Cape).

RELATED SPECIES

Distinguished from related level-ground species in the section *Minuscula* by its slightly larger, conspicuous bodies. The related level-ground species are usually well camouflaged among the lichen and moss-filled stone pockets.

ADAPTATIONS TO THE CLIFF ENVIRONMENT

Habit: Conspicuous dense clusters.

Size and weight: Clusters of light to medium weight.

Stem: Short, usually unexposed.

Leaves

Orientation: Fused into narrow, obcordate bodies, the apices with blunt keels, slightly curved and ornamented.

Colour and texture: Epidermis pale greyish green, with a few scattered dots, papillate.

Age and persistence: Plants long-lived perennials.

Armament and camouflage: Plants are soft-leaved bodies without conspicuous armament or camouflage properties and in comparison to level-ground species that are well camouflaged (*Conophytum swanepoelianum*, *C. minusculum*, *C. rubrolineatum*), this reduction in camouflage can be seen as an adaptation to the largely undisturbed cliff-face habitat.

Sexual reproduction

Flowers: Scentless, about 20 mm in diameter, diurnal, flowering in early autumn; petals in 1 or 2 series, up to 8×2 mm.

Fruit/Seed

Size: Seed $0.7 \times 0.5 \times 0.3$ mm, pustulate.

Dispersal: Hydrochory. Fruiting capsule 4- or 5-locular, 3 × 2 mm, angular, fragile, opening hygrochastically with rain but seeds dispersed by ‘wash-out dispersal’ (Hartmann 1988). The capsules have broad rectangular valve wings, no covering membranes. Rain fills the saucer-like cavity of the capsule and the seeds are washed out and down the cliffs, succumbing to gravity until they become wedged in a crevice. The large, pustulate seeds indicate adaptation to the cliff habitat and this method of dispersal, providing good anchorage for seedlings in the quartz crevices.

Time: Hygrochastical capsules releasing the seeds only during the rainy season, maximising establishment.

Vegetative reproduction: Plants increase vegetatively, forming small, dense, tight mats or clusters, the active vegetative growth an efficient vegetative dispersal backup and adaptation to the cliff face.

CONSERVATION STATUS

Common in the habitat, not threatened.

ADDITIONAL NOTES

Horticulture: *Conophytum tantillum* subsp. *amicorum* is best grown under controlled conditions in a greenhouse. Very easily cultivated and its growth vigour can be viewed as maximising survival. Propagate from seed, cuttings or by division. Keep dry from late spring to summer. Best grown in partial shade, in sandy soil in small containers.

VOUCHER

Barnhill, Hammer, Rogerson & Tribble 2296 (BOL).

ILLUSTRATIONS AND MAP

Figures 191a & 191b, Map 191.

192. *Conophytum taylorianum* (Dinter & Schwantes) N.E.Br. subsp. *ernianum* (Loesch & Tischer) de Boer ex S.A.Hammer, *The genus Conophytum: a conograph*: 240 (1993). (Hohenzollern obligate cremnophilous form.)

Crempnophyte growth form: Clustered, mat-forming (of light to medium weight, cliff hugger).

Growth form formula: A:S:Lar:Lf (vb) (r)

Etymology: The species was named after the British mesemb enthusiast Edward Taylor (1848–1928); the subspecific epithet honours Franz Sales Erni (1878–1952) from near Aus, Namibia.

DESCRIPTION AND HABITAT

Plants forming dense mats up to 400 mm in diameter. Roots fibrous. Leaves fused into laterally compressed, obcordate, bilobed, soft bodies, each body 15–35 × 12–20 × 10–14 mm,

lobes diverging at apex, unequal and chin-like, with sharp, sinuate, pinkish keels; epidermis grey-green, glabrous to finely papillate; summer sheath white, spotted. Flowers diurnal, up to 30 mm in diameter, bright rosy magenta. Petals numerous, in 2 or 3 series, up to 15×2 mm. Fruiting capsule 5-locular, 4×6 mm, depressed obovate, opening hygrochastically. Seed $0.8 \times 0.5 \times 0.4$ mm, tuberculate, dark brown. (Description based on Hammer 2002.)

Phenology: Flowering in autumn. Flowers slightly scented, conspicuous.

Pollinators: Insects.

Habitat and aspect: Confined to shady south-facing cliffs of the Hohenzollern Mountain where the plants grow in the fog belt. Summers are hot and dry but plants are 'misted' by fog from the Atlantic Ocean. The average daily maximum temperature is about 20°C and average daily minimum about 9°C , with frost absent from the habitat. Rainfall occurs mainly in winter (cyclonic cold fronts), 50–100 mm per annum.

Altitude: 600–1200 m.

Associated vegetation: Succulent Karoo.

Associated cremnophytes: Associated plants include *Conophytum angelicae* and *Crassula ausensis*.

Geology: Hard sandstone (Nama Group).

DISTRIBUTION

Conophytum taylorianum subsp. *ernianum* has a fairly wide distribution from the Sperrgebiet along the coast to Hohenzollern in the east.

RELATED SPECIES

Distinguished from related level-ground *Conophytum* species by its conspicuous globose clusters. The other level-ground *Conophytum* species are usually well camouflaged, often with sunken growth.

ADAPTATIONS TO THE CLIFF ENVIRONMENT

Habit: Conspicuous globose clusters in quartz crevices.

Size and weight: Clusters of light to medium weight.

Stem: Short, usually unexposed.

Leaves

Orientation: Fused into laterally compressed, obcordate, soft, bilobed bodies, the lobes diverging at the apex, unequal and chin-like with sharp sinuate pinkish keels.

Colour and texture: Epidermis grey-green, glabrous to finely papillate; summer sheath white, spotted.

Age and persistence: Plants slow-growing, long-lived perennials.

Armament and camouflage: Plants fragile, without conspicuous armament or camouflage properties, an adaptation to the largely undisturbed habitat.

Sexual reproduction

Flowers: Bright rosy magenta, up to 30 mm in diameter, diurnal; petals numerous, in 2 or 3 series, up to 15×2 mm.

Fruit/Seed

Size: Seed $0.8 \times 0.5 \times 0.4$ mm, tuberculate, dark brown.

Dispersal: Hydrochory. Hygrochastic capsules depressed obovate, 2×3 –4 mm, opening with rain but seeds dispersed by ‘wash-out dispersal’ (Hartmann 1988). The capsules have broad rectangular valve wings, no covering membranes. Rain fills the saucer-like cavity of the capsule and the seeds are washed out and down the cliffs, succumbing to gravity until they become wedged in a crevice. The large, tuberculate seeds indicate adaptation to the cliff habitat and this method of dispersal, providing good anchorage for seedlings in the quartz crevices (compared to other *Conophytum* species).

Time: Hygrochastic capsules releasing the seeds only during the rainy season, maximising establishment.

Vegetative reproduction: Plants increase vegetatively, forming small, dense, tight mats or clusters, the active vegetative growth an efficient vegetative dispersal backup and adaptation to the cliff face.

CONSERVATION STATUS

A little-known species, not threatened owing to the sheer cliff habitat and its distribution within the Richtersveld Transfrontier National Park.

ADDITIONAL NOTES

Horticulture: *Conophytum taylorianum* subsp. *ernianum* is best grown under controlled conditions in a greenhouse. Very easily cultivated and its growth vigour can be viewed as maximising survival. Propagate from seed, cuttings or by division. Keep dry from late spring to summer. Best grown in partial shade, in sandy soil in small containers.

VOUCHER

Van Jaarsveld 21032 (NBG).

ILLUSTRATIONS AND MAP

Plate 192, Figures 192a–192d, Map 192.

193. *Conophytum taylorianum* (Dinter & Schwantes) N.E.Br. subsp. *rosynense* S.A.Hammer, The genus *Conophytum*: a conograph: 265 (1993).

Crempnophyte growth form: Clustered, mat-forming growth (of light to medium weight, cliff hugger).

Growth form formula: A:S:Lar:Lf (vb) (r)

Etymology: The species was named after the British mesemb enthusiast Edward Taylor (1848–1928), and the subspecies after the Rosyntjieberg in the Richtersveld, Northern Cape.

DESCRIPTION AND HABITAT

Plants forming rounded clusters up to 80 mm in diameter. Roots fibrous. Leaves fused into laterally compressed, obcordate, bilobed, soft bodies, each body 10–25 × 12–18 × 10–12 mm, lobes diverging at apex, unequal, chin-like, with sharp, sinuate, reddish keels; epidermis grey-green, finely papillate; summer sheath pale brown. Flowers diurnal, up to 45 mm in diameter, bright rosy magenta. Petals numerous, in 2 or 3 series, 12–22 mm long. Fruiting capsule 5-locular, 2 × 3–4 mm, depressed obovate, opening hygrochastically. Seed 0.8 × 0.5 × 0.4 mm, tuberculate. (Description based on Hammer 2002.)

Phenology: Flowering in midsummer. Flowers slightly scented, conspicuous.

Pollinators: Insects.

Habitat and aspect: Confined to shady south-facing cliffs of the Rosyntjieberg, the plants growing in the fog belt. Summers are hot and dry but plants are ‘misted’ by fog from the Atlantic Ocean. The average daily maximum temperature is about 20°C and average daily minimum about 9°C, with frost absent from the habitat. Rainfall occurs mainly in winter (cyclonic cold fronts), 50–100 mm per annum.

Altitude: 600–1200 m.

Associated vegetation: Rosyntjieberg Succulent Shrubland of the Succulent Karoo Biome (Mucina *et al.* 2005).

Associated crempnophytes: Associated plants include *Aloe meyeri*, *Conophytum angelicae* subsp. *tetragonum*, *C. stephanii*, *Ficus ilicina* and *Trachyandra aridimontana*.

Geology: Hard quartz of the Rosyntjieberg Formation (Orange River Group).

DISTRIBUTION

Confined to the Rosyntjieberg Mountains north of the Richtersveld.

RELATED SPECIES

Distinguished from related level-ground *Conophytum* species by its conspicuous globose clusters. The level-ground *Conophytum* species are usually well camouflaged, often with sunken growth.

ADAPTATIONS TO THE CLIFF ENVIRONMENT

Habit: Conspicuous globose clusters in quartz crevices.

Size and weight: Clusters of light to medium weight.

Stem: Short, usually unexposed.

Leaves

Orientation: Fused into laterally compressed, obcordate, soft, bilobed bodies, the lobes diverging at the apex, unequal and chin-like with sharp, sinuate, reddish keels.

Colour and texture: Epidermis grey-green, finely papillate; summer sheath pale brown.

Age and persistence: Plants slow-growing, long-lived perennials.

Armament and camouflage: Plants fragile, without conspicuous armament or camouflage properties, an adaptation to the largely undisturbed habitat.

Sexual reproduction

Flowers: Conspicuous, bright rosy magenta, up to 45 mm in diameter, diurnal. The rich flowering and floriferous nature can be seen as an adaptation to the cliff environment, maximising visibility.

Fruit/Seed

Size: Seed $0.8 \times 0.5 \times 0.4$ mm, tuberculate.

Dispersal: Hydrochory. Hydrochastic capsules depressed obovate, $2 \times 3-4$ mm, opening with rain but seeds dispersed by 'wash-out dispersal' (Hartmann 1988). The capsules have broad rectangular valve wings, no covering membranes. Rain fills the saucer-like cavity of the capsule and the seeds are washed out and down the cliffs, succumbing to gravity until they become wedged in a crevice. The large, tuberculate seeds indicate adaptation to the cliff habitat and this method of dispersal, providing good anchorage for seedlings in the quartz crevices (compared to other *Conophytum* species).

Time: Hydrochastic capsules releasing the seeds only during the rainy season, maximising establishment.

Vegetative reproduction: Plants increase vegetatively, forming small, dense, tight mats or clusters, the active vegetative growth an efficient vegetative dispersal backup and adaptation to the cliff face.

CONSERVATION STATUS

A little-known species, not threatened owing to the sheer cliff habitat and its occurrence within the Richtersveld Transfrontier National Park.

ADDITIONAL NOTES

Horticulture: *Conophytum taylorianum* subsp. *rosynense* is best grown under controlled conditions in a greenhouse. Very easily cultivated and its growth vigour can be viewed as maximising survival. Propagate from seed, cuttings or by division. Keep dry from late spring to summer. Best grown in partial shade, in sandy soil in small containers.

VOUCHER

Van Jaarsveld 5518 (NBG).

ILLUSTRATIONS AND MAP

Plate 193, Figures 193a–193e, Map 193.

DELOSPERMA N.E.Br. emend Lavis

194. *Delosperma* sp. A

Cremonophyte growth form: Pendent to procumbent mats, rooting at nodes (of medium weight, cliff hanger).

Growth form formula: E:F:P:Els (vb) (r)

DESCRIPTION AND HABITAT

Plants mat-forming and pendent from cliff faces, with stems up to 500 mm long forming loose clusters. Roots fibrous. Branches 1.8–2.0 mm in diameter, soft, brittle, terete, at first reddish green, becoming grey-green; nodes 12–15(–30) mm apart; surface glabrous, or with scattered hairs when young. Leaves fleshy, dorsiventrally compressed, ovate, narrowly ovate to linear-ovate, occasionally elliptic to linear-oblongate, slightly cymbiform and with obscure keel, 25–35 × 7–12 mm, spreading to slightly recurved; surface smooth, shiny green, occasionally hairy when young becoming glabrescent; margin entire to ciliate, reddish towards apex; apex acute, with green to reddish mucro. Flowers axillary, solitary, 20–25 mm in diameter; pedicels 8–10 mm long. Receptacle cup-shaped, 3 mm deep, 10 mm in diameter, bearing 2 outer ovate sepals 7–8 × 4 mm and 3 smaller obovoid sepals 3 × 2.5 mm, with membranous margins and pointed apices, with scattered hairs. Petals magenta, mauve or yellow, in 2 series, the outer linear-lanceolate, up to 15 × 1.3–1.5 mm, the inner shorter and narrower, 5 × 0.2 mm. Stamens in 3 series, 3–5 mm long, at first overtopping stigmas; filaments white to light mauve, hairy; anthers 0.7–1.0 mm, yellowish. Ovary elevated to about 2 mm, 5-lobed; stigmas 5, lanceolate, 2 mm long, papillate; nectaries dark green, 2 × 0.3 mm. Capsule top-shaped, 8–10 mm in diameter, grey, with old petals persistent and becoming blackish; covering membranes lacking, valve wings present, closing bodies absent. Seed pear-shaped, 0.5 × 0.4 mm, tuberculate, pale brown.

Phenology: Flowering from spring to autumn with a peak in midsummer, but occasionally at other times of the year.

Pollinators: Insects.

Habitat and aspect: Sheltered cliffs, from coastal rivers to sunny kloofs (mainly eastern, southern and western aspects). Plants tend to root at the nodes and extend their range by runners. Temperatures are moderate and subtropical. Winters are cool but frost is absent. The average daily maximum temperature is about 24°C and the average daily minimum temperature is about 16°C. Rainfall occurs mainly in summer but at times also in winter, ranging from 1000–1250 mm per annum.

Altitude: 200–250 m.

Associated vegetation: Pondoland-Ugu Sandstone Coastal Sourveld.

Associated cremnophytes: At Mzamba (Eastern Cape), the habitat is shared with *Aloe arborescens*, *Bulbine natalensis*, *Cotyledon orbiculata*, *Crassula orbicularis*, *C. perfoliata* var. *minor*, *C. perforata* and *Gasteria croucheri*.

Geology: Quartzitic sandstone (light-coloured and smooth-textured), Natal Formation (Cape Supergroup).

DISTRIBUTION

Delosperma sp. A is confined to the coastal quartzitic sandstone gorges in southern KwaZulu-Natal (Mtamvuna region) and the northeastern extreme of the Eastern Cape (Mzamba River).

RELATED SPECIES

Delosperma sp. A is at once distinguished from *D. rogersii* by its procumbent growth, with larger, dorsiventrally flattened leaves and larger flowers of 20–25 mm in diameter. *Delosperma rogersii* form loose mats with decumbent, sturdy branches, oblong, triquetrous leaves 10–20 × 7 mm and smaller flowers about 19 mm in diameter. *Delosperma rogersii* is a widespread species common in the dry river valleys of the Eastern Cape such as the Bashee and Kei Rivers (shale and occasionally sandstone), and is especially common on cliffs and steep, exposed, rocky terrain. It also occurs in light shade of short shrubby vegetation. The associated vegetation is thicket and the plants are variable in leaf hairiness and flower colour. The leaves are sometimes densely arranged, almost imbricate, especially in exposed habitats. The flowers are mainly yellow, but pink- and mauve-flowered populations are also found. *Delosperma rogersii* is also cultivated locally as a ground cover. It is a long-lived perennial and is drought tolerant.

ADAPTATIONS TO THE CLIFF ENVIRONMENT

Habit: Plants bearing long, pendent, leafy stems, a habit that is retained in cultivation. A rapid-growing, fairly long-lived perennial.

Size and weight: Plants small.

Rootstock: Roots fibrous, no specialised features.

Stem: The internodes of the long, pendent branches are 12–30 mm long, an adaptation to the vertical cliff face without much competition or predation. Stems and leaves soft and fragile.

Leaves

Orientation: Spreading, sometimes somewhat recurved.

Colour and texture: Green, sometimes shiny, fleshy, soft, becoming turgid after rain, but withered during dry periods, an adaptation to the extreme, dry habitat. Leaves are hairy or glabrous, sometimes only the margin fringed with hairs.

Age and persistence: Leaves persistent and long-lived, eventually withering and resulting in apical grouping.

Armament: The plants have no obvious armament.

Sexual reproduction

Flowers: Mauve, pink or yellow, simple, axillary produced, conspicuous, with conspicuous yellow stamens, maximising visibility for successful pollination in the vertical cliff environment. Flowering time is long and flowers are regularly produced, ensuring a long and continual seed supply.

Fruit/Seed

Size: Seed 0.5×0.4 mm, pear-shaped, tuberculate, the size ideal for establishment in crevices.

Dispersal: Pale brown seeds locally dispersed by rainwater ('wash-out dispersal', Hartmann 1991), settling in crevices where they germinate.

Time: Seeds ripening throughout summer and autumn. Germination after 14–21 days.

Vegetative reproduction: Plants increase vegetatively, forming drooping mats rooting at nodes. This active vegetative growth will root when coming into contact with new crevices below, an effective vegetative dispersal backup and adaptation to the cliff face, ensuring long-term survival.

CONSERVATION STATUS

A local endemic, not threatened.

ADDITIONAL NOTES

Horticulture: Best for subtropical coastal gardens and ideal for embankments, balconies, window sills as well as hanging baskets. Best grown in partial shade. Propagate from cuttings in a sandy mixture. Plants thrive in cultivation. Its very easy growing nature maximises survival rate.

VOUCHER

Van Jaarsveld 19294 (NBG).

ILLUSTRATIONS AND MAP

Figures 194a–194c, Map 194.

195. *Delosperma* sp. B

Cremonophyte growth form: Pendent to procumbent leafy stems (of medium weight, cliff hanger).

Growth form formula: E:F:P:Els (vb)

DESCRIPTION AND HABITAT

Plants mat-forming and pendent from cliff faces with stems up to 800 mm long, forming loose clusters. Roots fibrous. Branches 1.8 mm in diameter, soft, brittle, terete, green to grey-green; nodes 12–55 mm apart (leaves crowded towards branch ends); surface hairy; hairs multicellular, translucent, up to 0.5 mm long. Leaves fleshy, dorsiventrally compressed, narrowly elliptic to linear-oblongate, slightly cymbiform and with obscure keel, 20–40 × 5–9 mm, ascending to recurved; surface dull green, densely hairy (velvety), sometimes slightly uneven and wrinkled; apex acute, with green to reddish, sharply pointed mucro. Flowers solitary, 20–25 mm in diameter; pedicels slender, 20–40 mm long. Receptacle cup-shaped, 2 mm deep, 5–6 mm in diameter, bearing 2 outer linear-lanceolate sepals 8 × 3 mm and 3 smaller obovoid sepals 3 × 4 mm, with membranous margins and pointed apices. Petals mauve, in 2 series, the outer linear-lanceolate, up to 12 × 1–1.3 mm, the inner shorter and narrower, 5 × 0.2 mm. Stamens in 3 series, 3–5 mm long, at first overtopping stigmas; filaments light mauve; anthers 0.7 mm long, yellowish. Ovary pointed, 1.8 mm high, 5-ridged; stigmas 5, lanceolate, 2.5 mm long, papillate; nectaries dark green, 1.5 × 0.3 mm. Capsule obconical, 9 mm in diameter; covering membranes lacking, valve wings present, closing bodies absent. Seed pear-shaped, up to 1 × 0.6–0.7 mm, tuberculate, pale brown.

Phenology: Flowering mainly from spring to autumn.

Pollinators: Insects.

Habitat and aspect: Cliffs of narrow shady kloofs (mainly eastern, southern and western aspects). Plants are rooted in crevices and on ledges, drooping over the rock faces. Winters are cool but frost is absent. Temperatures moderate, the average daily maximum about 24°C and average daily minimum about 16°C. Rainfall occurs mainly in summer, but occasionally also in winter, 1000–1250 mm per annum.

Altitude: 150–250 m.

Associated vegetation: Pondoland-Ugu Sandstone Coastal Sourveld of the Indian Ocean Coastal Belt (*Mucina et al.* 2005).

Associated cremnophytes: At Luputana (Eastern Cape), the habitat is shared with *Aloe arborescens*, *Bulbine natalensis*, *Cotyledon orbiculata*, *Crassula orbicularis*, *C. perfoliata* var. *minor* and *C. perforata*.

Geology: Quartzitic sandstone (light-coloured and smooth-textured), Natal Formation (Cape Supergroup).

DISTRIBUTION

Delosperma sp. B is a quartzitic sandstone endemic, as yet known only from the narrow Luputana Gorge (northern Transkei, Eastern Cape).

RELATED SPECIES

Related to *Delosperma* sp. A, *Delosperma obtusum* and *D. tradescantioides*. *Delosperma* sp. B is at once distinguished from *Delosperma* sp. A by its linear-oblongate, densely hairy leaves (surface often mat and wrinkled), slender pedicels 20–40 mm long, slightly smaller flowers of which the petals are 12×1.0 – 1.3 and larger seed of 1×0.6 – 0.7 mm. *Delosperma obtusum* is a much-branched, vigorous, scrambling species with semiterete leaves that grows at higher altitudes along the Drakensberg. *Delosperma tradescantioides* has larger, firmer, triangular-ovate leaves and is widespread in the Eastern Cape.

ADAPTATIONS TO THE CLIFF ENVIRONMENT

Habit: Plants with long, pendent, leafy stems, a habit that is retained in cultivation. A rapid-growing, fairly long-lived perennial.

Size and weight: Small.

Rootstock: Roots fibrous, no specialised features.

Stem: The internodes of the long, pendent branches are up to 55 mm long, an adaptation to the vertical cliff face without much competition or predation. Stems and leaves soft and fragile.

Leaves

Orientation: Ascending-spreading.

Colour and texture: Pale green, fleshy, soft, becoming turgid after rain, but withered during dry periods, an adaptation to the extreme, dry habitat.

Age and persistence: Leaves persistent and long-lived, eventually withering and resulting in apical grouping.

Armament: The unarmed plant is dependent on the protection of the cliff face against larger herbivores.

Sexual reproduction

Flowers: Mauve, simple, axillary produced, conspicuous, with conspicuous yellow stamens, maximising visibility for successful pollination in the vertical cliff environment. Flowering time is long and flowers are regularly produced, ensuring a long and continual seed supply.

Fruit/Seed

Size: Seed up to $1 \times 0.6\text{--}0.7$ mm, pear-shaped, tuberculate.

Dispersal: Pale brown seeds locally dispersed by water ('wash-out dispersal', Hartmann 1991).

Time: Seeds ripening throughout summer and autumn.

Vegetative reproduction: Plants increase vegetatively, forming dense mats that soon become pendent, the branches (vegetative growth) rooting where they find new crevices below, an efficient vegetative dispersal backup and adaptation to the cliff face, ensuring long-term survival.

CONSERVATION STATUS

A local endemic, not threatened.

ADDITIONAL NOTES

Horticulture: Best for subtropical coastal gardens and ideal for embankments, balconies, window sills and hanging baskets. Grow in partial shade. Propagate from cuttings in a sandy mixture. Plants do well in cultivation. Its very easy growing nature maximises its survival rate.

VOUCHER

Van Jaarsveld 16405 (NBG).

ILLUSTRATIONS AND MAP

Figures 195a–195d, Map 195.

196. *Delosperma esterhuyseniae* L.Bolus in *Journal of South African Botany* 25: 259–260 (1959).

Cremonophyte growth form: Pendent loose mats, succulent leaves crowded towards branch ends (of light to medium weight, cliff hanger).

Growth form formula: E:F:P:Els (vb) (r)

Etymology: After Elsie Esterhuysen (1912–2006) of the University of Cape Town, very prolific plant explorer, mountaineer and botanist.

DESCRIPTION AND HABITAT

Plants forming dwarf clusters with pendulous stems up to 120 mm long from a lignified semisucculent base up to 15 mm in diameter. Branches up to 3 mm in diameter, becoming corky and thicker with age, usually with 2 pairs of functional leaves at apices, withering from the base. Leaves thick, succulent, laterally compressed, club-shaped viewed from the side, cymbiform, with eccentric keel, up to 36×8 mm; surface minutely papillose, yellowish to purplish green; apex obtuse. Flowers solitary, up to 40 mm in diameter, with white to light pink Stamnodes. Receptacle top-shaped, about 10 mm in diameter, bearing 2 club-shaped sepals 6 mm long and 3 ovate sepals up to 5 mm long. Petals in 6 series, outer linear-lanceolate, up to 22×1.5 mm, inner shorter, narrower. Stamens in 3 series, up to 3 mm long; filaments yellowish green. Stigmas 5, lanceolate, 1.5–3 mm long, papillate. Capsule obconic, 9 mm in diameter; covering membranes lacking, valve wings present, closing bodies absent. Seed up to 1 mm in diameter, pale brown.

Phenology: Flowering mainly from spring to summer.

Pollinators: Insects.

Habitat and aspect: Cliffs of narrow shady kloofs (mainly eastern and western aspects). Plants are firmly rooted in crevices and size often depends on the growing space allowed by the crevice. Temperatures are high in summer and can reach 40°C. Winters are cooler but frost is absent. The average daily maximum temperature is 26–27°C and the average daily minimum about 9–11°C. Rainfall occurs throughout the year but with a peak in spring and summer (thunder showers or cyclonic winter rain), 200–300 mm per annum.

Altitude: 400–1200 m.

Associated vegetation: Kouga Grassy Sandstone Fynbos of the Fynbos Biome as well as Gamka Thicket and Groot Thicket of the Albany Thicket Biome (Mucina *et al.* 2005).

Associated cremnophytes: At Gert Smitskloof (Baviaanskloof), the habitat is shared with *Albuca cremnophila*, *Cotyledon tomentosa*, *Crassula perfoliata* var. *minor*, *C. perforata* and *Gasteria rawlinsonii*.

Geology: Quartzitic sandstone (light-coloured and smooth-textured), Peninsula Formation (Cape Supergroup). Plants tightly wedged in cracks, ledges and fissures.

DISTRIBUTION

Delosperma esterhuyseniae is a quartzitic sandstone endemic, confined to the narrow kloofs (north-south orientation) of the Aasvoëlberg northwest of Willowmore, Baviaanskloof and Groot Winterhoek Mountains of the Eastern Cape.

RELATED SPECIES

Related to *Delosperma ecklonis*, a much-branched, vigorous, scrambling dwarf shrub with hairy leaves and smaller flowers.

ADAPTATIONS TO THE CLIFF ENVIRONMENT

Habit: Plants firmly rooted in crevices, forming small, tight mats, often becoming drooping and with the soft, fragile leaves apically grouped. This habit is retained in cultivation. A rapid-growing, fairly long-lived perennial.

Size and weight: Heads small and within the miniature size range.

Rootstock: The slightly thickened rootstock grows firmly wedged in crevices.

Stem: The short branches (up to 40 mm) are grey, with older leaves withering. The stems are fibrous and strong.

Leaves

Orientation: Spreading-ascending.

Colour and texture: Pale green, glaucous, very fleshy, soft, becoming turgid after rain, but withered during dry periods, an adaptation to the extreme, dry habitat.

Age and persistence: Leaves becoming deciduous from the base, resulting in apical grouping.

Armament: The soft leaf texture suggests a reduction in armament in response to the undisturbed cliff habitat in contrast to the thorny but heavily grazed surrounding thicket vegetation.

Sexual reproduction

Flowers: White to light pink, simple, large for such a small plant, with conspicuous yellow stamens, maximising visibility for successful pollination on the shady vertical cliffs. Flowering time is long and flowers are regularly produced, ensuring a long and continual seed supply.

Fruit/Seed

Size: Seed up to 1mm in diameter, an ideal size for establishment in crevices.

Dispersal: Seeds dispersed by rainwater ('wash-out dispersal', Hartmann 1991), settling and germinating in crevices.

Time: Seeds ripening throughout summer and autumn, coinciding with the start of the rainy season. Germination after 14–21 days.

Vegetative reproduction: Plants increase vegetatively, the active vegetative growth rooting where it comes into contact with new crevices below, an efficient vegetative dispersal backup and adaptation to the cliff face, ensuring long-term survival.

CONSERVATION STATUS

Not threatened, a local endemic well protected by the habitat and furthermore occurring within a nature reserve.

ADDITIONAL NOTES

Horticulture: Best grown in thicket gardens, in rockeries or containers. Outside its native habitat, it is best grown under controlled conditions in a greenhouse. Propagate from cuttings or seed in a sandy mixture. It does well in cultivation and should preferably be kept in dappled shade. Its very easy growing nature maximises survival rate.

VOUCHER

Van Jaarsveld 7245, 16078 (NBG).

ILLUSTRATIONS AND MAP

Plate 196, Figures 196a–196d, Map 196.

197. *Delosperma knox-daviesii* Lavis in Journal of South African Botany 32: 209–210 (1966).

Crempnophyte growth form: Pendent leafy stems (of light to medium weight, cliff hanger).

Growth form formula: E:F:P:Els (vb)

Etymology: After Mr C.N. Knox-Davies.

DESCRIPTION AND HABITAT

Plants branched, soft, fragile, procumbent, fast-growing, short-lived, perennial shrublets, sometimes mat-forming on cliffs and becoming pendent, with stems up to 200 mm long; tips of flowering branches often dying back to central clusters. Roots fibrous. Branches glabrous, becoming woody, soft and green at first, terete; internodes on vegetative branches 10–30 mm long, spreading. Leaves decussate, sometimes crowded owing to short internodes, dorsiventrally flattened, linear-elliptic, linear-ob lanceolate to lanceolate-obovate, 15–35 × 6–8 mm; surface glabrous, abaxial surface convex; apex acute, mucronate. Flowers terminal, solitary or in loose apical cymes, 20–24 mm in diameter; pedicels 8–12 mm long. Receptacle top-shaped, 3 mm deep, bearing 2 outer linear-lanceolate sepals 4 × 1.5 mm and 3 much shorter sepals. Petals linear-lanceolate, up to 12 × 2–2.5 mm, mauve, centre white. Staminodes white, linear, overtopping stamens. Capsule top-shaped, up to 6 mm in diameter. Seed pear-shaped, up to 1 × 0.5–0.8 mm, tuberculate, brown.

Phenology: Flowering mainly from spring to summer.

Pollinators: Insects.

Habitat and aspect: Cliffs of the upper eastern escarpment margin (Mpumalanga), on all aspects. Plants are rooted in crevices and on ledges, drooping over rock faces. Temperatures moderate, average daily maximum about 24°C and average daily minimum about 12°C. Winters are cooler, with light frost. Rainfall mainly in summer, 700–800 mm per annum.

Altitude: 1500 m.

Associated vegetation: Northern Escarpment Quartzite Sourveld of the Grassland Biome (Mucina *et al.* 2005).

Associated cremnophytes: At Blyderivierspoort (Mpumalanga), the habitat is shared with *Aeollanthus parvifolius*, *Aloe arborescens*, *A. spicata*, *Bulbine natalensis*, *Cotyledon orbiculata*, *Crassula setulosa*, *C. swaziensis*, *Cyanotis speciosus*, *Otiophora cupheoides*, *Scilla natalensis*, *Senecio orbicularis* and *Thorncroftia succulenta*.

Geology: Quartzitic sandstone, Chuniespoort Group (Black Reef Formation, Transvaal Supergroup).

DISTRIBUTION

Delosperma knox-daviesii occurs on the escarpment edge in the Mpumalanga Drakensberg. It is confined to exposed cliffs.

RELATED SPECIES

Related to *Delosperma obtusum* and *Delosperma* sp. A, the former with semiterete leaves and from higher altitudes along the southern Drakensberg. *Delosperma* sp. A is a procumbent species with larger axillary flowers.

ADAPTATIONS TO THE CLIFF ENVIRONMENT

Habit: Plants forming mats and stems becoming pendent, the old flowering branches dying back. A fast-growing, short-lived perennial.

Size and weight: Plants small (200–300 mm in diameter).

Rootstock: Roots fibrous, no specialised features.

Stem: Short to long and sometimes drooping.

Leaves

Orientation: Spreading (shade), to densely crowded (full light).

Colour and texture: Pale to purplish green, soft and fragile, becoming turgid after rain, but withered during dry periods.

Age and persistence: Persistent.

Armament: The soft, fragile nature suggests a reduction in armament in response to the undisturbed cliff habitat in contrast to the grazed grassland and subtropical forest.

Sexual reproduction

Inflorescence and flowers: Mainly mauve but also pink or magenta, simple or in terminal cymes, conspicuous, maximising visibility for successful pollination in the cliff and ledge

environment. Flowering time is long and flowers are regularly produced, ensuring a long and continual seed supply.

Fruit/Seed

Size: Seed small, $1 \times 0.5\text{--}0.8$ mm, tuberculate.

Dispersal: Dark brown seeds locally dispersed by water ('wash-out dispersal', Hartmann 1991), ideal for establishment in crevices.

Time: Seeds ripening throughout summer and autumn.

Vegetative reproduction: Plants increase vegetatively, forming small, dense mats or clusters, the active vegetative growth rooting where it comes into contact with new crevices below, an efficient vegetative dispersal backup and adaptation to the cliff face, ensuring long-term survival.

CONSERVATION STATUS

Widespread and not threatened.

ADDITIONAL NOTES

Horticulture: Best for highveld hardens, grown in rockeries or containers. Outside its habitat, it should rather be grown under controlled conditions in a greenhouse. Plants easily grown from cuttings and thrive in cultivation. Its very easy growing nature maximises survival rate). Introduced to Kirstenbosch in 1934 (285/34).

VOUCHER

Van Jaarsveld 19360 (NBG).

ILLUSTRATIONS AND MAP

Figures 197a & 197b, Map 197.

198. *Delosperma laxipetalum* L.Bolus, Notes on Mesembryanthemum and allied genera 2: 66 (1929).

Cremonophyte growth form: Ascending shrublet (of medium weight, cliff squatter).

Growth form formula: E:F:As:S/H:Es (vb)

Etymology: The epithet *laxipetalum* refers to the lax floral petals.

DESCRIPTION AND HABITAT

Plants much-branched, compact shrublets up to 300 mm high. Roots fibrous. Branches minutely papillate, becoming woody, terete. Leaves decussate, subimbricate or crowded owing to short internodes, spreading, somewhat trigonous, dorsiventrally flattened, but with

distinct keel, elliptic-obovate, 10–15 × 4–7 mm; surface minutely papillate; apex rounded, apiculate. Flowers solitary (rarely in cymes of up to 3); pedicels short, 1–4 mm long, 12–14 mm in diameter. Receptacle top-shaped. Petals linear, 5–6 × 1 mm, white. Capsule top-shaped, 3–4 mm in diameter. Seed not seen.

Phenology: Flowering mainly from spring to autumn.

Pollinators: Insects.

Habitat and aspect: Vertical cliffs of narrow shady kloofs (all aspects) and river valleys. Plants are rooted in crevices and on ledges. Temperature moderate, the average daily maximum about 25°C and average daily minimum for the region about 15°C. Winters are cool but frost is absent. Rainfall occurs mainly in summer and winter, 400–500 mm per annum.

Altitude: 550–1100 m.

Associated vegetation: Groot Thicket of the Albany Thicket Biome (Mucina *et al.* 2005).

Associated cremnoophytes: At Gert Smitskloof (Baviaanskloof), the habitat is shared with *Bulbine natalensis*, *Cotyledon woodii*, *Crassula orbicularis*, *C. perforata*, *C. rupestris*, *Delosperma elsieae* and *Gasteria rawlinsonii*.

Geology: Quartzitic sandstone (light-coloured and smooth-textured), Table Mountain Group (Cape Supergroup).

DISTRIBUTION

Delosperma laxipetalum occurs widespread in the Eastern Cape, from the Baviaanskloof and Kouga in the south to the Suurberg in the northeast.

RELATED SPECIES

Related to *Delosperma rogersiae* with mauve or yellow flowers and linear leaves (glabrous or hairy).

ADAPTATIONS TO THE CLIFF ENVIRONMENT

Habit: Plants forming compact shrublets, well rooted in crevices and on ledges. A slow-growing, long-lived perennial.

Size and weight: Plants of medium weight.

Rootstock: Roots fibrous, no specialised features.

Stem: Becoming woody.

Leaves

Orientation: Spreading in shade, densely crowded and subimbricate when in full sun, triangular in cross section. Very adaptable.

Colour and texture: Pale green to green, fleshy, soft, becoming turgid after rain, but withered during dry periods, an adaptation to the extreme, dry habitat.

Age and persistence: Leaves persistent and long-lived, resulting in densely imbricate grouping.

Armament: No specific adaptation, but heavily grazed in non-cliff sites.

Sexual reproduction

Flowers: White, simple, terminally produced, conspicuous, maximising visibility for successful pollination in the vertical cliff environment. Flowering time is long and flowers are regularly produced, ensuring a long and continual seed supply.

Fruit/Seed

Size: Not seen.

Dispersal: Seeds locally dispersed by water ('wash-out dispersal', Hartmann 1991), ideal for establishment in crevices.

Time: Seeds ripening throughout summer and autumn.

Vegetative reproduction: Stems of *Delosperma laxipetalum* will root where they come into contact with the soil, a vegetative backup and adaptation to the very dry, harsh conditions on the cliff face.

CONSERVATION STATUS

Widespread and not threatened.

ADDITIONAL NOTES

Horticulture: Best for thicket and succulent karoo gardens, grown on steep embankments, rockeries or balconies. Plants rapid-growing and not shy to flower. Propagate from seed or cuttings. *Delosperma laxipetalum* does well in cultivation but outside its habitat, it is best grown under controlled conditions in a greenhouse.

VOUCHER

Van Jaarsveld 16074 (NBG).

ILLUSTRATIONS AND MAP

Figures 198a–198c, Map 198.

199. *Delosperma nubigenum* (Schltr.) L.Bolus, in Jacobsen, A handbook of succulent plants 3: 1103 (1960).

Cremonophyte growth form: Pendent to procumbent leafy stems (of medium weight, cliff hanger).

Growth form formula: E:F:P:Els (vb) (r)

Etymology: The epithet *nubigenum*, cloud-borne, refers to its high-altitude habitat.

DESCRIPTION AND HABITAT

Plants branched, soft, fragile, procumbent shrublets forming mats and drooping from cliffs, with stems up to 500 mm long. Roots fibrous. Branches glabrous, papillate, soft and green at first, terete. Leaves decussate, dorsiventrally flattened, 12–14 × 5–6 mm, pale to bright green; surface glabrous, minutely papillate, abaxial surface convex; apex acute, apiculate. Flowers terminal, solitary, 20–25 mm in diameter, shortly pedicellate. Petals linear-lanceolate, bright yellow; receptacle top-shaped. Capsule top-shaped.

Phenology: Flowering mainly from spring to summer.

Pollinators: Insects.

Habitat and aspect: Cliffs of the eastern escarpment of the central Drakensberg (all aspects). Plants are rooted in crevices and on ledges, drooping over the rock faces. Temperature very low in winter, with snow. An average daily maximum of 18°C has been recorded. The average daily minimum temperature for the region is 5°C. Rainfall occurs mainly in summer, 1000–1500 mm per annum.

Altitude: 3000–3400 m.

Associated vegetation: Drakensberg Afroalpine Heathland of the Grassland Biome (Mucina *et al.* 2005).

Associated cremonophytes: *Aloe aristata*, *A. pratensis*, *Cotyledon orbiculata*, *Crassula setulosa*, *Merwillia plumbea* and *Senecio orbicularis*.

Geology: Basalt.

DISTRIBUTION

Delosperma nubigenum occurs on the escarpment edge in the KwaZulu-Natal Drakensberg. It is confined to exposed cliffs.

RELATED SPECIES

Related to *Delosperma obtusum* which has mauve flowers and larger leaves.

ADAPTATIONS TO THE CLIFF ENVIRONMENT

Habit: Plants forming mats, with stems becoming pendent. A fast-growing, cold-tolerant species and fairly long-lived perennial.

Size and weight: Plants small.

Rootstock: Roots fibrous, no specialised features.

Stem: Becoming long and drooping.

Leaves

Orientation: Spreading-ascending.

Colour and texture: Bright green, soft and fragile, becoming turgid after rain, but withered during dry periods.

Age and persistence: Persistent.

Armament: The soft, fragile nature suggests a reduction in armament in response to the undisturbed cliff habitat in contrast to the grazed grassland.

Sexual reproduction

Flowers: Bright yellow, simple, conspicuous, maximising visibility for successful pollination in the cliff and ledge environment. Flowering time in summer and autumn is long and flowers are regularly produced, ensuring a long and continual seed supply.

Fruit/Seed

Size: Not seen.

Dispersal: Seeds locally dispersed by water ('wash-out dispersal', Hartmann 1991), ideal for establishment in crevices.

Time: Seeds ripening throughout summer and autumn.

Vegetative reproduction: Plants increase vegetatively, forming dense mats that soon become pendent, the branches (vegetative growth) rooting where they find new crevices below, an efficient vegetative dispersal backup and adaptation to the cliff face, ensuring long-term survival.

CONSERVATION STATUS

Not threatened owing to the safe habitat.

ADDITIONAL NOTES

Horticulture: Best for cool temperate to warm temperate gardens, grown in full sun on steep embankments. Its dense mat-like growth is ideal for preventing soil erosion. Propagate from

cuttings in a sandy mixture. Plants thrive in cultivation. Its very easy growing nature maximises survival rate.

VOUCHER

Van Jaarsveld 17000 (NBG).

ILLUSTRATIONS AND MAP

Figures 199a–199e, Map 199.

200. *Delosperma saxicola* Lavis in Journal of South African Botany 35,3: 145–148 (1969).

Cremonophyte growth form: Pendent leafy stems, occasionally spreading, cluster-forming shrublet (of medium weight, cliff hanger).

Growth form formula: E:F:P:Els (vb)

Etymology: The epithet *saxicola*, dwelling among rocks, pertains to its habitat.

DESCRIPTION AND HABITAT

Plants much cluster-forming, spreading shrublets up to 250 mm in diameter and 50 mm high. Roots fibrous. Branches minutely hairy at first, becoming glabrescent and grey, woody, 2 mm in diameter; nodes 4–8 mm apart. Leaves very crowded and subimbricate (owing to short internodes), club-shaped (oblanceolate, dorsiventrally viewed), 14–19 × 6–8 mm, trigonous, distinctly keeled, up to 8 mm deep; surface minutely hairy, becoming glabrescent; apex acute, apiculate. Flowers solitary, often monochasial, 20–24 mm in diameter; pedicels 5 mm long. Receptacle obconical. Petals 8 × 1 mm, white, light pink, or apices pinkish. Capsule top-shaped, fragile, 5 mm in diameter. Seed globose, 1 × 0.8 mm in diameter, surface tuberculate.

Phenology: Flowering mainly from spring to summer.

Pollinators: Insects.

Habitat and aspect: Exposed, vertical to near vertical, coastal (sea-facing), quartzitic, sandstone cliffs. The aspect is south-facing. Plants are rooted in crevices and on ledges, occasionally drooping over the rock faces. Temperatures are moderate and an average daily maximum of 25°C has been recorded. The average daily minimum temperature for the region is 12–14°C. Rainfall occurs mainly in winter and summer, ranging from 700–800 mm per annum.

Altitude: 50–100 m.

Associated vegetation: Tsitsikamma Sandstone Fynbos of the Fynbos Biome (Mucina *et al.* 2005).

Associated cremnophytes: At Lotteringriviermond, the following plants have been recorded: *Crassula orbicularis*, *Drosanthemum candens*, *Gazania rigens* var. *leucolaena*, *Lobelia cuneifolia*, *Oedera imbricata* and *Passerina* sp.

Geology: Quartzitic sandstone (Table Mountain Group, Cape Supergroup).

DISTRIBUTION

Delosperma saxicola is endemic to the coastal cliffs just north and south of the Lotteringriviermond of the Tsitsikamma National Park in the Western Cape. Although locally common, it is a rare endemic.

RELATED SPECIES

Related to *Delosperma pattersoniae* to the east and *D. littoralis* to the west. It is immediately distinguished from these two coastal species by its densely (almost imbricate) arranged leaves (short internodes). The others are procumbent, mat-forming (forming much larger mats) and the leaves are much further apart.

ADAPTATIONS TO THE CLIFF ENVIRONMENT

Habit: Small cluster-forming mats (occasionally with stems becoming pendent). A slow-growing, long-lived perennial.

Size and weight: Plants small (up to 250 mm in diameter).

Rootstock: Roots fibrous, no specialised features.

Stem: Short to long and sometimes drooping.

Leaves

Orientation: Densely crowded (subimbricate), an adaptation to the semi-arid cliff-face environment.

Colour and texture: Green, firm, minutely hairy, becoming turgid after rain, but withered during dry periods.

Age and persistence: Persistent.

Armament and camouflage: No armament or camouflage.

Sexual reproduction

Inflorescence and flowers: Mainly white to light pink or mauve, simple or in a simple terminal monochasium, conspicuous, maximising visibility for successful pollination in the cliff environment. Flowering time is long and flowers are regularly produced, ensuring a long and continual seed supply.

Fruit/Seed

Size: Seed small, 1×0.8 mm, tuberculate.

Dispersal: Dark brown seeds locally dispersed by water ('wash-out dispersal', Hartmann 1991), ideal for establishment in crevices.

Time: Seeds ripening throughout summer and autumn. Germination after 14–21 days.

Vegetative reproduction: Plants increase vegetatively, forming dense mats that soon become pendent, the branches (vegetative growth) rooting where they come into contact with new crevices below, an efficient vegetative dispersal backup and adaptation to the cliff face, ensuring long-term survival.

CONSERVATION STATUS

Very localised, well protected by the cliff-face environment.

ADDITIONAL NOTES

Horticulture: Best for coastal fynbos gardens, grown in full sun on steep embankments. Does well in containers. Outside its habitat, it should rather be grown under controlled conditions in a greenhouse. Propagate from cuttings in a sandy mixture. Grows best in slightly acid, mineral-poor soil. Plants thrive in cultivation. Its very easy growing nature maximises survival rate.

VOUCHER

Van Jaarsveld 19217 (NBG).

ILLUSTRATIONS AND MAP

Figures 200a–200d, Map 200.

201. *Delosperma subpetiolatum* L.Bolus, Notes on Mesembryanthemum and allied genera 2: 168 (1930).

Cremnophyte growth form: Pendent to procumbent leafy stems (of medium weight, cliff hanger).

Growth form formula: E:F:P:Els (vb) (r)

Etymology: The epithet *subpetiolatum* (*sub*, almost, and *petiolatum*, bearing a petiole) refers to the very short petiole.

DESCRIPTION AND HABITAT

Plants branched, soft, fragile, procumbent shrublets, mat-forming and drooping from cliffs, with stems up to 500 mm long. Roots fibrous. Branches glabrous, papillate, soft and reddish green at first, terete. Leaves ascending-spreading, decussate, dorsiventrally flattened, $10\text{--}15 \times 5\text{--}8$ mm,

bright green; adaxial surface flat, abaxial surface convex; surface glabrous, minutely papillate; apex acute, apiculate; petiole up to 1 mm long. Flowers terminal, solitary, 18 mm in diameter; pedicels 10 mm long. Receptacle top-shaped. Petals linear-lanceolate, pink. Capsule top-shaped.

Phenology: Flowering mainly from spring to summer.

Pollinators: Insects.

Habitat and aspect: Sheltered cliffs of the Eastern Cape Drakensberg (all aspects). Plants are rooted in crevices and on ledges, drooping over the rock faces. Temperatures are low in winter, with snow. The average daily maximum temperature is about 22°C and average daily minimum 12°C. Rainfall occurs mainly in summer, 1000–1200 mm per annum.

Altitude: 1000–1400 m.

Associated vegetation: Amathole Mountain Grassland of the Grassland Biome (Mucina *et al.* 2005).

Associated cremnophytes: *Aloe maculata*, *Cotyledon orbiculata* and *Crassula nudicaulis*.

Geology: Beaufort shale (Tarkastad Subgroup).

DISTRIBUTION

Delosperma subpetiolatum occurs on the Katberg and adjacent mountains in the Eastern Cape (part of the southern Drakensberg). It is confined to exposed cliffs.

RELATED SPECIES

Related to *Delosperma repens* with white to red flowers.

ADAPTATIONS TO THE CLIFF ENVIRONMENT

Habit: Forming mats, growing on ledges and fissures and with stems becoming pendent. A fast-growing, cold-tolerant species and fairly long-lived perennial.

Size and weight: Plants small.

Rootstock: Fibrous, no specialised features.

Stem: Becoming long and drooping.

Leaves

Orientation: Spreading-ascending.

Colour and texture: Bright green, soft and fragile, becoming turgid after rain, but withered during dry periods.

Age and persistence: Persistent.

Armament: The soft, fragile nature suggests a reduction in armament in response to the undisturbed cliff habitat in contrast to the grazed grassland.

Sexual reproduction

Flowers: Bright pink, simple, conspicuous, maximising visibility for successful pollination in the cliff and ledge environment. Flowering time in summer and autumn is long and flowers are regularly produced, ensuring a long and continual seed supply.

Fruit/Seed

Size: Not seen.

Dispersal: Seeds locally dispersed by water ('wash-out dispersal', Hartmann 1991), ideal for establishment in crevices.

Time: Seeds ripening throughout summer and autumn.

Vegetative reproduction: Plants increase vegetatively, forming dense mats that soon become pendent, the branches (vegetative growth) rooting when they find new crevices below, an efficient vegetative dispersal backup and adaptation to the cliff face, ensuring long-term survival.

CONSERVATION STATUS

Widespread and not threatened.

ADDITIONAL NOTES

Horticulture: Best for highveld gardens, grown in full sun. Suitable for growing in containers and hanging baskets. Plants thrive in cultivation and are easily propagated from cuttings in a sandy mixture.

VOUCHER

Van Jaarsveld 16921 (NBG).

ILLUSTRATIONS AND MAP

Figures 201a–201c, Map 201.

202. *Delosperma tradescantioides* (A.Berger) L.Bolus in *The Flowering Plants of South Africa* 7: t. 261 (1937).

Cremonophyte growth form: Pendent to procumbent leafy stems and loose mats (of medium weight, cliff hanger).

Growth form formula: E:F:P:Els (vb)

Etymology: The epithet *tradescantioides* refers to its resemblance to the genus *Tradescantia* (Commelinaceae).

DESCRIPTION AND HABITAT

Plants pendulous from cliff faces, with stems up to 1 m long, forming loose curtains. Roots fibrous. Branches 2 mm in diameter, maroon-green to green when young, glabrous or hairy, becoming grey when mature, terete; nodes 5–30(–40) mm apart. Leaves fleshy, sessile, dorsiventrally flattened, ascending-spreading, ovate to ovate-cordate or ovate-lanceolate, 20–30 × 12–17; surface glabrous or hairy, adaxial surface slightly convex, abaxial surface flat to slightly convex, except for central midrib, rounded; apex acute, mucronate; base subcordate. Flowers solitary, 25–30 mm in diameter; pedicels short, angular, 3–4 mm long, glabrous or hairy. Petals up to 17 × 1.5 mm, bright magenta (rarely red) to white. Sepals fleshy (covering ovary after flowering), 2 outer broad and up to 12 mm long, 3 inner smaller (7 mm long). Capsule 3–4 mm, obconical, 9 mm in diameter; covering membranes lacking, valve wings present, closing bodies absent. Seed pear-shaped, 0.8 × 0.5 mm in diameter, dark brown.

Phenology: Flowering mainly from spring to autumn.

Pollinators: Insects.

Habitat and aspect: Cliffs of river gorges (mainly eastern and southern aspects). Plants are rooted in crevices and on ledges, drooping over the rock faces. Temperatures are moderate, the average daily maximum about 22°C and average daily minimum for the region 14°C. Winters are cool but frost is absent. Rainfall occurs mainly in summer but at times also in winter, ranging from 600–800 mm per annum.

Altitude: 400–1440 m.

Associated vegetation: Eastern Valley Bushveld of the Savanna Biome (Mucina *et al.* 2005).

Associated cremnophytes: *Aloe arborescens*, *Bulbine natalensis*, *Cotyledon orbiculata*, *Crassula orbicularis*, *C. perfoliata* var. *minor*, *C. perforata* and *Gasteria excelsa*.

Geology: Quartzitic sandstone and shale.

DISTRIBUTION

Delosperma tradescantioides is confined to the coastal river gorges (Kei River and surrounding region) of the Eastern Cape.

RELATED SPECIES

Related to *Delosperma lebomboensis* which differs in leaf shape (also slightly smaller) and lacks indumentums. The latter is widespread in northern KwaZulu-Natal, Swaziland and Mpumalanga (especially the Lebombo Mountains), usually with white flowers.

ADAPTATIONS TO THE CLIFF ENVIRONMENT

Habit: Plants with long, pendent, leafy stems, a habit that is retained in cultivation. A rapid-growing, fairly long-lived perennial.

Size and weight: Plants forming small mats drooping from the cliff.

Rootstock: Roots fibrous, no specialised features.

Stem: The internodes of the long, pendent branches are reddish purple (grey in older plants) and up to 1 m long, an adaptation to the cliff face where the plants experience little competition or predation. Stems and leaves soft and fragile, a character that can be viewed as an adaptation to a little-disturbed environment.

Leaves

Orientation: Ascending-spreading.

Colour and texture: Pale green and flattened, adapted to grow in shade, thus ideal for the often shady cliff habitats. The fleshy leaves are soft, becoming turgid after rain, but withered during dry periods, an adaptation to the extreme, dry habitat.

Age and persistence: Persistent, long-lived, eventually withering.

Armament: Leaves soft and fragile, without armour.

Sexual reproduction

Flowers: Mauve, reddish or white, simple, axillary produced, conspicuous. Flowering time is long and flowers are regularly produced, ensuring a long and continual seed supply.

Fruit/Seed

Size: Seed 0.8×0.5 mm, tuberculate, the size ideal for establishment in crevices.

Dispersal: Dark brown seeds locally dispersed by rainwater ('wash-out dispersal', Hartmann 1991), settling and germinating in crevices.

Time: Seeds ripening throughout summer and autumn. Germination after 14–21 days.

Vegetative reproduction: Plants increase vegetatively, forming dense mats that soon become pendent, the branches (vegetative growth) rooting when they reach new crevices below, an efficient vegetative dispersal backup and adaptation to the cliff face, ensuring long-term survival.

CONSERVATION STATUS

A local endemic, not threatened.

ADDITIONAL NOTES

Horticulture: Plants easily grown from seed or cuttings and thrive in cultivation. Its very easy growing nature maximises survival rate.

VOUCHER

Van Jaarsveld 7157 (NBG).

ILLUSTRATIONS AND MAP

Plate 202, Figure 202a, Map 202.

203. *Delosperma velutinum* L.Bolus, Notes on Mesembryanthemum and allied genera 2: 39 (1929).

Cremnophyte growth form: Pendent to procumbent leafy stems (of medium weight, cliff hanger).

Growth form formula: E:F:P:Els (vb)

Etymology: The epithet *velutinum* pertains to the velvety indumentum of the leaf.

DESCRIPTION AND HABITAT

Plants compact shrublets, forming longer spreading branches, sometimes pendent from cliff face, with stems up to 300 mm long. Roots fibrous. Branches 2.2 mm in diameter, green when young, with short dense hairs or glabrous, becoming grey when mature, terete; internodes very short. Leaves fleshy, ascending-spreading, crowded at branch tips, subimbricate, subsessile, dorsiventrally flattened, ovate to ovate-lanceolate, 15–22 × 8–12 mm; surface densely hairy (velutinous), adaxial surface slightly convex, abaxial surface keeled; apex acute, apiculate; base cuneate; old leaves persistent. Flowers solitary, 25–30 mm in diameter; pedicels short, angular, 3–4 mm long, glabrous or hairy. Petals up to 14 mm in diameter, white or mauve.

Phenology: Flowering mainly from spring to autumn.

Pollinators: Insects.

Habitat and aspect: Cliffs of the eastern escarpment margin (Kranskop, Thukela), also river gorges (northern aspects). Plants are rooted in crevices and on ledges. Temperatures are moderate, the average daily maximum about 24°C and average daily minimum for the region 12°C. Winters are cool but frost is absent or light. Rainfall mainly in summer but at times also in winter, ranging from 700–800 mm per annum.

Altitude: 100–1550 m.

Associated vegetation: Eastern Valley Bushveld of the Savanna Biome (Mucina *et al.* 2005).

Associated cremnophytes: *Aloe arborescens*, *Bulbine natalensis*, *Crassula expansa* subsp. *fragilis* and *C. perfoliata* var. *heterotricha*.

Geology: Quartzitic sandstone and shale.

DISTRIBUTION

Delosperma velutinum occurs widespread, from the escarpment margin overlooking the Thukela River basin to Shongweni and Oribi Gorge in coastal and southern KwaZulu-Natal.

RELATED SPECIES

Related to *Delosperma tradescantioides*, with distinctly flat leaves, and *D. echinatum* of the Eastern Cape, the latter with long distinct trichomes and oval to globular leaves.

ADAPTATIONS TO THE CLIFF ENVIRONMENT

Habit: A fairly long-lived, perennial shrublet. Plants also producing longer spreading stems, rooting and colonising new crevices.

Size and weight: Plants forming small shrublets firmly wedged in crevices.

Rootstock: Roots fibrous, no specialised features.

Stem: Becoming woody, sturdy shrublets.

Leaves

Orientation: Grouped and almost imbricate, at ends of branches.

Colour: Pale green.

Armament: Leaves soft and fragile, without armour.

Sexual reproduction

Flowers: White to mauve, simple, solitary, axillary, conspicuous. Flowering time is long and flowers are regularly produced, ensuring a long and continual seed supply.

Fruit/Seed

Size: Not seen.

Dispersal: Seeds dispersed by water ('wash-out dispersal', Hartmann 1991).

Time: Seeds ripening throughout summer and autumn.

Vegetative reproduction: Plants increase vegetatively, forming dense mats that soon become pendent, the branches (vegetative growth) rooting when they find new crevices below, an efficient vegetative dispersal backup and adaptation to the cliff face, ensuring long-term survival.

CONSERVATION STATUS

A local endemic, not threatened.

ADDITIONAL NOTES

Horticulture: Best for dry bushveld gardens, on steep embankments and rockeries. Outside its habitat, it is best grown under controlled conditions in a greenhouse. Propagate from cuttings. Thrives in containers. Its easy growing nature maximises survival rate.

VOUCHER

Van Jaarsveld 18048 (NBG).

ILLUSTRATIONS AND MAP

Figures 203a–203c, Map 203.

204. *Delosperma waterbergense* L.Bolus in Journal of South African Botany 29: 48 (1963).

Cremonophyte growth form: Pendent leafy stems to cluster-forming (of light weight, cliff hanger).

Growth form formula: E:F:P:Els (vb)

Etymology: After its habitat, the Waterberg, Limpopo Province.

DESCRIPTION AND HABITAT

Plants compact shrublets (sometimes becoming pendent) up to 100 mm high. Rootstock swollen. Stems minutely papillate. Leaves ascending, subterete, linear, 25–34(–50) × 2–4 mm, (4 mm at widest point); abaxial surface canaliculate; apex acute. Flowers solitary, 30–40 mm in diameter; pedicels 6–16 mm long. Petals linear-spathulate, up to 22 × 2 mm, pink. Filaments pink. Capsule 5 mm in diameter. Seed pear-shaped, 0.5 × 0.3 mm, tuberculate, dark brown.

Phenology: Flowering mainly in summer.

Pollinators: Insects.

Habitat and aspect: South-facing cliffs of the Waterberg (Limpopo Province) plateau margin. Plants are rooted in crevices and on ledges. Temperatures are moderate, the average daily maximum about 27°C and average daily minimum for the region about 12°C. Winters are cool but frost is absent or light. Rainfall mainly in summer, 700–800 mm per annum.

Altitude: 1500–1800 m.

Associated vegetation: Waterberg Magaliesberg Summit Sourveld of the Grassland Biome (Mucina *et al.* 2005).

Associated cremnophytes: In its native habitat at Marakele National Park, it grows in association with *Aeollanthus buchnerianus*, *A. parvifolius*, *Agapanthus coddii*, *Aloe arborescens*, *Bulbine natalensis*, *Crassula cymbiformis*, *C. sarcocaulis*, *C. setulosa*, *C. swaziensis*, *Lobelia aquamontanus*, *Teedia pubescens*, *Tetradenia brevispicata*.

Geology: Quartzitic sandstone, Matlabas Subgroup (Waterberg Group).

DISTRIBUTION

Delosperma waterbergense is endemic to the Waterberg (Limpopo Province).

RELATED SPECIES

Delosperma waterbergense is related to *D. zoutpansbergense* but is at once distinguished by its compact growth with a swollen rootstock.

ADAPTATIONS TO THE CLIFF ENVIRONMENT

Habit: A long-lived, cluster-forming shrublet well anchored in fissures, crevices and ledges.

Size and weight: Plants forming small shrublets firmly wedged in crevices, sometimes becoming pendent.

Rootstock: Roots fleshy, providing anchorage and storage from which damaged branches can perennate.

Stem: Herbaceous, becoming slightly woody.

Leaves

Orientation: Ascending-spreading, crowded, linear, subterete, an adaptation to the dry habitat.

Colour: Green.

Armament: Leaves soft and fragile, without armour.

Sexual reproduction

Flowers: Simple, larger than those of most other *Delosperma* species, thus rich flowering attracting insect pollinators to the cliff-face habitat. Flowering time is in the growing season, fairly long, and flowers are regularly produced, ensuring a long and continual seed supply.

Fruit/Seed

Size: Seed 0.5×0.3 mm, pear-shaped, tuberculate.

Dispersal: Dark brown seeds dispersed by water ('wash-out dispersal', Hartmann 1991).

Time: Seeds ripening throughout summer and autumn.

Vegetative reproduction: Plants increase vegetatively, forming small mats that become pendent, the branches (vegetative growth) rooting when coming into contact with soil, an efficient vegetative dispersal backup and adaptation to the cliff face, ensuring long-term survival.

CONSERVATION STATUS

A local endemic, not threatened.

ADDITIONAL NOTES

Horticulture: Best for highveld gardens, grown in containers or rockeries. Outside its habitat, it is best grown under controlled conditions in a greenhouse. Propagate from cuttings. Does well in containers, in dappled shade or full sun. Its ease of growth maximises survival rate.

VOUCHER

Van Jaarsveld 17953 (NBG).

ILLUSTRATIONS AND MAP

Plate 204, Figures 204a–204c, Map 204.

205. *Delosperma zoutpansbergense* L.Bolus in Journal of South African Botany 25: 372 (1959).

Cremnophyte growth form: Pendent to procumbent leafy stems (of medium weight, cliff hanger).

Growth form formula: E:F:P:Els (vb)

Etymology: After its habitat, the Soutpansberg, Limpopo Province.

DESCRIPTION AND HABITAT

Plants procumbent, mat-forming, up to 30 mm high, without swollen rootstock. Stems with shiny papillae; nodes 20–40(–45) mm apart. Leaves spreading ascending, subterete, linear, 10–50 × 2–4 mm; surface papillate, adaxial surface channelled; apex acute. Flowers solitary, 27–30 mm in diameter; pedicels up to 15 mm long. Petals linear-spathulate, 10–13 × 0.75–1.25 mm, pink. Filaments pink; apices white. Capsule not seen. Seed not seen.

Phenology: Flowering mainly in summer.

Pollinators: Insects.

Habitat and aspect: Upper sheltered south-facing cliffs of the Zoutpansberg (Limpopo Province). Plants are rooted in crevices and on ledges. Temperatures are moderate, the average daily maximum about 25°C and average daily minimum for the region 10°C. Winters are cool but frost is absent or light. Rainfall occurs mainly in summer, 1250–1500 mm per annum.

Altitude: 1500–1730 m.

Associated vegetation: Soutpansberg Summit Sourveld (Mucina *et al.* 2005).

Associated cremnoophytes: *Aeollanthus buchnerianus*, *Aloe arborescens*, *Crassula swaziensis*, *Kalanchoe crundallii*, *Plectranthus mutabilis* and *Thorncroftia succulenta*.

Geology: Protozoic quartzitic sandstone (Soutpansberg Group, Wyllies Poort Formation).

DISTRIBUTION

Delosperma zoutpansbergensis appears to be endemic to the upper south-facing cliffs of the Soutpansberg (Limpopo Province), growing on ledges, in crevices and fissures.

RELATED SPECIES

Related to *Delosperma waterbergense* but is at once distinguished by its smaller flowers and lack of a tuberous base.

ADAPTATIONS TO THE CLIFF ENVIRONMENT

Habit: A soft, procumbent, mat-forming plant.

Size and weight: Small, soft, fragile mats firmly wedged in crevices.

Rootstock: Roots fibrous, providing anchorage in crevices.

Stem: Herbaceous, becoming slightly woody.

Leaves

Orientation: Ascending-spreading, soft, linear, subterete, an adaptation to the seasonally dry habitat.

Colour: Pale green.

Armament: Leaves soft and fragile, without armour.

Sexual reproduction

Flowers: Simple but conspicuous, thus rich flowering attracting insect pollinators to the cliff-face habitat. Flowering time is during the growing season, fairly long, and flowers are regularly produced, ensuring a long and continual seed supply.

Fruit/Seed

Size: Seed 0.5×0.3 mm, pear-shaped, tuberculate.

Dispersal: Dark brown seeds dispersed by water ('wash-out dispersal', Hartmann 1991).

Time: Seeds ripening throughout summer and autumn.

Vegetative reproduction: Plants increase vegetatively, forming small mats that become pendent, the branches (vegetative growth) rooting where they touch the soil, an efficient vegetative dispersal backup and adaptation to the cliff face, ensuring long-term survival.

CONSERVATION STATUS

A local endemic, not threatened.

ADDITIONAL NOTES

Horticulture: Best for highveld gardens, grown in containers or rockeries. Outside its habitat, it is best grown under controlled conditions in a greenhouse. Propagate from cuttings. Thrives in containers, in dappled shade or full sun. Its ease of growth maximises survival rate.

VOUCHER

Van Jaarsveld 19776 (NBG).

ILLUSTRATIONS AND MAP

Figures 205a–205d, Map 205.

DROSANTHEMUM Schwantes

206. *Drosanthemum anemophilum* Van Jaarsv. & S.A.Hammer in *Cactus and Succulent Journal* (U.S.) 76,4: 204 (2004).

Cremnophyte growth form: Erect, spindly shrub (of medium weight to heavy, cliff squatter).

Growth form formula: E:F:As:W:Ev

Etymology: The epithet *anemophilum*, wind-loving, pertains to the wind-dispersed seed.

DESCRIPTION AND HABITAT

Erect, virgate, spindly shrubs up to 1.5 m tall, with leaves and fertile parts carried at tips of branches. Main branch up to 18 mm thick, terete, sometimes slightly angular, with smooth purplish brown bark; young branches bubbly papillate, papillae subsiding with age; older branches glabrescent. Leaves opposite, equal, papillate, compressed, 3-angled, $10\text{--}16 \times 2\text{--}2.5 \times 2$ mm, dark dull green, never reddened, ascending-spreading; apices slightly incurved,

obtuse. Flowers diurnal, appearing in late spring and early summer (October to early November), solitary, apical; pedicels 2–8(–15) mm long. Sepals 5, triangular, 3 × 3 mm, margins thin, aging to a dull purple. Petals linear, 10–14 × 0.5 mm, blunt, spreading, in 2 series: a longer outer one and a shorter inner erect one, mauve pink to white, shiny. Filamentous staminodes in a central cone; filaments about 2 mm long, white; anthers 0.3 mm long, white, not overtopping stigmas. Ovary conical, 5-angled, raised to about 2.5 mm, reddish when fresh; stigmas 5, ascending-spreading, lanceolate, 1.5–2 mm long. Capsule globose to top-shaped, 5-locular, placentation parietal, 9–11 × 7–9 mm when fresh, reduced to about 7–8 × 5–8 mm when dried, loculi deep and slightly narrowing to the 4 mm wide apex (vs 5–6 mm at widest point of capsule), hard and bone-like, ivory-coloured when dried, difficult to break open with the fingers, hygroscopic; valves triangular, 2 × 2 mm, without wings, remaining erect once opened; expanding keels contiguous, parallel, loculi deep (4–5 mm), without covering membranes, central axis and loculi roofs raised to almost as high as open erect valves. Seed 1.3 × 0.75 × 0.40 mm, minutely tuberculate, slightly flattened, brownish.

Phenology: Flowering mainly in spring.

Pollinators: Insects.

Habitat and aspect: Steep south-facing aspects, on and below sandstone cliffs, up to altitudes of about 1000 m. Plants rooted in crevices and on ledges. Temperature high in summer, warm with cold nights in winter. Average daily maximum temperature about 29°C and average daily minimum about 14°C. Rainfall in winter and summer, 200–300 mm per annum.

Altitude: 800–1000 m.

Associated vegetation: Western Little Karoo of the Succulent Karoo Biome (Mucina *et al.* 2005).

Associated cremnoophytes: Associated species at the type locality at Rooinek Pass include *Crassula atropurpurea* var. *purcellii*, *C. brachystachya*, *Othonna triplinervia* and *Senecio articulatus*.

Geology: Quartzitic sandstone, Table Mountain Group (Cape Supergroup).

DISTRIBUTION

Drosanthemum anemophilum is a quartzitic sandstone endemic, confined mainly to the south-facing cliffs on the Rooinek Pass, south of Laingsburg (Western Cape).

RELATED SPECIES

Not closely related to any other *Drosanthemum*. See note below.

ADAPTATIONS TO THE CLIFF ENVIRONMENT

Habit: Erect, very sparsely branched, virgate growth habit up to 1.5 m high.

Size and weight: Plants of medium weight to heavy in large specimens.

Rootstock: With central taproot, thus firmly anchored on cliff faces. Roots fibrous.

Stem: Erect, soon becoming woody.

Leaves

Orientation: Ascending-spreading.

Colour: Pale green.

Age and persistence: Leaves persistent and long-lived, eventually withering.

Armament: No armament.

Sexual reproduction

Flowers: Flowers are solitary at branch ends, conspicuous, maximising visibility for successful pollination in the cliff environment. Flowering time is in spring (October–November).

Fruit/Seed

Size: Seed $1.3 \times 0.75 \times 0.40$ mm, brownish, minutely tuberculate.

Dispersal: Capsule remaining open, the slightly flattened seed dispersed by wind and jactitation (Van der Pijl 1982).

Time: Seeds ripening throughout summer and autumn, in time for winter rains. Germination after 14–21 days.

Vegetative reproduction: Absent.

CONSERVATION STATUS

A local endemic, not threatened.

ADDITIONAL NOTES

Note: Not only is it an unusual *Drosanthemum*, it is unique in the Mesembryanthemaceae in several ways. It is unusually tall for a mesemb. The fruit capsules are bone-like in texture, hygroscopic and anemochorous. Their valves lack wings, and the deep loculi have small fragmentary roofs in an erect position. After opening, the valves remain open and in an erect position, allowing easy egress for the unusually large, somewhat flattened seeds, which are dispersed by strong gusts of wind. This is the first record of anemochory in the genus *Drosanthemum*.

Horticulture: Plants easily grown from seed, thriving in cultivation. It has a rapid growth rate and flowers after the third year of sowing.

VOUCHER

Van Jaarsveld 13695 (NBG).

ILLUSTRATIONS AND MAP

Figure 206a, Map 206.

207. *Drosanthemum expersum* (N.E.Br.) Schwantes in Zeitschrift für Sukkulantenkunde 3: 30 (1927).

Cremonophyte growth form: Pendent to procumbent leafy stems (of medium weight, cliff hanger).

Growth form formula: E:F:P:Els (vb) (r)

Etymology: The epithet *expersum*, devoid of, pertains to the capsules, which are without covering membranes.

DESCRIPTION AND HABITAT

Plants much-branched, long-lived, mat-forming, pendulous shrublets from cliff faces, with stems up to 400 mm long forming loose mats. Roots fibrous; main root (taproot) succulent, up to 5 mm in diameter, cylindrical, about up to 120 mm long. Branches 1 mm in diameter, maroon at first, becoming dark purplish brown, soft, brittle, terete; nodes 5–12 mm apart; surface papillate; hairs multicellular, translucent. Leaves fleshy, subterete, linear, papillate, 9–14 × 2 mm, ascending-spreading; surface papillate, green, adaxial surface somewhat flattish; apex obtuse. Flowers solitary, up to 35 mm in diameter; pedicels 18–65 mm long. Receptacle cup-shaped, 2 mm deep, 8 mm in diameter, bearing 2 outer triangular-lanceolate sepals 5 × 3.5 mm and 3 smaller sepals 3 × 2 mm. Petals bright magenta, 10–15 × 0.5–1.5 mm. Ovary pointed; stigmas 5, lanceolate, 4.0–5.5 mm long, papillate; nectaries green. Capsule cup-shaped, 8 mm in diameter (open 12 mm), top pyramidal; covering membranes lacking, valve wings present, closing bodies absent. Younger fruits reddish, 10–12 mm in diameter before desiccating. Seed up to 0.8 mm in diameter, pale brown.

Phenology: Flowering mainly in spring.

Pollinators: Insects.

Habitat and aspect: Sheltered south- and east-facing cliffs of the upper slopes of the central and northern Cape Fold Belt mountains. Plants are rooted in crevices and on ledges, drooping over the rock faces. Temperatures relatively low, with snow in winter. The average daily maximum temperature is about 20°C and average daily minimum about 8°C. Rainfall occurs mainly in winter, estimated to be above 1000–1500 mm per annum.

Altitude: 1200–2000 m.

Associated vegetation: North Hex Sandstone Fynbos of the Fynbos Biome (Mucina *et al.* 2005).

Associated cremnophytes: Associated species include *Crassula nudicaulis*, *C. pellucida* subsp. *spongiosa* and *Esterhuysenia drepanophylla*.

Geology: Quartzitic sandstone, Table Mountain Group (Cape Supergroup).

DISTRIBUTION

Drosanthemum exspersum is a quartzitic sandstone endemic, confined mainly to south-facing cliffs from Tafelberg (Cold Bokkeveld, Western Cape) to Bobbejaansberg and Matroosberg in the south (Western Cape) and northwards to the Calvinia district (Northern Cape).

RELATED SPECIES

Not closely related to any other *Drosanthemum*. A unique feature setting it apart from most other members of the genus, is the absence of covering membranes and hence its former placement in the genus *Delosperma*. Could perhaps be related to the deciduous cremnophilous *Drosanthemum inornatum* of the Hunsberg in southern Namibia with smaller, puce-coloured flowers and capsules without covering membranes.

ADAPTATIONS TO THE CLIFF ENVIRONMENT

Habit: Plants with pendent, leafy stems, a habit that is retained in cultivation. A rapid-growing, fairly long-lived perennial, sprouting from the basal portion of the stem.

Size and weight: Plants of medium weight.

Rootstock: With central taproot, thus firmly anchored on cliff face. Roots fibrous. Perennial rootstock long-lived and re-sprouting, thus differing from most other short-lived *Drosanthemum* species.

Stem: Pendent and forming loose mats on ledges. Stems and leaves soft and fragile, a character that can be viewed as a reduction in armament as a result of the undisturbed habitat.

Leaves

Orientation: Ascending-spreading, somewhat recurved.

Colour: Pale green.

Age and persistence: Leaves persistent and long-lived, eventually withering and resulting in apical grouping.

Armament: The softer leaf texture suggests a reduction in armament in response to the undisturbed cliff habitat in contrast to the grazed grassland and subtropical forest.

Sexual reproduction

Flowers: Flowers simple, borne at branch ends or axillary produced, conspicuous, maximising visibility for successful pollination on the vertical cliffs. Flowering time is in spring.

Fruit/Seed

Size: Seed up to 0.8 mm in diameter, an ideal size for establishment in crevices.

Dispersal: Seeds dispersed by rainwater ('wash-out dispersal', Hartmann 1991), settling and germinating in crevices.

Time: Seeds ripening throughout summer and autumn, in time for winter rains. Germination after 14–21 days.

Vegetative reproduction: Plants increase vegetatively, forming small mats that become pendent, the branches (vegetative growth) rooting where they come into contact with soil, an efficient vegetative dispersal backup and adaptation to the cliff face, ensuring long-term survival.

CONSERVATION STATUS

A local endemic well protected in the habitat, not threatened.

ADDITIONAL NOTES

Horticulture: Best for cool fynbos and other temperate gardens, grown in containers or on rockeries. Outside its habitat, it is best grown under controlled conditions in a greenhouse. Propagate from cuttings. *Drosanthemum expersum* does well in containers, in dappled shade or full sun. Its ease of growth maximises survival rate.

VOUCHERS

Van Jaarsveld 18413, 18621, 19210, 20059 (NBG).

ILLUSTRATIONS AND MAP

Plate 207, Figures 207a–207i, Map 207.

208. *Drosanthemum inornatum* (L.Bolus) L.Bolus in *Journal of South African Botany* 30: 33–44 (1964). (Hunsberg form.)

Crempnophyte growth form: Pendent leafy stems from tuberous roots (of medium weight, cliff hanger).

Growth form formula: E:F:P:Els:D (vb) (eg)

Etymology: The epithet *inornatum* pertains to its generally unattractive features.

DESCRIPTION AND HABITAT

Plants much-branched, long-lived, pendulous (from cliff faces), summer-deciduous shrublets with stems up to 500 mm long forming loose mats. Main branch up to 8 mm in diameter. Roots tuberous (main root or taproot) succulent, up to 5 mm in diameter. Branches 1.8–2.5 mm in diameter, 3.5 mm in diameter (basally up to 4 mm) at swollen nodes, at first green, with

translucent papillate epidermis, becoming brownish, longitudinally fissured, becoming dark purplish brown, slightly articulated at nodes, soft and brittle, terete; nodes 7–25 mm apart. Leaves summer-deciduous, fleshy, green, spreading, pendent, subterete, linear, papillate, 12–18(–25) × 2 mm, drooping; surface papillate, green, adaxial surface somewhat flattish; apex obtuse. Flowers solitary, up to 20 mm in diameter; pedicels 8–10 mm long. Receptacle cup-shaped, 2–3 mm deep, 4 mm in diameter, bearing fleshy sepals with membranous wings. Petals puce, 8 × 1–1.5 mm. Stigmas 5 mm long, papillate; nectaries green. Capsule top-shaped, fragile, 5–6 mm in diameter, about 3–4 mm deep (open 9 mm in diameter, at top); covering membranes lacking, valve wings broad, 2 × 2 mm, closing bodies absent. Seed 0.6 × 0.4 mm, light brown.

Phenology: Flowering mainly in spring.

Pollinators: Bees (Hartmann 1991).

Habitat and aspect: Confined to south-facing cliffs, the plants growing on ledges and crevices. Temperature warm to high in summer and mild to warm in winter, but regularly cooled by fog from the Atlantic. The average daily maximum temperature is about 24°C and the average daily minimum temperature for the region 10°C. Winters are cooler but frost is absent. Rainfall occurs mainly in winter and about 50–75 mm per annum (mainly cyclonic winter rain). Regular fog provides extra moisture.

Altitude: 800–1100 m.

Associated vegetation: Succulent Karoo.

Associated cremnophytes: *Drosanthemum inornatum* shares its habitat at the type locality (at Konsertinaberg) with *Crassula sladenii*, *C. tomentosa* var. *tomentosa*, an undescribed *Hartmanthus* sp., *Tylecodon buchholzianus* and *T. singularis*.

Geology: Dolomite cliffs of the Port Nolloth Zone (Gariiep Supergroup).

DISTRIBUTION

Southern Namibia, east of Rosh Pinah, confined to dolomite.

RELATED SPECIES

Not closely related to any other *Drosanthemum*. A unique feature distinguishing it from most other members of the genus, is the absence of covering membranes. In this respect it is similar to *D. expersum*, another cremnophyte occurring from Nieuwoudtville to Matroosberg in the south. Another unusual feature is the deciduous nature of the plants.

ADAPTATIONS TO THE CLIFF ENVIRONMENT

Habit: Plants with pendent, leafy stems, a habit that is retained in cultivation.

Size and weight: Plants of medium weight.

Rootstock: Tuberous roots ensure good anchorage and long-term survival.

Stem: Pendent, forming loose mats on ledges. Stems and leaves soft and fragile, young stems with a fleshy, translucent layer, the epidermis covered in papillae, a character that can be viewed as an adaptation to the shady, south-facing cliffs during its cooler growing season. The reduction in armament (fragility) can be viewed as a result of the undisturbed cliff-face habitat.

Leaves

Orientation: Drooping from the drooping stems, an adaptation to the vertical cliff face.

Colour and texture: Bright green, papillate.

Age and persistence: Leaves deciduous towards summer.

Armament: The absence of armament and the soft leaf texture suggest a response to the undisturbed cliff habitat.

Sexual reproduction

Flowers: Simple, in leaf axils. Flowering in winter and spring.

Fruit/Seed

Size: Seed 0.6×0.4 mm, an ideal size for establishment in crevices.

Dispersal: Seeds dispersed by rainwater ('wash-out dispersal', Hartmann 1991), settling and germinating in crevices.

Time: Seeds ripening throughout spring.

Vegetative reproduction: Absent.

CONSERVATION STATUS

A local endemic, not threatened.

ADDITIONAL NOTES

Horticulture: Best grown in containers under controlled conditions in a greenhouse. It has little ornamental value and is grown as a curiosity plant. Propagate from cuttings in sandy soil. Sow seed in autumn. Plants easily grown from cuttings, doing well in cultivation. Its very easy growth maximises survival rate.

VOUCHER

Van Jaarsveld 19915 (NBG).

ILLUSTRATIONS AND MAP

Figures 208a & 208b, Map 208.

EREPSIA N.E.Br.

209. *Erepsia heteropetala* (Haw.) Schwantes in Gartenflora 77: 68 (1928).

Cremnophyte growth form: Pendent, cluster-forming (of medium weight, cliff hanger).

Growth form formula: E:F:As:W:Ev

Etymology: The epithet *heteropetala* refers to the variable length of the petals.

DESCRIPTION AND HABITAT

Plants much-branched, cushion-shaped or pendent shrublets up to 300 mm in diameter. Roots fibrous. Stems reddish brown, up to 4.5 mm in diameter, soft at first becoming woody; nodes 5–30 mm apart. Leaves ascending, fleshy, pale green (margins and leaf tips sometimes reddish), triquetrous, slightly laterally compressed (8 mm wide), falcate to subfalcate, 35(–50) × 7 mm; margin serrate-denticulate; surface smooth, adaxial surface somewhat flat to slightly channelled; apex mucronate, reddish at tips. Flowers solitary or up to 3 in apical cymes, up to 40 mm in diameter; pedicels 6 mm long (in fruit). Petals purplish pink, linear, merging with staminodes. Capsule top-shaped, 15 mm deep, 15 mm in diameter at top; closing body absent, covering membranes present, valves light brown, valve wings narrow. Seed 1.5 × 1.2 mm in diameter, somewhat laterally compressed (0.5 mm) tuberculate, pale brown.

Phenology: Flowering mainly in spring and summer.

Pollinators: Insects.

Habitat and aspect: Mainly south- and west-facing cliffs of the central Cape Fold Belt mountains. Plants are rooted in crevices and on ledges, sometimes drooping over the rock faces. Temperatures are relatively low, with occasional snow in winter. The average daily maximum temperature is about 20°C and the average daily minimum for the region about 10°C. Rainfall occurs mainly in winter and is estimated to be above 1000–1500 mm per annum.

Altitude: 400–1300 m.

Associated vegetation: Hawekwas Sandstone Fynbos of the Fynbos Biome (Mucina *et al.* 2005).

Associated cremnophytes: Associated species include *Crassula pellucida* subsp. *alsinoides*, *C. nudicaulis*, *C. pellucida* subsp. *spongiosa*, *Esterhuysenia stokoei*, *Oscularia caulescens* and *O. deltoides*.

Geology: Quartzitic sandstone, Table Mountain Group (Cape Supergroup).

DISTRIBUTION

Erepsia heteropetala is a quartzitic sandstone endemic, confined to the south- and east-facing cliffs in the Du Toitskloof and adjacent regions of the southwestern Cape (Western Cape).

RELATED SPECIES

Related to *Erepsia lacera* in shape, colour and size of the leaves, but the latter is an erect shrublet from Paarlberg. Two smaller species, *E. forficata* (Table Mountain) and *E. inclaudens* (Kogelberg), also occur frequently on cliff faces in the Western Cape.

ADAPTATIONS TO THE CLIFF ENVIRONMENT

Habit: Plants with compact cushion or becoming pendent, this habit retained in cultivation. A rapid-growing, fairly long-lived perennial.

Size and weight: Plants of medium weight.

Rootstock: Fibrous, no specialised features.

Stem: Stems and leaves softer and more fragile than those of the closely related *Erepsia lacera*, a character that can be viewed as a reduction in armament as a result of the undisturbed habitat.

Leaves

Orientation: Ascending-spreading.

Colour: Pale green, somewhat glaucous.

Age and persistence: Leaves persistent and long-lived, eventually withering and resulting in apical grouping.

Armament: Plants without obvious armament.

Sexual reproduction

Inflorescence and flowers: Flowers simple or in cymes of 3, at branch ends or axillary produced, conspicuous, thus maximising visibility for successful pollination in the vertical cliff environment. Flowering time is in late spring and summer and flowers are regularly produced, ensuring a long and continual seed supply.

Fruit/Seed

Size: Seed large, 1.5 mm in diameter, with tuberculate surface ideal for establishment in crevices.

Dispersal: Seeds locally dispersed by rainwater ('wash-out dispersal', Hartmann 1991), but their compressed nature appears to be an adaptation for wind dispersal as well.

Time: Seeds ripening throughout summer and autumn, in time for winter rains.

Vegetative reproduction: Absent.

CONSERVATION STATUS

A local endemic, not threatened (Hilton-Taylor 1996).

ADDITIONAL NOTES

Horticulture: Plants easily grown from seed or cuttings, thriving in cultivation. Its very easy growing nature maximises survival rate.

VOUCHERS

Van Jaarsveld 18419, 18421 (NBG).

ILLUSTRATIONS AND MAP

Figures 209a–209e, Map 209.

ESTERHUYSENIA L.Bolus

210. *Esterhuysenia stokoei* (L.Bolus) H.E.K.Hartmann in *Bradleya* 16: 44–91 (1998).

Cremonophyte growth form: Pendent to procumbent leafy stems (of light weight, cliff squatter).

Growth form formula: E:F:P:Els (vb) (r)

Etymology: After Thomas Stokoe (1868–1959), mountaineer and plant collector.

DESCRIPTION AND HABITAT

Plants much-branched, pendulous, glabrous shrublets on cliff faces, with stems up to 300 mm long forming loose mats. Roots fibrous. Branches 1 mm in diameter (main branch up to 5 mm in diameter), yellowish at first, becoming brown, soft, brittle, terete; nodes 5–30 mm apart; surface smooth. Leaves fleshy, trigonous, linear, falcate to subfalcate, grey-green, reddish at tips, 8–14 × 3 mm, ascending-spreading; surface finely papillate, green, adaxial surface somewhat flat; apex mucronate. Flowers solitary, 30–45 mm in diameter; pedicels 10–50 mm long (in fruit). Petals purplish pink, 4–20 × 0.25–2.5 mm. Filaments absent; anthers yellow. Capsule top-shaped, 5 mm deep, 6–8 mm in diameter (open 12–13 mm); closing body absent, covering membranes lacking, but with closing ledges, valves light brown, valve wings narrow. Seed 1.5 × 1.3 mm in diameter, echinulate, dark brown.

Phenology: Flowering mainly in late spring.

Pollinators: Insects.

Habitat and aspect: Mainly sheltered south-facing cliffs. Plants are rooted in crevices and on ledges, drooping over the rock faces. Temperatures moderate in summer, with cold winters and occasional snow. An average daily maximum temperature of about 20°C has been

recorded. The average daily minimum temperature for the region is about 8°C. Rainfall occurs mainly in winter and is estimated to be above 1000–1500 mm per annum.

Altitude: 800–1500 m.

Associated vegetation: North Hex Sandstone Fynbos of the Fynbos Biome (Mucina *et al.* 2005).

Associated cremnophytes: Associated species include *Crassula alsinoides* subsp. *alsinoides*, *C. nudicaulis*, *C. pellucida* subsp. *spongiosa*, *Erepsia heteropetala* and *Oscularia deltoides*.

Geology: Quartzitic sandstone, Table Mountain Group (Cape Supergroup).

DISTRIBUTION

Esterhuysenia stokoei is a quartzitic sandstone endemic, confined to south-facing cliffs in the Du Toitskloof and Franschhoek regions of the southwestern Cape (Western Cape).

RELATED SPECIES

Not closely related to any of the other three *Esterhuysenia* species. *Esterhuysenia drepanophylla* also commonly occurs on cliffs in the Western Cape but it is a shrublet with very different leaves.

ADAPTATIONS TO THE CLIFF ENVIRONMENT

Habit: Plants with pendent, leafy stems, a habit that is retained in cultivation. A rapid-growing, fairly long-lived, perennial.

Size and weight: Plants of light weight.

Rootstock: Central taproot and branches rooting where touching the ground. Roots fibrous, no specialised features.

Stem: Pendent and forming loose mats. Stems and leaves soft and fragile, a character that can be viewed as a reduction in armament as a result of the undisturbed habitat.

Leaves

Orientation: Ascending-spreading.

Colour: Pale green, somewhat glaucous.

Age and persistence: Leaves persistent and long-lived, eventually withering and resulting in apical grouping.

Armament: The softer leaf texture (compared to other *Esterhuysenia* species) suggests a reduction in armament in response to the undisturbed cliff habitat in contrast to the surrounding accessible fynbos.

Sexual reproduction

Inflorescence and flowers: Flowers simple, at branch ends or axillary produced, conspicuous, thus maximising visibility for successful pollination in the vertical cliff environment. Flowering time is in late spring and flowers are regularly produced, ensuring a long and continual seed supply.

Fruit/Seed

Size: Seed large, 1.5 mm in diameter, the echinulate surface ideal for establishment in crevices.

Dispersal: Seeds dispersed by rainwater ('wash-out dispersal', Hartmann 1991), settling and germinating in crevices.

Time: Seeds ripening throughout summer and autumn, in time for winter rains.

Vegetative reproduction: Plants increase vegetatively, forming small mats that become pendent, the branches (vegetative growth) rooting where they touch the soil, an efficient vegetative dispersal backup and adaptation to the cliff face, ensuring long-term survival.

CONSERVATION STATUS

A local endemic, not threatened owing to the safe, sheer cliff face.

ADDITIONAL NOTES

Horticulture: Best for cool fynbos and other temperate gardens, grown in containers or rockeries. Outside its habitat, it is best grown under controlled conditions in a greenhouse. Propagate from cuttings. Does well in containers, in dappled shade or full sun. Its ease of growth maximises survival rate.

VOUCHER

Van Jaarsveld 18436 (NBG).

ILLUSTRATIONS AND MAP

Figures 210a–210f, Map 210.

JENSENOBOTRYA A.G.J.Herre

211. *Jensenobotrya lossowiana* A.G.J.Herre in *Sukkulentenkunde* 4: 79 (1951).

Crempnophyte growth form: Pendent clusters (of medium weight to heavy, cliff hanger).

Growth form formula: E:P:F:Els (ft) (vb)

Etymology: First part of genus name honours Emil Jensen, succulent enthusiast of Lüderitz; the Greek *botrys* (a bunch of grapes) refers to the club-shaped leaves, resembling bunches of grapes. The specific epithet honours Otto von Lossow, physician from Luderitz.

DESCRIPTION AND HABITAT

Much-branched, densely leaved shrubs pendent from cliffs or procumbent on ledges up to a 2.18 m in diameter. Roots fibrous. Branches woody, brittle, dark brown to blackish, with flaking, longitudinally fissured bark (bare for up to two thirds of their length in old specimens), 1 m long; main branch up to 70 mm in diameter; younger branches with internodes 5–10 mm long, spongy internodes 5 mm in diameter, brownish at first and with remnants of old persistent leaves. Leaves decussate, crowded, with 1 or 2 functional pairs at each branch end, basally connate, oblong trigonous-clavate (linear-oblongate viewed from the top) to subglobose, somewhat laterally compressed, 20–30 mm long, 15–18 mm in diameter at apex (base 8 mm in diameter); apices faintly keeled; surface grey-, pinkish to purplish green, smooth, turgid; second or third pair withering (as moisture recycled to first pairs); the upper half of older leaves often covered with blackish fungal growth; epidermis flat, stomata not sunken; apex obtuse. Flowers light to dark pink, terminal, solitary, 20–25(–35) mm in diameter when fully opened, ebracteate, buds reddish, opening during the day; pedicel 10 mm long, terete, 3 mm in diameter. Sepals 5, obtuse, 4–5 mm long, reddish purple, inner hyaline. Petals in 2 series, 10–12 × 2 mm. Filamentous staminodes absent; stamens diffuse, numerous, 3–4 mm long, white. Ovary flat or concave; glands annular, in a dark green lophomorphic ring (crenulate); stigmas 5, subulate; placenta parietal. Fruiting capsule 10–12 mm in diameter, funnel-shaped, flat at top, opening hygrochastically, soft and disintegrating soon; valve wings broad, expanding keels contiguous, diverging, ending in coiled tape-like awns, locules 5, covering membranes absent. Seed oval to subglobose, 0.5 × 0.8–1 mm, papillate, reddish brown.

Phenology: Flowering sparsely but continuous throughout year.

Pollinators: Insects (generalist).

Habitat and aspect: The main and best developed stands are found on south- and southeast-facing cliffs at Dolphin Head (Spencer Bay) and northwards to Arkona, at altitudes of 15–200 m. Plants grow in crevices and on ledges of the lower and upper slopes, in ample sandy soil, the branches often covered in lichens. The climate is typical of the southern Namib Desert and rainfall is below 25 mm per annum, but the vegetation is dependent on regular fog from the cold Benguela Current. It remains cool throughout the year except when onshore berg winds cause temperatures to rise above 40°C. The average daily maximum temperature is about 19°C and average daily minimum about 10°C, with frost absent from the habitat. Rainfall occurs mainly in winter (cyclonic cold fronts), 15–20 mm per annum.

Altitude: 15–200 m.

Associated vegetation: Succulent Karoo Biome.

Associated cremnophytes: Other cremnophytes observed at Dolphin Head include *Dicoma spinulosa*, *Pelargonium ceratophyllum*, *P. cortusifolium* and *Tylecodon schaeferi*. At the coastal sandstone ridges at Arkona, plants found in association are *Brownanthus marlothii*, *Capparis hereroensis* and *Drosanthemum luederitzii*.

Geology: Coarse brittle quartzitic sandstone of the Spencer Bay Formation (Nossop Group, Damara Sequence).

DISTRIBUTION

Localised at Dolphin Head and northwards to Arkona, confined to the coast.

RELATED SPECIES

Related to the genus *Delosperma*.

ADAPTATIONS TO THE CLIFF ENVIRONMENT

Habit: Conspicuous pendent, much-branched, fragile, brittle shrubs with pendent clusters of grape-like leaves. The heavy branches are perfectly adapted to a pendent and procumbent growth (on ledges).

Size and weight: Clusters medium-sized to large.

Stem: Up to 1 m long.

Leaves

Orientation: Leaves without teeth, fragile and plants easily damaged. The very succulent, club-shaped leaves remain turgid owing to the regular supply of moisture in the form of fog and are adapted to the dry, almost rainless climate. Like many mesembs adapted to arid conditions, the moisture from the older leaf pair is absorbed (recycled) by the younger pair. Plants were observed during morning fog, the plants and lichens moist, with moisture dripping from the leaf apices. Their turgid nature, even in December when rainfall is least expected, clearly points to their dependency on fog. The leaf epidermis is flat, without sunken stomata (Hartmann 2001b), an indication of a regular fog supply. When covered in moisture, the stomata are able to absorb moisture, a possible explanation for the turgid status of the leaves throughout the year. The thick layer of wax on the epidermis protects the plant from moisture loss under dry berg wind conditions when temperatures can suddenly rise.

Colour: Reddish to greyish green. Plants becoming reddish to greyish green (production of anthocyanins), an adaptation that reduces penetration of light that may be harmful.

Age and persistence. Slow-growing, long-lived perennials; leaves annually replaced.

Armament and camouflage: Plants fragile, extremely brittle and without armament or camouflage properties.

Sexual reproduction

Flowers: Melittophilous (Hartmann 1991). Flowering sparsely but throughout the year, probably because of the regular fog supply and almost seasonless climate.

Fruit/Seed

Size: Seed small, 0.5×0.8 –1 mm, reddish brown to yellowish, ovoid to subglobose.

Dispersal: Hydrochory (ombrohydrochory). Hygrochastic capsules opening with rain but seeds dispersed by ‘wash out dispersal’ (Hartmann 1988). The capsules have no covering membranes. Rain fills the bowl-like cavity of the capsule and seeds are washed or splashed out. This dispersal strategy would ensure local dispersal on the cliffs, the seeds succumbing to gravity and eventually becoming wedged in crevices, ideal for establishment. The papillate surface and small size of the seeds are indications of adaptation and successful dispersal in the cliff habitat where the seeds are washed into crevices, providing good anchorage for the seedlings. According to Burgoyne (1998) the coiled, ribbon-like awns arising from the end of the expanding keels help to remove the seeds from the capsules. As the valves open, the hygroscopic, coiled, ribbon-like awns tear loose from the centre and uncoil, removing some of the seeds from their cavities, thus aiding dispersal.

Time: Seeds released throughout the year but especially in winter, coinciding with autumn or winter rains, thus during the cool season and maximising establishment.

Vegetative reproduction: Plants increase vegetatively, forming dense mats or clusters up to 1 m in diameter and occasionally rooting when coming into contact with soil, an efficient vegetative dispersal backup and adaptation to the cliff face.

CONSERVATION STATUS

Classified as near threatened (Loots 2005). A little-known species, not threatened owing to the safe, remote habitat without disturbances by herbivores or humans.

ADDITIONAL NOTES

The habitat: Today Dolphin Head forms a promontory but it was once an island. The main population of *Jensenobotrya lossowiana* grows on the sheer cliffs and steep slopes but because of a lack of disturbance (even today there are no herbivores), plants are also found on non-cliff sites. Dolphin Head has a breeding colony of the Cape fur seal (*Arctocephalus pusillus*), and the only other larger mammals are black-backed jackal (*Canis mesomelas*) and brown hyena (*Hyaena brunnea*). In my opinion, many of the plants consequently migrated to non-cliff sites owing to a lack of disturbance (no baboons, gemsbok or small game such as hare). However, during times of increased rainfall and an increase in herbivores, the main population will continue their growth on the cliff faces.

Horticulture: Best for cool coastal succulent karoo gardens, ideal for embankments and hanging baskets. Very easily cultivated from cuttings or seed. Grow in full sun or light shade. Water sparingly in winter and summer.

VOUCHER

Van Jaarsveld 21148 (WIND).

ILLUSTRATIONS AND MAP

Plate 211, Figures 211a–211f, Map 211.

LAMPFRANTHUS N.E.Br.

212. *Lampranthus affinis* L.Bolus in Journal of South African Botany 28: 12–14 (1962).

Cremonophyte growth form: Decumbent shrublet (of medium weight, cliff squatter).

Growth form formula: E:F:As:W:Ev (r)

Etymology: The epithet *affinis* pertains to its close affinity to members of *Lampranthus* section *Haworthia* (*L. stipulaceum*, *L. coralliflorus*, *L. productus* and *L. haworthii*).

DESCRIPTION AND HABITAT

Erect, moderately branched shrublets up to 400 mm high, branched from base and with short, decumbent side branches along erect stems. Roots fibrous. Stems cylindrical, woody, up to 12 mm in diameter, becoming grey; younger leafy branches terete, purplish, 2.5–3 mm in diameter. Leaves numerous, crowded, erect to slightly falcate, ascending, trigonous, terete to somewhat laterally compressed, 35–45 × 3–4 mm; surface smooth, glaucous, covered with powdery bloom, becoming pink when stressed, persistent when dry. Inflorescence cymose, at tips of main branches. Flowers up to 70 mm in diameter, light pink to white, conspicuous. Petals linear-oblongate, 25–30 × 2.5 mm. Staminodes numerous, petal-like; stamens numerous, light yellow, initially covering stigma. Capsule hygroscopic, woody, 8 mm deep, 8–12 mm in diameter, opening once and remaining open, occasionally closing halfway. Seed pear-shaped, slightly depressed, 1–1.3 mm in diameter.

Phenology: Flowering in spring and early summer (October–November). Seeds wind-dispersed.

Pollinators: Insects.

Habitat and aspect: Cliffs in dry river valleys or narrow shady kloofs (all aspects). Plants are firmly rooted in crevices and size often depends on the growing space allowed by the crevice. Temperatures are high in summer and the average daily maximum is about 27°C and average daily minimum about 12°C. Winters are cool but frost is absent. Rainfall occurs throughout the year but with a peak in spring and summer (thunder showers or cyclonic winter rain), ranging from 200–300 mm per annum.

Altitude: 300–1050 m.

Associated vegetation: Mainly Gamka Thicket and Groot Thicket of the Albany Thicket Biome (Mucina *et al.* 2005).

Associated cremonophytes: At Geelhoutboskloof (Baviaanskloof, Eastern Cape), the following plants have been recorded: *Albuca cremonophila*, *Bulbine cremonophila*, *Cotyledon tomentosa*, *Crassula perfoliata* var. *minor*, *C. perforata* and *Gasteria rawlinsonii*.

Geology: Quartzitic sandstone of the Peninsula Formation (Cape Supergroup).

DISTRIBUTION

Lampranthus affinis is a quartzitic sandstone endemic, confined to the narrow kloofs (north-south orientation) of the Baviaanskloof and Swartberg Mountains of the Eastern and Western Cape Provinces (Grootrivierspoort to Seweweekspoort).

RELATED SPECIES

Lampranthus affinis is related to *L. coralliflorus* but is immediately distinguished by the large, rich-flowering inflorescences and by the fruiting capsules that remain open after initially opening. In fact, this character distinguishes it from any other *Lampranthus*.

ADAPTATIONS TO THE CLIFF ENVIRONMENT

Habit: Plants with erect to decumbent stems. A rapid-growing, fairly long-lived perennial. No noticeable vegetative adaptation to the cliff environment.

Size and weight: Plants of medium weight.

Stem: The short branches are grey and covered by persistent old leaves.

Leaves

Orientation: Ascending-spreading to erect, subterete.

Colour and texture: Glaucous (reflecting the light), with powdery bloom. Their slight translucent nature allows light to penetrate deeply, an adaptation enabling the plants to cope with the shady cliff environment. Leaves are soft and fleshy, becoming turgid after rain, but pinkish during dry periods, an adaptation to the extreme, dry habitat. The waxy bloom is another adaptation to the very dry habitat.

Age and persistence: Dry leaves persistent.

Armament: Plants with no conspicuous armament, suggesting a response to the undisturbed cliff habitat in contrast to the thorny but heavily grazed surrounding thicket vegetation.

Sexual reproduction

Inflorescence and flowers: Inflorescence ascending to spreading, with large, conspicuous light pink to white flowers (rich flowering). Unlike the flowers of most species of *Lampranthus*, these flowers open in shady positions. This phenomenon together with the conspicuous light-coloured flowers can be related to the shady cliff environment, maximising insect pollination.

Fruit/Seed

Size: Seed 1.0–1.3 mm in diameter, depressed, the size ideal for establishment in crevices.

Dispersal: Capsules initially hygrochastic, but remaining open (occasionally closing again). The seeds are shaken from the capsules and dispersed by water, wind and also by jactitation. This is unlike other *Lampranthus* species, which are mostly rain-dispersed.

Time: Seeds ripening in summer. Germination after 21 days.

Vegetative reproduction: Stems of *Lampranthus affinis* will root where they come into contact with the soil, a vegetative backup strategy for survival under the very dry, harsh conditions on the cliff face.

CONSERVATION STATUS

Locally abundant.

ADDITIONAL NOTES

Horticulture: Best for thicket, dry fynbos and succulent karoo gardens, grown on steep embankments, rockeries or balconies. Plants are rapid-growing and not shy to flower, even in shady positions. Propagate from seed or cuttings. *Lampranthus affinis* thrives in cultivation but outside its habitat it is best grown under controlled conditions in a greenhouse.

VOUCHERS

Van Jaarsveld 16086, 17379 (NBG).

ILLUSTRATIONS AND MAP

Figures 212a–212d, Map 212.

MACHAIROPHYLLUM Schwantes

213. *Machairophyllum brevifolium* L.Bolus, Notes on Mesembryanthemum and allied genera 3: 126 (1938).

Cremonophyte growth form: Rounded cluster (of medium weight, cliff hugger).

Growth form formula: A:Lper:R:C:La (vb) (r)

Etymology: Latin *brevi*, short, and *folium*, leaf, pertaining to the short leaves (shortest in the genus).

DESCRIPTION AND HABITAT

Plants much-branched, round, firm, cluster-shaped, 70 mm high, 120 mm wide. Roots fibrous. Stems short. Leaves ascending, very fleshy, trigonous, slightly laterally compressed (laterally viewed 15 mm wide), falcate to subfalcate, 10–30 × 10–26 mm, with a prominent keel; epidermis whitish green to pale green (margins and leaf tips sometimes reddish); surface smooth, adaxial surface flat to slightly convex; apex mucronate. Flowers solitary; pedicels up

to 15 mm long, 40–45 mm in diameter. Petals lorate, 13–20 × 1–2 mm. Capsule top-shaped, 9–12 mm in diameter, 6-locular; covering membranes present, closing body absent.

Phenology: Flowering in spring.

Pollinators: Insects.

Habitat and aspect: Mainly south-facing cliffs and cliff tops. Plants are rooted in crevices and on ledges. It is warm in summer and colder in winter, with occasional light frost. The average daily maximum temperature is about 32°C and average daily minimum about 15°C. Rainfall occurs mainly in summer and winter and is estimated at 200–300 mm per annum.

Altitude: 500–600 m.

Associated vegetation: Gamka Thicket of the Albany Thicket Biome (Mucina *et al.* 2005).

Associated cremnohytes: Associated species include *Crassula capitella* subsp. *thyrsiflora*, *C. nudicaulis*, *C. perforata* and *C. rupestris*.

Geology: Conglomerate (Enon, Uitenhage Group).

DISTRIBUTION

Machaiophyllum brevifolium is endemic to cliffs on the conglomerate hills in the Oudtshoorn district of the Western Cape.

RELATED SPECIES

Immediately distinguished from other *Machaiophyllum* species by its short, compact leaves.

ADAPTATIONS TO THE CLIFF ENVIRONMENT

Habit: Plants with compact, rounded cushions. A slow grower and long-lived perennial.

Size and weight: Small plants (of medium weight).

Rootstock: Fibrous, no specialised features.

Leaves

Orientation: Ascending-spreading.

Colour: Whitish green, somewhat glaucous.

Age and persistence: Leaves persistent and long-lived, eventually withering and resulting in apical grouping.

Armament: No armament.

Sexual reproduction

Flowers: Vespertine, like those of its relatives, opening late afternoon, pollinated by insects.

Fruit/Seed

Size: Not seen.

Dispersal: Seeds locally dispersed. Capsules hygrochastic and seeds dispersed by falling rain drops.

Time: Seeds ripening throughout summer and autumn, in time for winter rains.

Vegetative reproduction: Absent.

CONSERVATION STATUS

A local endemic, not threatened (Hilton-Taylor 1996).

ADDITIONAL NOTES

Horticulture: Best for succulent karoo gardens, grown in rockeries or containers. Outside its habitat, it is best grown under controlled conditions in a greenhouse. Propagate from seed or stem cuttings.

VOUCHER

Van Jaarsveld 15227 (NBG).

ILLUSTRATIONS AND MAP

Figures 213a & 213b, Map 213.

OSCULARIA Schwantes

214. *Oscularia cremnophila* Van Jaarsv., Desmet & A.E.van Wyk in *Bothalia* 35,2: 160–163 (2005c).

Cremnophyte growth form: Pendent leafy stems (heavy, cliff hanger).

Growth form formula: E:F:P:Els (vb) (r)

Etymology: Greek *kremnos*, cliff, and Greek *phileein*, to love, pertaining to its cliff habitat.

DESCRIPTION AND HABITAT

Densely branched, glabrescent, succulent shrub pendent from cliffs, 600–750(–1000) mm tall. Old stems woody, up to 30 mm in diameter, basal portion with rough bark, very corky, with

prominent longitudinal cork ridges (wings), leafless for up to 250 mm, becoming thinner with leaves distally; young stems green at first, soon becoming brown, woody and longitudinally fissured. Leaves sessile, united at base, decussate, crowded (almost touching), entire, ascending, spreading, 2 or 3 pairs (with persistent withered older pair), thick, club-shaped, trigonous, 10–15 × 6–10 mm, pale yellowish grey-green; surface minutely papillate; apex obtuse, mucronate; edges of keel and margin sometimes reddish, keel 7–9 mm deep, falcate. Inflorescences in lax to dense, laterally spreading cymes forming panicles, 40–50 × 25–40 mm, with up to 23 flowers on bibracteate peduncles up to 20 mm long; flowers in 3-flowered cymes of (10–)15–17 mm diameter, central flower opening first, remaining open; bracts leaf-like, club-shaped. Flowers diurnal, pleasantly scented; pedicels 3–5(–8) mm long. Sepals 5, unequal, with translucent margins, outer 2 triangular-club-shaped, 5–7 × 3.0–3.5 mm, inner 3 triangular-lorate, 3.5–4.0 × 3.0 mm. Petals pink, in 1 series, spreading, linear-lanceolate, 6–7 × 1.4–2.0 mm; apices obtuse to subacute. Stamens: staminodes filamentous, in a central cone; filaments 3 mm long, distal third pink, basal two thirds translucent, white, clasping ovary; anthers 0.6–0.7 mm long, yellow, not completely overtopping stigmas. Gynoecium 4 mm in diameter, with 5 raised, obtuse sutures, minutely papillate, pale translucent green, elevated up to 1.2 mm; nectaries narrow, 2 mm long, crenulate, surrounding ovary; placentation parietal; stigmas 5, arising from centre between sutures or lobes, tapering, erect, dark maroon, papillate, not completely concealed by stamens. Capsule 5-locular, hygrochastical, globose to top-shaped, 5 mm in diameter, 6–7 mm deep, top rounded, when open then up to 9 mm in diameter; covering membranes complete, valve wings broad. Seeds pear-shaped, 0.6–0.8 mm in diameter, tapering, minutely tuberculate, brownish.

Phenology: Flowering in early spring (August–September).

Pollinators: Insects.

Habitat and aspect: Coastal cliffs of two quartzitic sandstone inselbergs, mainly east-facing. Plants are rooted in crevices and on ledges, drooping over the rock faces. Temperature moderate, with frequent coastal fog. The average daily maximum temperature is about 20°C and average daily minimum temperature about 12°C. Rainfall occurs mainly in winter and is estimated at about 300–400 mm per annum.

Altitude: 50–100 m.

Associated vegetation: Namaqualand Strandveld of the Fynbos Biome (Mucina *et al.* 2005).

Associated cremnophytes: Associated species include *Crassula alsinoides* subsp. *alsinoides*, *C. nudicaulis* and *C. pellucida* subsp. *spongiosa*.

Geology: Quartzitic sandstone, Table Mountain Group (Cape Supergroup).

DISTRIBUTION

Oscularia cremnophila is a quartzitic sandstone endemic, confined to the east-facing cliffs of a single inselberg near Elands Bay (Western Cape).

RELATED SPECIES

Related to *Oscularia vredenburgensis*, a spreading shrub of Saldanha with grey-green leaves not as densely arranged and turgid as those of *O. cremnophila*.

ADAPTATIONS TO THE CLIFF ENVIRONMENT

Habit: Plants with dense, leafy, pendent stems and this habit is retained in cultivation. A long-lived perennial with a medium to rapid growth rate.

Size and weight: Large plants with drooping stems sometimes weigh more than 1 kg, but are firmly wedged in crevices.

Rootstock: Fibrous, no specialised features.

Stem: Base of stem with marked corkification, the function of which is not understood currently.

Leaves

Orientation: Ascending-spreading.

Colour: Pale yellowish green, somewhat glaucous.

Age and persistence: Persistent and long-lived, eventually withering.

Armament: Leaves softer and more fragile than those of the closely related *Oscularia vredenburgensis*, suggesting a reduction in armament as a result of the undisturbed habitat.

Sexual reproduction

Inflorescence and flowers: Flowers in cymes, conspicuous, maximising visibility for successful pollination in the vertical cliff environment. Flowering time is in spring.

Fruit/Seed

Size: Seed 0.6–0.8 mm in diameter, tuberculate.

Dispersal: Brown seeds dispersed by raindrops (ombrohydrochory) (Hartmann 1991).

Time: Seeds ripening throughout summer and ready for dispersal at the onset of autumn rains. Germination within 3 weeks.

Vegetative reproduction: Plants become pendent, the branches (vegetative growth) rooting when coming into contact with soil, an efficient vegetative dispersal backup and adaptation to the cliff face, ensuring long-term survival.

CONSERVATION STATUS

A local endemic of which the population is so small that it might become threatened.

ADDITIONAL NOTES

Horticulture: Best for fynbos gardens, grown on steep embankments, balconies, containers or rockeries. Outside its habitat, it is best grown under controlled conditions in a greenhouse. Propagate from cuttings. Does well in containers, in full sun or dappled shade. Its ease of growth maximises survival rate.

VOUCHER

Van Jaarsveld 19003 (NBG).

ILLUSTRATIONS AND MAP

Plate 214, Figures 214a–214e, Map 214.

RUSCHIA Schwantes

215. *Ruschia knysnana* (L.Bolus) L.Bolus, Notes on Mesembryanthemum and allied genera 1: 146 (1929).

Cremonophyte growth form: Cushion-shaped to pendent or mat-forming, succulent-leaved (of medium weight, cliff squatter).

Growth form formula: E:F:As:W:Ev (vb)

Etymology: After Knysna, Western Cape, where this species occurs.

DESCRIPTION AND HABITAT

Plants much-branched, cushion-shaped or pendent shrublets up to 600 mm in diameter. Roots fibrous. Stems reddish brown at first, becoming grey, up to 2 mm in diameter; nodes 5–15 mm apart. Leaves connate at base, often in compact groups, becoming deciduous on older stems and not persistent, ascending, fleshy, bright green (margins and keels translucent, and leaf tips sometimes reddish), triquetrous, slightly laterally compressed (up to 8 mm wide), subfalcate, 20–30(–40) × 4–6 mm; margin and keel entire except tips sometimes obscurely serrate-denticulate; surface smooth, adaxial surface flat; apex aristate or apiculate. Flowers solitary, 12–15 mm in diameter; pedicels 5 mm long (in fruit). Petals purplish pink, 10 × 0.8 mm, merging with staminodes. Filaments 3–5 mm long, light pink. Anthers 1 × 0.2 mm. Stigmas surrounded by a ring of nectaries. Capsule top-shaped, rounded at top, 7 mm in diameter; closing body absent, covering membranes present, valves light brown, valve wings narrow. Seed pear-shaped, 1 mm in diameter, pale brown.

Phenology: Flowering mainly in spring and summer.

Pollinators: Insects.

Habitat and aspect: Coastal cliffs and steep near vertical slopes (mainly south-facing). Plants are firmly rooted in crevices and size often depends on the growing space allowed by

the crevice. Temperature moderate throughout the year. Winters are cooler but frost is absent. The average daily maximum temperature is about 21°C and average daily minimum about 11°C. Rainfall occurs throughout the year (cyclonic in winter, but also with occasional thunder showers in summer), ranging from 600–700 mm per annum.

Altitude: 50–650 m.

Associated vegetation: Tsitsikamma Sandstone Fynbos and Loerie Conglomerate Fynbos (Knysna) (Mucina *et al.* 2005).

Associated cremnophytes: At Oubosstrand, *Ruschia knysnana* grows with *Bulbine latifolia*, *Crassula nudicaulis* and *C. perforata*.

Geology: Quartzitic sandstone (Cape Supergroup) or Enon Conglomerate.

DISTRIBUTION

Ruschia knysnana is distributed from Knysna (Western Cape) to Oubosstrand (Eastern Cape), growing on coastal cliffs.

RELATED SPECIES

No close relatives.

ADAPTATIONS TO THE CLIFF ENVIRONMENT

Habit: Plants with compact cushion or becoming pendent and this habit is retained in cultivation. A rapid-growing, fairly long-lived perennial.

Size and weight: Plants of medium weight.

Rootstock: Fibrous, no specialised features.

Stem: No apparent unique cliff adaptation.

Leaves

Orientation: Ascending-spreading.

Colour: Bright green.

Age and persistence: Leaves persistent and long-lived, eventually withering and resulting in apical grouping.

Armament: The lack of sufficient armament an apparent response to the undisturbed cliff habitat in contrast to the surrounding accessible fynbos.

Sexual reproduction

Inflorescence and flowers: Flowers simple, occasionally on elongated flowering branches, at branch ends or axillary produced, conspicuous, maximising visibility for successful pollination in the vertical cliff environment. Flowering time is in late spring and summer and flowers are regularly produced, ensuring a long and continual seed supply also coinciding with rainfall in the region.

Fruit/Seed

Size: Seed 1 mm in diameter, an ideal size for establishment in crevices.

Dispersal: Seeds dispersed by rainwater ('wash-out dispersal', Hartmann 1991). The compressed shape is an adaptation for wind dispersal as well, the seeds settling and germinating in crevices.

Time: Seeds ripening throughout summer and autumn, in time for winter rains.

Vegetative reproduction: Absent.

CONSERVATION STATUS

A local endemic, not threatened (Hilton-Taylor 1996).

ADDITIONAL NOTES

Horticulture: Best for fynbos gardens, grown on steep embankments, rockeries or balconies. Plants are rapid-growing and not shy to flower. Propagate from seed or cuttings. *Erepsia knysnana* thrives in cultivation, but outside its habitat it is best grown under controlled conditions in a greenhouse.

VOUCHER

Van Jaarsveld 18658 (NBG).

ILLUSTRATIONS AND MAP

Figures 215a & 215b, Map 215.

216. *Ruschia promontorii* L.Bolus, Notes on Mesembryanthemum and allied genera 2: 121 (1929).

Cremonophyte growth form: Pendent leafy mats (of medium weight, cliff hanger).

Growth form formula: E:F:P:Els:Ev (vb)

Etymology: The epithet *promontorii* refers to the Cape Peninsula, especially Cape Point, a promontory where the plant occurs.

DESCRIPTION AND HABITAT

Plants much-branched, mat-forming, glabrous shrublets becoming pendent from cliff faces, with stems up to 500 mm long forming loose mats, leaves crowded at branch ends (2 or 3 pairs). Roots fibrous. Branches 3.5 mm in diameter (main branch up to 5 mm in diameter), reddish at first, biconvex, becoming mottled grey and woody but remaining flaccid; nodes 15–25 mm apart; surface smooth. Leaves fleshy, trigonous, falcate to subfalcate owing to deep prominent keel (5–7 mm), green to yellowish green, reddish at tips and keels, 10–20 × 5–7 mm (viewed dorsally, triangular-ovate), ascending; surface smooth, adaxial surface somewhat flat; apex acute, bearing prominent mucro. Flowers solitary, up to 30 mm in diameter; pedicels 7 mm long. Petals purplish pink. Anthers yellow. Capsule top-shaped, 7–9 mm in diameter, 5–6 mm deep; closing body absent. Seed pear-shaped, 1.5 × 1 mm, minutely tuberculate, light brown.

Phenology: Flowering mainly in spring, to end of October.

Pollinators: Insects.

Habitat and aspect: Sea-facing cliffs (all aspects, mainly northern). Plants are rooted in crevices and on ledges, drooping over the rock faces. Temperature relatively low throughout the year. The average daily maximum temperature is 20°C and average daily minimum for the region 12°C. Rainfall occurs mainly in winter and is estimated to be above 300–400 mm per annum.

Altitude: 120–400 m.

Associated vegetation: Hangklip Sand Fynbos (Mucina *et al.* 2005).

Associated cremnophytes: Near the light house at Cape Point, *Ruschia promontorii* shares its habitat with *Cotyledon orbiculata* var. *orbiculata*, *Crassula nudicaulis*, *Cussonia thyrsiflora*, *Tylecodon grandiflorus* and *T. paniculatus*.

Geology: Quartzitic sandstone, Table Mountain Group (Cape Supergroup).

DISTRIBUTION

Ruschia promontorii is a quartzitic sandstone endemic, confined mainly to east facing coastal cliffs in the Cape Point Nature Reserve (Western Cape). Outside of the National Park it grows on west-facing cliffs (Scarborough to Chapman's Peak).

RELATED SPECIES

Related to *Ruschia rubricaulis*, a ascending to sprawling shrublet occurring among sandstone outcrops.

ADAPTATIONS TO THE CLIFF ENVIRONMENT

Habit: Plants with pendent, leafy stems, this habit retained in cultivation. A rapid-growing, fairly long-lived perennial.

Rootstock: Central taproot and branches rooting where touching the ground. Roots fibrous, no specialised features.

Stem: Pendent and forming loose mats. Stems and leaves soft and flaccid, a character that can be viewed as a reduction in armament as a result of the undisturbed habitat.

Leaves

Orientation: Ascending-spreading.

Colour: Bright green to yellowish green.

Age and persistence: Leaves persistent and long-lived, eventually withering and resulting in apical grouping.

Armament: No armament.

Sexual reproduction

Flowers: Flowers are simple at branch ends, conspicuous, maximising visibility for successful pollination in the vertical cliff environment. Flowering time is in winter and spring, ensuring a long and continual seed supply.

Fruit/Seed

Size: Seed large, 1.5 mm in diameter, and minutely tuberculate, a size and surface ideal size for establishment in crevices.

Dispersal: Seeds dispersed by rainwater (ombrohydrochory, Hartmann 1991), settling and germinating in crevices.

Time: Seeds ripening throughout summer and autumn, in time for winter rains. Germination within 3 weeks.

Vegetative reproduction: Plants increase vegetatively, forming small mats that become pendent, the branches (vegetative growth) rooting where they touch the soil, an efficient vegetative dispersal backup and adaptation to the cliff face, ensuring long-term survival.

CONSERVATION STATUS

A local endemic, not threatened (Hilton-Taylor 1996).

ADDITIONAL NOTES

Horticulture: Best for cool fynbos and other temperate gardens, grown in containers or rockeries. Outside its habitat, it is best grown under controlled conditions in a greenhouse. Propagate from cuttings. Does well in containers, in dappled shade or full sun. Its ease of growth maximises survival rate.

VOUCHER

Van Jaarsveld 19954 (NBG).

ILLUSTRATIONS AND MAP

Figures 216a–216c, Map 216.

SCOPELOGENA L. Bolus

217. *Scopelogenia bruynsii* Klak in *Bothalia* 30,1: 35–42 (2000).

Cremnophyte growth form: Decumbent shrublet (of medium weight, cliff squatter).

Growth form formula: E:F:As:W:Ev (vb) (r)

Etymology: The genus name ‘*Scopelogenia*’, Latin, ‘*scopulus*’, a cliff, pertaining to its habitat. After Dr Peter Bruyns, specialist in Asclepiadaceae and succulent plants.

DESCRIPTION AND HABITAT

Decumbent, branched shrublets up to 500 mm in diameter, about 300 mm high, branched from base, with short side branches along stems. Roots fibrous. Stems cylindrical, woody, up to 10 mm in diameter, becoming purplish grey; younger leafy branches terete, purplish, 4 mm in diameter. Leaves crowded, erect to slightly incurved, ascending, subterete to 3-angled, up to 45 × 8 mm, persistent when dry; surface smooth, glaucous, covered with powdery bloom, becoming yellowish when stressed. Inflorescence cymose, at ends of main branches. Flowers up to 18 mm in diameter, yellow to pink or reddish, flowering in masses, conspicuous. Staminodes numerous; petaloid staminodes linear-oblongate, 7 × 1.5 mm; stamens numerous, light yellow. Stigmas 5.3 mm long. Capsule top-shaped, hygrochastic, 5-locular, soft, up to 4.5 mm in diameter, top dome-shaped; covering membranes present. Seed 1 mm in diameter, tuberculate, pear-shaped.

Phenology: Flowering in spring and early summer (September–October).

Pollinators: Insects.

Habitat and aspect: Sheltered south-facing cliffs. Temperatures are high in summer (average daily maximum about 26°C; average daily minimum about 10°C). Winters are cooler but frost is absent. Rainfall occurs mainly in winter (cyclonic winter rain), ranging from 200–300 mm.

Altitude: 120–400 m.

Associated vegetation: Succulent Karoo.

Associated cremnophytes: At Rooiberg, northern Knersvlakte (red flowered population), *Scopelogenia bruynsii* shares its habitat with *Cotyledon orbiculata* var. *orbiculata*, *Crassula pseudohemisphaerica* and *Tylecodon nolteei*.

Geology: Quartzitic sandstone of the Nardouw Subgroup (Table Mountain Group), Witpoort Formation (Witteberg Group), the latter two of the Cape Supergroup and also the Kwanous Formation in the Kamiesberg (Vanrhynsdorp Group).

DISTRIBUTION

Scopelogenia bruynsii is confined to quartzitic sandstone mountains ranging from the Kamiesberg (Northern Cape) to the mountains of the Little Karoo in the Western Cape.

RELATED SPECIES

See differences under *Scopelogenia verruculata*.

ADAPTATIONS TO THE CLIFF ENVIRONMENT

Habit: Plants with erect to decumbent stems, with a cushion-like growth. A rapid-growing, fairly long-lived perennial. No noticeable vegetative adaptation to the cliff environment.

Size and weight: Plants of medium weight or heavy.

Stem: The short branches are grey and covered by persistent old leaves.

Leaves

Orientation: Ascending, subterete.

Colour and texture: Glaucous (reflecting the light), with powdery bloom. Their slight translucent nature allows light to penetrate deeply, an adaptation enabling the plants to cope with the shady cliff environment. Leaves are soft and fleshy, becoming turgid after rain, but yellowish during dry periods, an adaptation to the extreme, dry habitat.

Age and persistence: Old, dry leaves persistent.

Armament: No conspicuous armament, suggesting a response to the undisturbed cliff habitat in contrast to the thorny but heavily grazed surrounding thicket vegetation.

Sexual reproduction

Inflorescence and flowers: Inflorescence ascending to spreading, with conspicuous yellow to pink flowers. The plants are floriferous and flower in masses. Unlike the flowers of most species of *Scopelogenia*, these flowers open in shady positions. This phenomenon together with the conspicuous light-coloured flowers can be related to the shady cliff environment, maximising insect pollination.

Fruit/Seed

Size: Seed 1 mm in diameter, depressed, pear-shaped, the size ideal for establishment in crevices.

Dispersal: Seeds forced out of capsules by water action and then locally dispersed.

Time: Seeds ripening in summer.

Vegetative reproduction: Branches finding a crevice will rapidly root.

CONSERVATION STATUS

Locally abundant.

ADDITIONAL NOTES

Horticulture: Best for dry fynbos or succulent karoo gardens, grown on steep embankments, rockeries or balconies. Plants are rapid-growing and not shy to flower, even in shade. Propagate from cuttings. *Scopelogenia bruynsii* thrives in cultivation, but outside its habitat it is best grown under controlled conditions in a greenhouse.

VOUCHER

Van Jaarsveld 17812 (NBG).

ILLUSTRATIONS AND MAP

Figure 217a, Map 217.

218. *Scopelogenia verruculata* (L.) L.Bolus in Journal of South African Botany 28: 9–11 (1962).

Cremonophyte growth form: Decumbent shrublet (of medium weight to heavy, cliff squatter).

Growth form formula: E:F:As:W:Ev (vb) (r)

Etymology: Latin *verrucula*, a small wart, pertaining to the leaves; Linnaeus cited Dillenius who named this species *Mesembryanthemum foliis verruculiformibus*.

DESCRIPTION AND HABITAT

Decumbent, branched shrublets up to 1 m in diameter and about 200 mm high, branched from base, with short side branches along stems. Roots fibrous. Stems cylindrical, woody, up to 12 mm in diameter, becoming purplish grey; younger leafy branches terete, purplish, 4 mm in diameter. Leaves numerous, erect to slightly falcate, ascending, subterete, up to 40 × 7 mm; surface smooth, glaucous, covered with powdery bloom, becoming yellowish when stressed, persistent when dry. Inflorescence cymose, at ends of main branches, up to 90 mm long, 80 mm in diameter. Flowers up to 18 mm in diameter, yellow, flowering in masses, conspicuous. Staminodes numerous; petaloid staminodes linear-oblongate, 7 × 1.5 mm; stamens numerous, light yellow. Stigmas 5.3 mm long. Capsule hygroscopic, woody, 5 mm deep, 7 mm in diameter, opening once, remaining open. Seed 1.2 mm in diameter, pear-shaped, flat, wind-dispersed.

Phenology: Flowering in spring and early summer (October–November).

Pollinators: Insects.

Habitat and aspect: Mainly sheltered cliffs (mostly south- and east-facing aspects). Plants are firmly rooted in crevices. Temperature relatively low in summer. Winters are cooler but frost is absent. The average daily maximum temperature is about 18°C and average winter temperature 8–10°C. Rainfall occurs mainly in winter (cyclonic winter rain), ranging from 1000–1500 mm per annum.

Altitude: 100–1000 m.

Associated vegetation: Peninsula Sandstone Fynbos (Mucina *et al.* 2005).

Associated cremnohytes: On cliffs on Table Mountain, it grows with the following cliff-dwelling species: *Bulbine lagopus*, *Crassula coccinea*, *C. pellucida* subsp. *alsinoides*, *Lampranthus multiradiatus* and *Oscularia falcata*.

Geology: Quartzitic sandstone (light-coloured and smooth-textured), Peninsula Formation (Cape Supergroup).

DISTRIBUTION

Scopelogenia verruculata is a quartzitic sandstone endemic, confined to rock faces from the Cape Peninsula to Riversdale in the east (Western Cape mountains).

RELATED SPECIES

Related to *Scopelogenia bruynsii*, but differs in the fruiting capsules remaining open, not closing again after initial opening. Related to the genus *Lampranthus* but immediately distinguished by the subterete, linear leaves.

ADAPTATIONS TO THE CLIFF ENVIRONMENT

Habit: Plants with erect to decumbent stems with a cushion-like growth. A rapid-growing, fairly long-lived perennial.

Size and weight: Plants of medium weight to heavy.

Stem: The short branches are grey and covered by persistent old leaves.

Leaves

Orientation: Ascending, subterete.

Colour and texture: Glaucous, with powdery bloom. Their slight translucent nature allows light to penetrate deeply, an adaptation enabling the plants to cope with the shady cliff environment. Leaves are soft and fleshy, becoming turgid after rain, but yellowish during dry periods, an adaptation to the extreme, dry habitat.

Age and persistence: Old, dry leaves persistent.

Armament: Plants without conspicuous armament, suggesting a response to the undisturbed cliff habitat in contrast to the thorny but heavily grazed surrounding thicket vegetation. Branches are not brittle and, unlike those of many *Lampranthus* species, difficult to detach owing to their strong fibrous nature.

Sexual reproduction

Inflorescence and flowers: Inflorescence ascending to spreading, with conspicuous yellow flowers. The plants are floriferous and flower in masses. Flowering in shady positions together with the conspicuous light-coloured flowers (rich flowering) can be related to the shady cliff environment, maximising insect pollination.

Fruit/Seed

Size: Seeds 1.2 mm in diameter, flat, pear-shaped, the size ideal for establishment in crevices.

Dispersal: Light seeds shaken from the capsules and dispersed by wind. This is unlike other related Mesembryanthemaceae such as members of the genus *Lampranthus* of which the seeds are rain-dispersed, an adaptation to the cliff environment.

Time: Seeds ripening in summer.

Vegetative reproduction: Branches finding a new crevice will rapidly root, filling ledges, a vegetative backup strategy enabling the plants to survive the harsh cliff-face environment.

CONSERVATION STATUS

Locally abundant and not threatened.

ADDITIONAL NOTES

Horticulture: Best for fynbos gardens, grown on steep embankments, rockeries or balconies. Plants are rapid-growing and not shy to flower, even in shade. Propagate from cuttings. *Scopelogenia verruculata* does well in cultivation, but outside its habitat it is best grown under controlled conditions in a greenhouse. Plants easily grown from cuttings. It grows very easily, maximising survival rate.

VOUCHER

Van Jaarsveld 17628 (NBG).

ILLUSTRATIONS AND MAP

Figures 218a–218d, Map 218.

OXALIDACEAE

Oxalis L.

219. *Oxalis pocockiae* L.Bolus

OXALIS L.

219. *Oxalis pocockiae* L.Bolus in Journal of Botany, British and Foreign 68: 75 (1930).

Cremonophyte growth form: Dwarf-sized rosette (of light weight, cliff hugger).

Growth form formula: A:B:D:C:La (vb)

Etymology: After Mary Agard Pocock (1886–1977), botanist who specialised in algae.

DESCRIPTION AND HABITAT

Plants dwarf-sized, semisucculent geophytes up to 140 mm high, with shortly exerted stems from rhizome 40–100 mm long. Bulb narrowly ovoid, with 4 longitudinal wings; tunics numerous, hard, dark brown, the outer adpressed at margins and forming the wings; numerous aerial winged bulbs produced in leaf axils. Leaves basal to loosely imbricate, glabrous or sparsely hairy; petiole up to 25 mm long; leaflets 3, sessile, broadly cuneate-rotund, 3–6 × 5–10 mm, green, often purplish below, the medial usually emarginate. Peduncles extending beyond leaves. Sepals oblong-lanceolate, obtuse, 4.5–7.0 mm long. Corolla 12–24 mm long, rose to white; tube funnel-shaped, yellow. Ovary glabrous or pubescent; styles pubescent. Stamens 9–10. Seed endospermous. (Description based on Salter 1944.)

Phenology: Flowering in winter and spring. Seed wind-dispersed.

Pollinators: Insects.

Habitat and aspect: A chasmophyte occurring in rock crevices, often on vertical sandstone cliffs. The bulbs are firmly rooted in crevices and on rocky ledges. The winters are cool but frost is a rarity or absent. The average daily maximum temperature is about 22°C and the average daily minimum 15°C. Rainfall occurs mainly in winter, occasionally in summer, 750–2000 mm per annum.

Altitude: 350–600 m.

Associated vegetation: Mainly Sandstone Fynbos in Peninsula Sandstone Fynbos, Fynbos Biome (Mucina *et al.* 2005).

Associated cremonophytes: *Aloe succotrina*, *Cotyledon orbiculata*, *Crassula nudicaulis*, *Drosanthemum stokoei* and *Ruschia promontorii*.

Geology: Mainly quartzitic sandstone, Peninsula Formation (Cape Supergroup), also on granite.

DISTRIBUTION

Oxalis pocockiae is confined to quartzitic cliff faces and rocky outcrops in the Western Cape, from Prince Albert in the east to Malmesbury in the west.

RELATED SPECIES

Related to *Oxalis depressa*, but at once distinguished by its winged vegetative bulbils.

ADAPTATIONS TO THE CLIFF ENVIRONMENT

Habit: Compact, rosulate growth, the rhizome deeply embedded in rock crevices. The bulb ensures its survival during the long summer droughts. The vegetative winged bulbils are formed near the stem apex, brittle and easily detached.

Size and weight: Dwarf-sized clusters.

Leaves

Orientation: Spreading-ascending.

Colour: Green, often purplish below.

Armament: Absent.

Sexual reproduction

Flowers: Corolla 12–24 mm long, rose to white; tube funnel-shaped, yellow.

Fruit/Seed

Size: Very fine dust diaspores.

Dispersal: Seeds dispersed by wind.

Time: Dispersal in winter and spring.

Vegetative reproduction: *Oxalis pocockiae* regenerates from brittle, winged bulbils that are dispersed by wind, a unique feature among cremnophilous succulent and bulbous succulent plants. When these winged bulbils become detached and fall into adjacent crevices, they will root and establish new plants. This regeneration is a vegetative backup strategy, aiding long-term survival.

CONSERVATION STATUS

Localised and confined to cliffs where it is not threatened owing to the inaccessible habitat.

ADDITIONAL NOTES

Horticulture: Grown as a curiosity plant, with potential to become a weed in succulent collections. Easily grown, but not an ornamental species.

VOUCHER

Van Jaarsveld 19660 (NBG).

ILLUSTRATIONS AND MAP

Figures 219a–219d, Map 219.

PORTULACACEAE

Anacampseros L.

220. *Anacampseros scopata* G. Will.

ANACAMPSEROS L.

220. *Anacampseros scopata* G. Will. in *Cactus and Succulent Journal* (U.S.) 66: 20–23 (1994).

Cremonophyte growth form: Dwarf-sized compact herb, leaf and stem succulent (of light weight, cliff hugger).

Growth form formula: A:S:Lper:Lc:Ca:B (vb) (ft)

Etymology: The epithet *scopata*, densely covered with bristly hairs, pertains to the heads covered in hairs.

DESCRIPTION AND HABITAT

Plants dwarf-sized perennials with flattened tubers, 25 × 12 mm, due to rock fissures. Branches up to 8, arising from tubers, truncate, up to 1.5 mm long, 5 mm in diameter. Leaves numerous, embedded among dense mass of white, woolly hairs (up to 5 mm long); lamina broadly elliptic to narrowly ovate, about 2–3 mm long, fleshy, ascending, glabrous, dark to greenish brown. Peduncles up to 10 mm long, 6 mm in diameter. Flowers apically produced, solitary, white to light pink. Sepals 2.5 × 2.5 mm, hooded, triangular, pink brown, fleshy. Petals: upper petal 2.3 mm long, 3 mm wide, triangular, subacute; lateral petals 2.5 × 2.3, triangular, subacute. Stamens 1.5 mm long, clasping base of ovary. Ovary globose, 1 mm in diameter, bright green; style 1 mm long. Seed obovate, 0.8 mm in diameter, tuberculate, straw-coloured.

Phenology: Flowering in autumn and winter.

Pollinators: Insects.

Habitat and aspect: In fissures of horizontally layered quartz on the eastern cliffs of Vyftienmyl se Berge. Winters cool but frost is a rarity or absent. Average daily maximum temperature is 19°C, average daily minimum 10°C. Rainfall mainly in winter and spring, 25–50 mm per annum. Precipitation in the form of regular fog from the nearby Atlantic Ocean.

Altitude: 350–450 m.

Associated vegetation: Vyftienmyl se Berge Succulent Shrubland, Succulent Karoo Biome (Mucina *et al.* 2005).

Associated cremonophytes: *Conophytum stephanii*, *Crassula muscosa*, *C. pseudohemisphaerica*, *Gasteria pillansii* var. *ernesti-ruschii*, *Haworthia arachnoidea*, *Plectranthus strigosus* and *Tylecodon buchholzianus*.

Geology: Stinkfontein Subgroup (Gariiep Supergroup).

DISTRIBUTION

Anacampseros scopata is known only from east-facing cliffs of the low coastal Oograbies mountain range near Port Nolloth along the Atlantic coast where it is subject to regular fog.

RELATED SPECIES

Anacampseros scopata is related to another dwarf-sized plant, *A. bayeri*, the latter lacking the dense woolly hairs and occurring in shallow pans, not on cliffs.

ADAPTATIONS TO THE CLIFF ENVIRONMENT

Habit: Compact succulent growth in the horizontal quartz layers ensures a safe, undisturbed habitat (from larger herbivores). Dense, woolly hairs help to trap the low clouds of fog.

Size and weight: Clusters dwarf-sized, of light weight.

Leaves

Orientation: Ascending-spreading.

Colour: Dark to greenish brown, covered in dense, white, woolly hairs.

Armament: Absent.

Sexual reproduction

Inflorescence and flowers: Flowers apically produced, solitary, white to light pink.

Fruit/Seed

Size: Seed small diaspores, 0.8 mm in diameter.

Dispersal: Seeds dispersed by wind.

Time: Winter and spring.

Vegetative reproduction: Absent.

CONSERVATION STATUS

Localised and confined to cliffs where it is not threatened owing to the inaccessible habitat.

ADDITIONAL NOTES

Horticulture: Best for greenhouses, grown under controlled conditions. Keep in light shade, dry in summer, but mist regularly. Plants easily grown in small containers, but need regular attention owing to their minute size. Thrives in a cool desert climate but must be protected from frost.



VOUCHER

G. & F. Williamson 4600 (NBG).

ILLUSTRATIONS AND MAP

Figures 220a–220c, Map 220.

OUTGROUPS (NON-SUCCULENTS)
(Pedaliaceae, Scrophulariaceae)

PEDALIACEAE

Dewinteria Van Jaarsv. & A.E.van Wyk

221. *Dewinteria petrophila* (De Winter) Van Jaarsv. & A.E.van Wyk

DEWINTERIA Van Jaarsv. & A.E.van Wyk

221. *Dewinteria petrophila* (De Winter) Van Jaarsv. & A.E.van Wyk in *Bothalia* 37,2: 198–201 (2007a).

Cremonophyte growth form: Squat, somewhat trailing chasmocremnophyte (of light weight, cliff squatter).

Growth form formula: E:F:As:S/H:Es:De (vb) (r) (fn)

Etymology: Greek *petra*, a rock, and *philein*, to love, after its rock habitat.

DESCRIPTION AND HABITAT

Soft, somewhat trailing, branched, biennial (or annual) plant, up to 200 mm long; most parts covered with mucilage glands; base of stem slightly swollen (semisucculent, somewhat ovate, up to 5 mm in diameter), often compressed owing to narrow crevices. Roots fibrous. Branches 3–4 mm in diameter at base. Specialist branchlets filiform, 0.25 mm in diameter, basally produced, trailing, negatively phototropic, annual, usually dying back after fruiting. Leaves on main branches opposite (internodes 8–14 mm long), broadly cordate to kidney-shaped, up to 40 × 55 mm, grey-green; margin coarsely dentate; petiole 20–60 mm long; axils mostly with paired or solitary extrafloral nectary. Leaves on specialist branchlets (arising as accessory shoots below extrafloral nectary and flower) small, entire, ovate, 2–4 × 0.6–1.7 mm; petiole 3–4 mm long, sometimes becoming slightly longer but then leaves becoming broader and coarsely toothed. Flowers on main branch axillary (mostly solitary, rarely in pairs), conspicuous, trumpet-shaped, 30–70 mm long; pedicel 1.2–4.0 mm long. Calyx slightly zygomorphic, persistent, 5-partite; lobes oblong-triangular, up to 3 mm long. Corolla slightly swollen at base, sparsely covered with mucilage glands, cream-coloured (pale yellow in bud stage) and maroon-purple in throat and tube; lobes 5, broadly ovate, somewhat 2-lipped, lower pair slightly larger than upper 3. Stamens 4, arising from base of corolla tube, with short staminode between the pairs; filaments filiform, slightly flattened, up to 12 mm long, pilose; anthers basifixed. Ovary elongate-conical, 2-chambered, placentation axile, with 3–5 seriate ovules; style up to 23 mm long; stigma capitate, up to 1.5 mm in diameter. Cleistogamous flowers on specialist branchlets 2 mm long, light yellowish green, remaining a reduced bud; pedicel up to 1.5 mm long. Capsules on main branches lanceolate in side view, 18–25 mm long, tapering into curved apex, laterally flattened, dehiscing loculicidally; valves 2, chartaceous. Specialist capsules flattened, ovate to ovate-cordate, 5–8 × 4.0–5.5 mm, brown; both carpels dehiscing loculicidally, false septa nearly completely reduced to small

seams at base of capsule. Seeds of main branch capsules linear-oblong to club-shaped, slightly flattened, 2.0–2.2 mm long, minutely reticulate, brownish. Specialist seeds oblong-obovoid, 2.5–3.0 mm long, fringed. (Description based partly on De Winter 1961.)

Phenology: Flowering in summer (January–April).

Pollinators: The long-tubed white corolla with its distinct maroon-purple centre suggests a specialist insect pollinator.

Habitat and aspect: Rock fissures, cracks and crevices. All aspects of cliffs but more prominent on shady, south-facing cliffs. Temperatures correspond to those of the tropics and it is very hot in summer. Winters are cooler but frost is absent. The average daily maximum temperature is 30–38°C and average daily winter temperature 18–28°C. Rainfall in summer, ranging from 50–150 mm per annum.

Altitude: 600–1500 m.

Associated vegetation: Mosaic of arid mopane savanna (*Colophospermum mopane* dominant) and Namib Desert vegetation.

Associated cremnophytes: *Aeollanthus haumannii* and *Tetradenia kaokoensis*.

Geology: Granite (Fransfontein Granite Suite).

DISTRIBUTION

Otjihipa Mountains, northwestern Kaokoveld, Namibia.

RELATED SPECIES

Related to *Rogeria* but immediately distinguished by its unique atelechorous and anemochorus dispersal strategies. This is a remarkable adaptation and the first of its kind recorded for an obligate cremnophilous species. It is further distinguished from *Rogeria* by its soft fragile growth, soft capsules and small, linear to club-shaped seeds. All *Rogeria* species are annual or biennial, with erect woody growth, and are usually found on disturbed sites. They have very firm, armoured capsules and flattened seed.

ADAPTATIONS TO THE CLIFF ENVIRONMENT

Habit: Soft, fragile, squat, somewhat trailing growth. It has a flattened, semisucculent, perennial stem base, well wedged in the small rock cracks and well protected from disturbances such as wind or large herbivores. Plants grow in summer when flowering and fruiting takes place, with a resting period in winter and spring. The habitat of small fissures and cracks in boulders presents little competition from other cliff-dwelling plant species.

Size and weight: Usually 100–250 mm in diameter, size also depending on the amount of rain.

Stem: Soft and fragile, sometimes becoming pendent if growing from an overhang. Additionally, the elongating, wandering, filiform accessory stems, which also appear in summer,

are phototropically negative and will grow into any available (adjacent or the same) crevice. Small cleistogamous flowers result in different smaller, ovate seed capsules deeply buried within the crevice and with larger seeds than those produced by the normal aerial capsules.

Leaves

Orientation: Ascending to spreading.

Colour and texture: Glaucous, grey-green, covered with mucilage glands, well adapted to the xeric habitat.

Age and persistence: Weakly perennial, rapid-growing during the short wet periods but dying back to the base under unfavourable conditions.

Armament and camouflage: Plants without conspicuous armament or camouflage properties. The fruiting capsules of the two related *Rogeria* species in the region are very hard and armoured. The extrafloral nectaries attract ants, which provide additional protection against phytophagous insects (plants at Kirstenbosch continually visited by local ants).

Sexual reproduction

Remarkable reproductive biology: *Dewinteria petrophila* displays a remarkable reproductive biology, an adaptation to its arid cliff-face habitat. The safe (ensured) atelechorous (blastochory) cloned seed placement near the mother plant (or adjacent crevices) and aerial anemochorous (dust diaspores) dispersal ensure long-term survival.

Inflorescence and flowers: Flowers axillary, large in comparison to plant size, thus rich flowering ensuring cross fertilisation. The large, tubular, trumpet-shaped standard flowers suggest a specific insect pollinator. The dwarf cleistogamous flowers are 2 mm long, with pedicels up to 1.5 mm long, on slender, negatively phototropic, filiform branches bearing ovate, dwarf-sized, sometimes toothed leaves.

Fruit/Seed

Capsules: Capsules on arboreal branches tapering and flattened, those on specialist accessory branches flattened, much smaller, ovate to ovate-cordate; both capsules dehiscent loculicidally.

Size: Seed from aerial capsules 2.0–2.2 mm long, linear-oblong to club-shaped, slightly flattened, minutely reticulate, brownish (more than 50 per capsule). Seed from smaller capsules on accessory branches 2.5–3.0 mm long, oblong-obovoid, fringed (up to 5 per capsule).

Dispersal: The smaller seeds from the normal aerial capsules are shaken from their capsules by wind (anemochorous). The higher numbers (more than 50) improve chances of seeds landing in a suitable crevice site. The larger seeds from cleistogamous flowers and smaller capsules are locally dispersed (blastochory), the lower number of seeds (less than 5 per capsule) well secured, 'planted' deep in the fissure by the plant itself. Here the seeds remain, germinating when conditions become favourable (with the next good rains), an adaptation that could be compared to a long-term insurance policy. In

this way, the plant can afford to produce fewer but larger, more secure seed but of the exact genetic stock as the mother plant.

Establishment: Mucilage on the surface of the seed may play a role in anchorage of seedlings and in absorption of moisture in both seed types.

Time: Seeds released during the rainy season from summer to autumn.

Vegetative reproduction: Absent.

CONSERVATION STATUS

Plants are fairly common on cliff faces in the habitat and are not threatened.

ADDITIONAL NOTES

Horticulture: An attractive ornamental species that would be excellent for dry desert gardens, grown in rock fissures. Grow from seed, but germination is erratic. Best grown in dappled shade under controlled conditions in a greenhouse. Flowering in summer and autumn.

VOUCHERS

Van Jaarsveld 17520, 19413, 19527, 22102, 22106 (NBG).

ILLUSTRATIONS AND MAP

Plate 221, Figures 221a–221e, Map 221.

SCROPHULARIACEAE

Stemodiopsis Engl.

222. *Stemodiopsis rivae* Engl.

STEMODIOPSIS Engl.

222. *Stemodiopsis rivae* Engl. in *Annuario Reale del Istituto Botanico di Roma* 7: 25 (1897).

Cremonophyte growth form: Trailing chasmophyte (of light weight, cliff hugger).

Growth form formula: E:F:As:S/H:Es:De (vb) (fn)

Etymology: After the Italian botanist Domenico Riva (1856–1895), who collected the type.

DESCRIPTION AND HABITAT

Soft, perennial, branched, trailing herb up to 400 mm in diameter; stems and leaves strigose. Branches somewhat 4-angled. Leaves slightly fleshy; lamina triangular-ovate to ovate, 5–18 × 2–18 mm; margin serrate-dentate with 2–4 teeth; apex acute; base cuneate to subtruncate; petiole 3–12 mm long. Flowers solitary; bracteole up to 1.5 mm, subulate; pedicels 4–9 mm long, becoming decurved in fruiting stage. Calyx lobes subequal. Corolla 2-lipped, up to 10 mm long, white; throat pink to mauve; tube up to 6.5 mm long, 1.5 mm at base, widening to 4 mm at throat, sparsely pilose; upper lip about 3 mm long, triangular-ovate, lower lip 4.0–4.5 mm long, shortly trilobed, minutely pubescent. Capsule 4–5(–9) mm long (including beak), minutely pubescent. Seed oblong, 1 × 0.3 mm, slightly curved, yellowish brown. (Partly based on Philcox 1990.)

Phenology: Flowering in summer (January–April).

Pollinators: Insects.

Habitat and aspect: Rock cracks and crevices. All aspects, but mainly on shady south-facing cliffs. Temperatures correspond to those of the tropics and it is very hot in summer. Winters are cooler but frost is absent. The average daily maximum is 29°C and average daily winter temperature 17°C. Rainfall in summer, ranging from 300–400 mm per annum.

Altitude: 400–1675 m.

Associated vegetation: Soutpansberg Mountain Bushveld of the Savanna Biome (Mucina *et al.* 2005).

Associated cremonophytes: On the farm Little Leigh (near Wyllies Poort), it grows with the following cliff-dwelling plants: *Adromischus umbraticola* subsp. *ramosa*, *Aeollanthus buchnerianus* and *Crassula setulosa*.

Geology: Sandstone of the Wyllies Poort Formation (Soutpansberg Group).

DISTRIBUTION

Restricted to cliffs near Wyllies Poort and also in Zambia, Zimbabwe, Mozambique and Malawi.

RELATED SPECIES

The only *Stemodiopsis* species occurring in South Africa. The negatively phototropic fruit stalks are unique among the family Scrophulariaceae in South Africa.

ADAPTATIONS TO THE CLIFF ENVIRONMENT

Habit: Soft, fragile, trailing perennial growth in narrow crevices, also from the roof of overhanging rocks. It is well wedged in small rock crevices and cracks where it is well protected from disturbances such as wind or large herbivores. Plants grow in summer, when flowering and fruiting takes place, with a resting period in winter and spring. There is little competition from other cliff-dwelling plant species in its habitat of small fissures and crevices in boulders.

Size and weight: Usually 100–400 mm in diameter, size also depending on the amount of rain.

Stem: Soft, fragile, sometimes becoming pendent if growing from an overhang.

Leaves

Orientation: Ascending spreading.

Colour and texture: Green, leathery, somewhat fleshy.

Age and persistence: Plants perennial, rapid-growing during the short wet periods but dying back to the base under unfavourable conditions.

Armament: Plants without armament or camouflage properties.

Sexual reproduction

Inflorescence and flowers: Flowers axillary, small, in 2- or 3-flowered cymes. The flowers suggest a specific insect pollinator.

Fruit/Seed

Capsules: After fertilisation, the sharply rostrate, ellipsoid-conical capsules become recurved or directed downward towards the crevice. The pedicels are negatively phototropic, bending the capsule towards the crevice.

Size: Seed 1 mm long, narrowly oblong, slightly curved.

Dispersal: Yellowish brown seeds are shaken from the small capsules and dispersed by wind (explaining the large number of seeds) but the capsules are directed towards the crevice, thus ensuring a better chance of establishment (blastochory).

Establishment: The small, oblong seeds become wedged in crevices where they germinate when conditions are favourable.

Time: Seeds released during the rainy season from summer to autumn.

Vegetative reproduction: Absent.

CONSERVATION STATUS

Plants are fairly common and widespread and are not threatened.

ADDITIONAL NOTES

Horticulture: No attempt has been made to cultivate the plants.

VOUCHERS

Van Jaarsveld 19763, 19822 (NBG).

ILLUSTRATIONS AND MAP

Plate 222, Figures 222a–222c, Map 222.

1. *Pyrrosia schimperiana*



PLATE 1

Pyrrosia schimperiana. Drawn from plants in the Kirstenbosch cliff-plant collection (material from a sandstone cliff face at Blyderivierspoort, *Van Jaarsveld 17246*, collected 28 February 2002). Artist: Jeanette Loedolff.

2. *Cyrtanthus falcatus*



PLATE 2

Cyrtanthus falcatus. Drawn from plants in the Kirstenbosch cliff-plant collection (material from Mzinga Waterfall, KwaZulu-Natal Drakensberg, collected 11 October 2003, *Van Jaarsveld 18266*). Artist: Vicki Thomas.

3. *Cyrtanthus flammus*



PLATE 3

Cyrtanthus flammus. Drawn from plants in the Kirstenbosch cliff-plant collection (material from a ledge at the Kouga Dam, type plant!). Artist: Lisa Strachan.

5. *Cyrtanthus herrei*



PLATE 5

Cyrtanthus herrei. Painted from plants in the Kirstenbosch cliff-plant collection (material from a ledge on Kuamsibberg, Hunsberg, southern Namibia, collected 7 July 2007 by Paul Ems). Artist: Vicki Thomas.

7. *Cyrtanthus junodii*



PLATE 7

Cyrtanthus junodii. Drawn from a plant in flower in the Kirstenbosch cliff-plant collection (material from Wolkberg, Limpopo Province, collected 21 July 1999, Van Jaarsveld 16231). Artist: Vicki Thomas.

8. *Cyrtanthus labiatus*



PLATE 8

Cyrtanthus labiatus. Drawn from plants in the Kirstenbosch cliff-plant collection (material from a ledge at the Kouga Dam, Eastern Cape, collected 18 September 1990, *Van Jaarsveld 11070*). Artist: Lisa Strachan.

12. *Haemanthus paucifolius*



PLATE 12

Haemanthus paucifolius. Plant in flower and in fruit. Note the vegetative spread of young bulbs at the base of the plant (from Kaaprivierspoort, Barberton, *Van Jaarsveld 19371*). Artist: Vicki Thomas.

13. *Aloe arborescens* subsp. *mzimnyati*



PLATE 13

Aloe arborescens subsp. *mzimnyati*. Painted from a plant on a scree below a cliff face at Mzimnyati River, KwaZulu-Natal (*Van Jaarsveld 18211*). Artist: Lisa Strachan.

15. *Aloe challisii*



PLATE 15

Aloe challisii. Drawn from a plant from Steenkampsberg, Mpumalanga (collected by Chris Challis). Artist: Lisa Strachan.

16. *Aloe corallina*

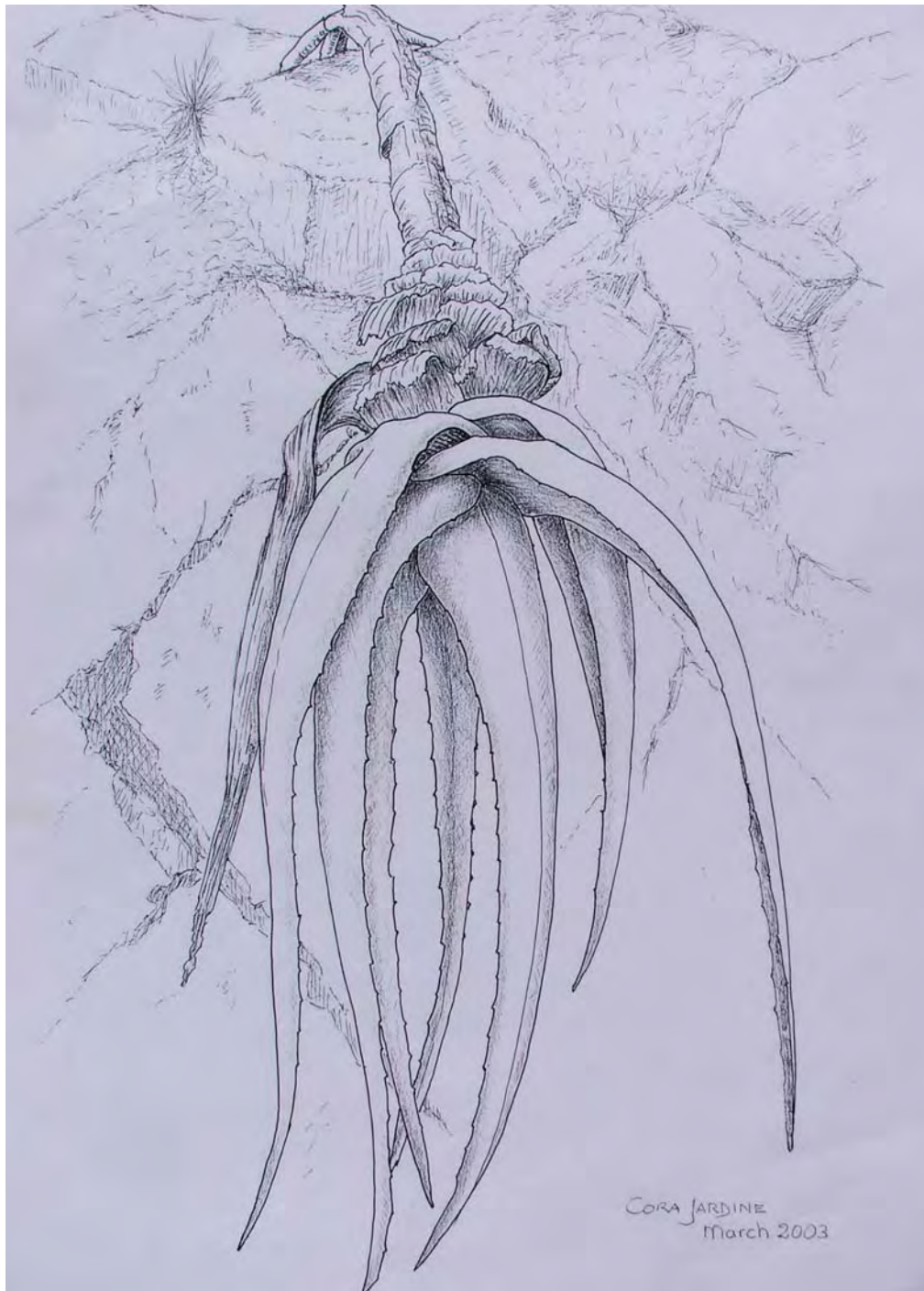


PLATE 16

Aloe corallina. Sketched from digital images of the original site (Otjiboronbongo, Kaakoveld, northern Namibia, *Van Jaarsveld 16482*). Artist. Cora Jardine.

17. *Aloe dabenorisana*



PLATE 17

Aloe dabenorisana. Painted from the type plant (Dabenorisberg, Bushmanland, Northern Cape). Artist: Ellaphie Ward-Hilhorst.



20. *Aloe hardyi*



PLATE 20

Aloe hardyi. Shown in habitat at Kromellenboog, Limpopo Province (*Van Jaarsveld 16242*). Artist: Eric Judd.

22. *Aloe meyeri*



PLATE 22

Aloe meyeri. Painted from the type plant (Rosyntjieberg, Richtersveld). Artist: Ellaphie Ward-Hilhorst.



24. *Aloe nubigena*



PLATE 24

Aloe nubigena. Depicted in its habitat near Angle Station, Barberton, Mpumalanga (from a plant collected by Phillip Nel). Artist: Eric Judd.

25. *Aloe omavandae*



PLATE 25

Aloe omavandae. Shown in habitat on a sandstone cliff on the Baynes Mountains at Omavanda (painted from the type plant). Artist: Gillian Condy.



26. *Aloe pavelkae*

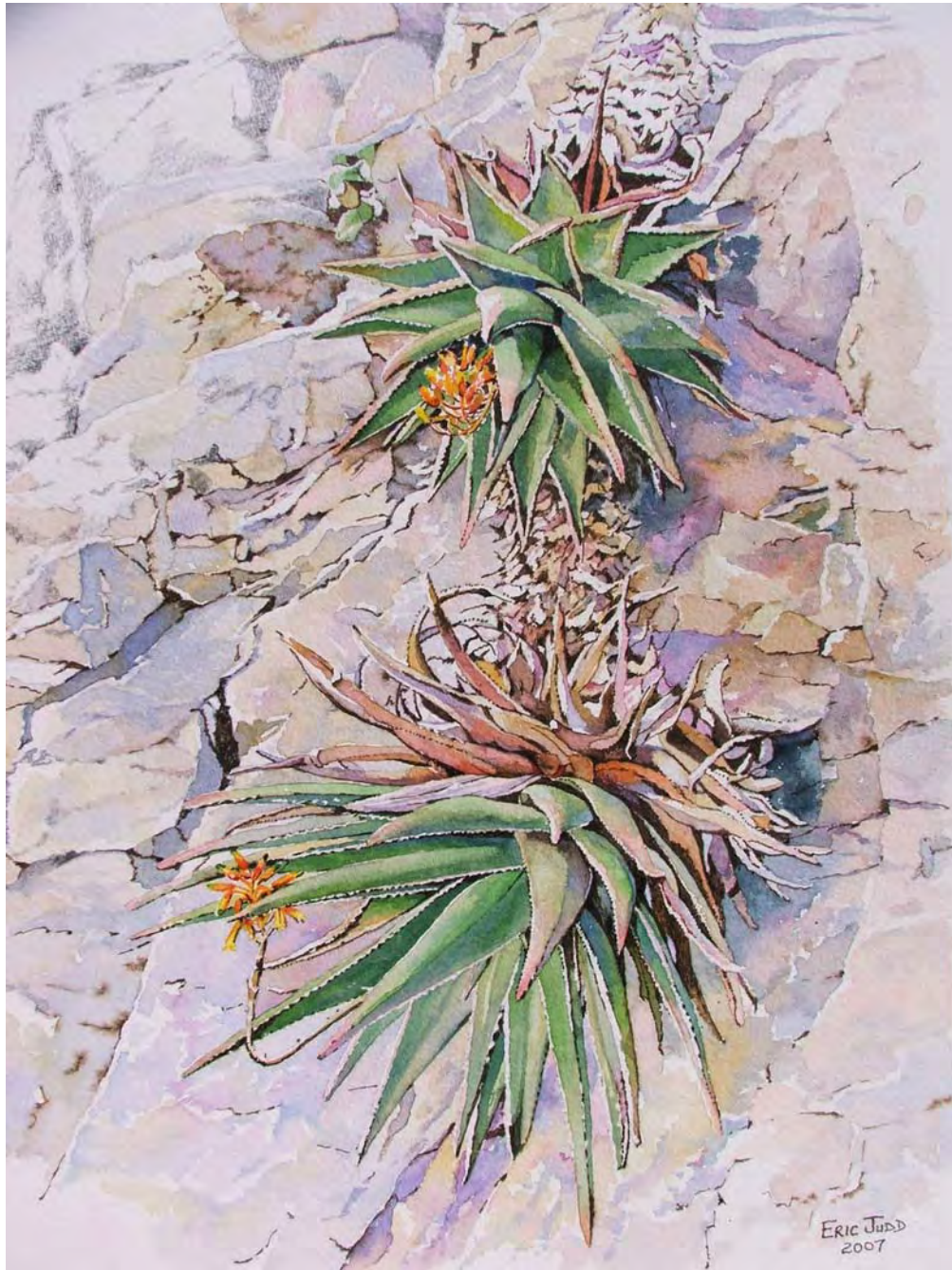


PLATE 26

Aloe pavelkae. Depicted in habitat in the Ai-Ais Richtersveld Transfrontier National Park (Kuamsibberg, Hunsberg, southern Namibia, *Van Jaarsveld 19919*). Artist: Eric Judd.



26a. *Aloe petrophila*



PLATE 26a

Aloe petrophila. Shown in habitat at Wyllies Poort, Soutpansberg, Limpopo Province (collected by Ernst van Jaarsveld). Artist: Eric Judd.



27. *Aloe pictifolia*



PLATE 27

Aloe pictifolia. Depicted in habitat at the Kouga Dam, Eastern Cape (*Van Jaarsveld 11046*)
Artist: Eric Judd.

28. *Aloe reynoldsii*



PLATE 28

Aloe reynoldsii. Painted from a plant at the Mbashe River, Eastern Cape (*Van Jaarsveld 16907*). Artist: Eric Judd.

31. *Bulbine cremnophila*



PLATE 31

Bulbine cremnophila. Drawn from a plant in Gertsmitzkloof, Baviaanskloof, Eastern Cape (Van Jaarsveld 7238). Artist: Vicki Thomas.

32a. *Bulbine latifolia* (Great Fish River, cliff form)



PLATE 32a

Bulbine latifolia. Depicted on cliffs at the Great Fish River, north of Grahamstown, Eastern Cape (Van Jaarsveld 16813). Artist: Vicki Thomas.

32. *Bulbine latifolia* var. *curvata*



PLATE 32

Bulbine latifolia var. *curvata*. Drawn from a plant at the Kouga Dam, Eastern Cape (Van Jaarsveld 13806). Artist: Vicki Thomas.

33. *Bulbine meiringii*



PLATE 33

Bulbine meiringii. Drawn from a plant from Meiringspoort, Western Cape (Van Jaarsveld, Vlok & Nanni 12762). Artist: Vicki Thomas.

35. *Bulbine pendens*



PLATE 35

Bulbine pendens. Depicted in the Skaaprivierspoort, Northern Cape (Van Jaarsveld, Harrower, Nicolson & Xaba 12762). Artist: Vicki Thomas.

36. *Bulbine ramosa*



PLATE 36

Bulbine ramosa. Shown in habitat at Badspoort south of Calitzdorp, Western Cape (Van Jaarsveld 16120). Artist: Vicki Thomas.

39. *Bulbine suurbergensis*



PLATE 39

Bulbine suurbergensis. Depicted in its habitat in the Suurberg, Eastern Cape (Van Jaarsveld 19228). Artist: Vicki Thomas.

40. *Bulbine thomasiae*



PLATE 40

Bulbine thomasiae. Depicted as it grows at Collywobbles, Eastern Cape (Van Jaarsveld 16850). Artist: Vicki Thomas.

41. *Gasteria batesiana* var. *batesiana*



PLATE 41

Gasteria batesiana var. *batesiana*. Drawn from plants in the Kirstenbosch cliff-plant collection. Artist: Ellaphie Ward-Hilhorst.

42. *Gasteria batesiana* var. *dolomitica*



PLATE 42

Gasteria batesiana var. *dolomitica*. Drawn from plants in the Kirstenbosch cliff-plant collection (material from Penge, Olifants River, Limpopo Province, *Van Jaarsveld & Hankey 15081*). Artist: Jeanette Loedolff.

43. *Gasteria croucheri* subsp. *pendulifolia*



PLATE 43

Gasteria croucheri subsp. *pendulifolia*. Painted from plants at Shongweni Dam, KwaZulu-Natal. Artist: Ellaphie Ward-Hilhorst.



43a. *Gasteria croucheri* subsp. *pendulifolia*



PLATE 43a

Gasteria croucheri subsp. *pendulifolia*. Depicted in cultivation at Kirstenbosch (gathered at Mamba Valley, Umgeni River, KwaZulu-Natal, *Van Jaarsveld, Baijnath & Heigeldorf* 9838). Artist: Tamlin Blake.

44. *Gasteria doreeniae*



PLATE 44

Gasteria doreeniae. Painted from material collected by Doreen Court from Swartwaterspoort, Eastern Cape. Artist: Ellaphie Ward-Hilhorst.

46. *Gasteria glomerata*



PLATE 46

Gasteria glomerata. Shown in its habitat at the Kouga Dam, Eastern Cape (Van Jaarsveld & Sardien 11054). Artist: Jeanette Loedolff.

47. *Gasteria pillansii* var. *ernesti-ruschii*



PLATE 47

Gasteria pillansii var. *ernesti-ruschii*. Painted from a plant from southern Namibia. Artist: Ellaphie Ward-Hilhorst.

48. *Gasteria rawlinsonii*



PLATE 48

Gasteria rawlinsonii. Drawn from a plant from Gertsmit-skloof, Baviaanskloof, Eastern Cape (*Van Jaarsveld 7215*). Artist: Jeanette Loedolff.

49. *Gasteria tukhelensis*

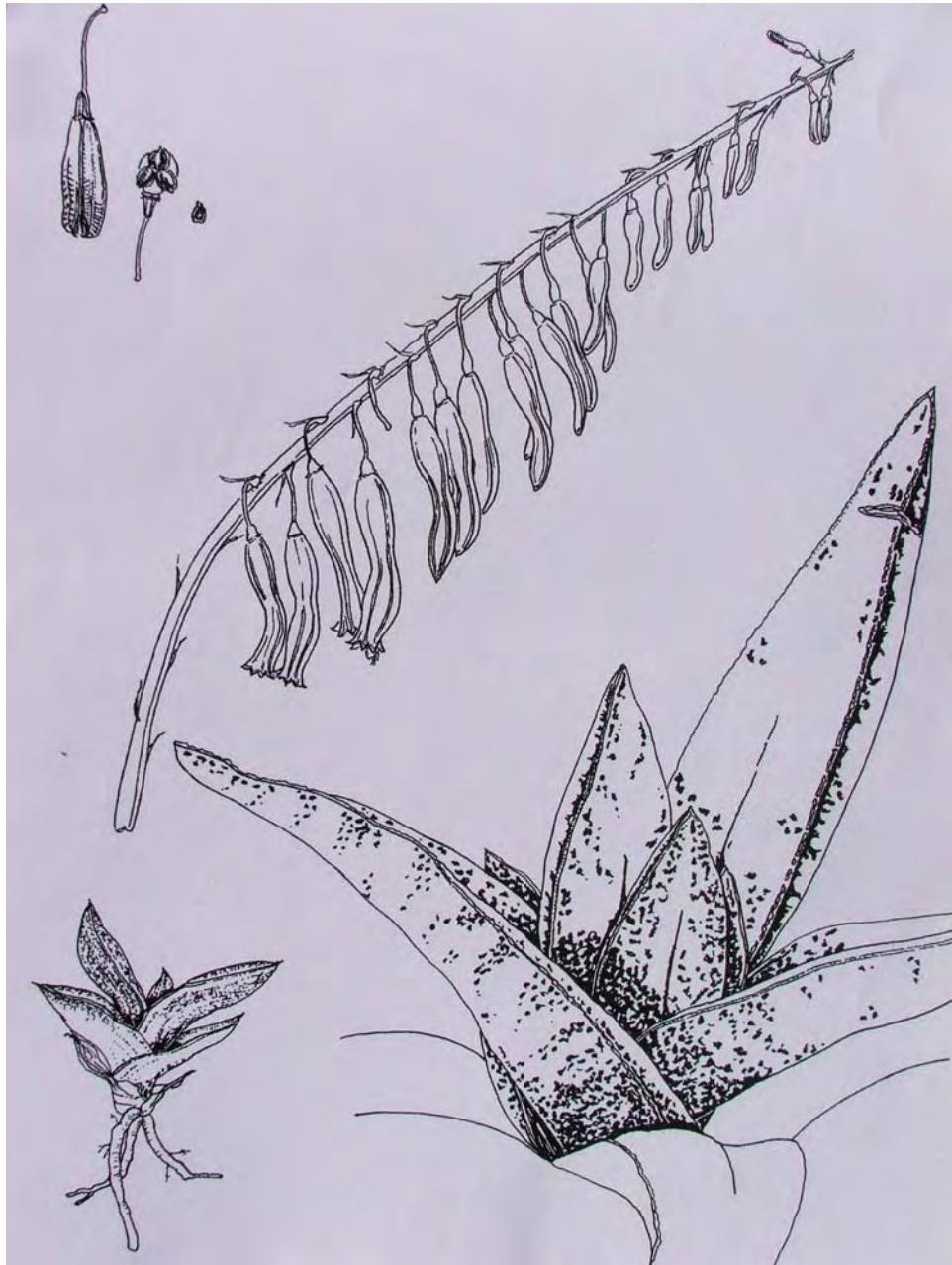


PLATE 49

Gasteria tukhelensis. Drawn from material from Ntshongweni, Thukela River, KwaZulu-Natal (*Van Jaarsveld 17996*). Artist: Lisa Strachan.

51. *Haworthia attenuata* (Enon form)



PLATE 51

Haworthia attenuata. Depicted in habitat at the Enon River, Eastern Cape (Van Jaarsveld 17833, 365/03). Artist: Gerhard Marx.

62. *Trachyandra tabularis*



PLATE 62

Trachyandra tabularis. Shown in habitat above Window Gorge, Table Mountain, Cape Peninsula, Western Cape (*Van Jaarsveld 22891*). Artist: Vicki Thomas.

63. *Albuca batteniana*



PLATE 63

Albuca batteniana. Drawn from material grown at Kirstenbosch (from coastal cliffs near Morgan's Bay, Eastern Cape, *Van Jaarsveld 16617*). Artist: Vicki Thomas.

64. *Albuca cremnophila*



PLATE 64

Albuca cremnophila. From Baviaanskloof, Eastern Cape (Van Jaarsveld 12171). Artist: Tamlin Blake.

65. *Albuca crudenii*



PLATE 65

Albuca crudenii. Drawn from plants grown in the Kirstenbosch cliff-plant collection (material collected by Tony Dold near Grahamstown, Eastern Cape). Note the production of bulbils at the base of the bulb (cloning). Artist: Lisa Strachan.



68. *Albuca thermarum*



PLATE 68

Albuca thermarum. Grown in the Kirstenbosch cliff-plant collection (type material from Badspoort, near Calitzdorp).
Artist: Vicki Thomas.

69. *Drimia cremnophila*

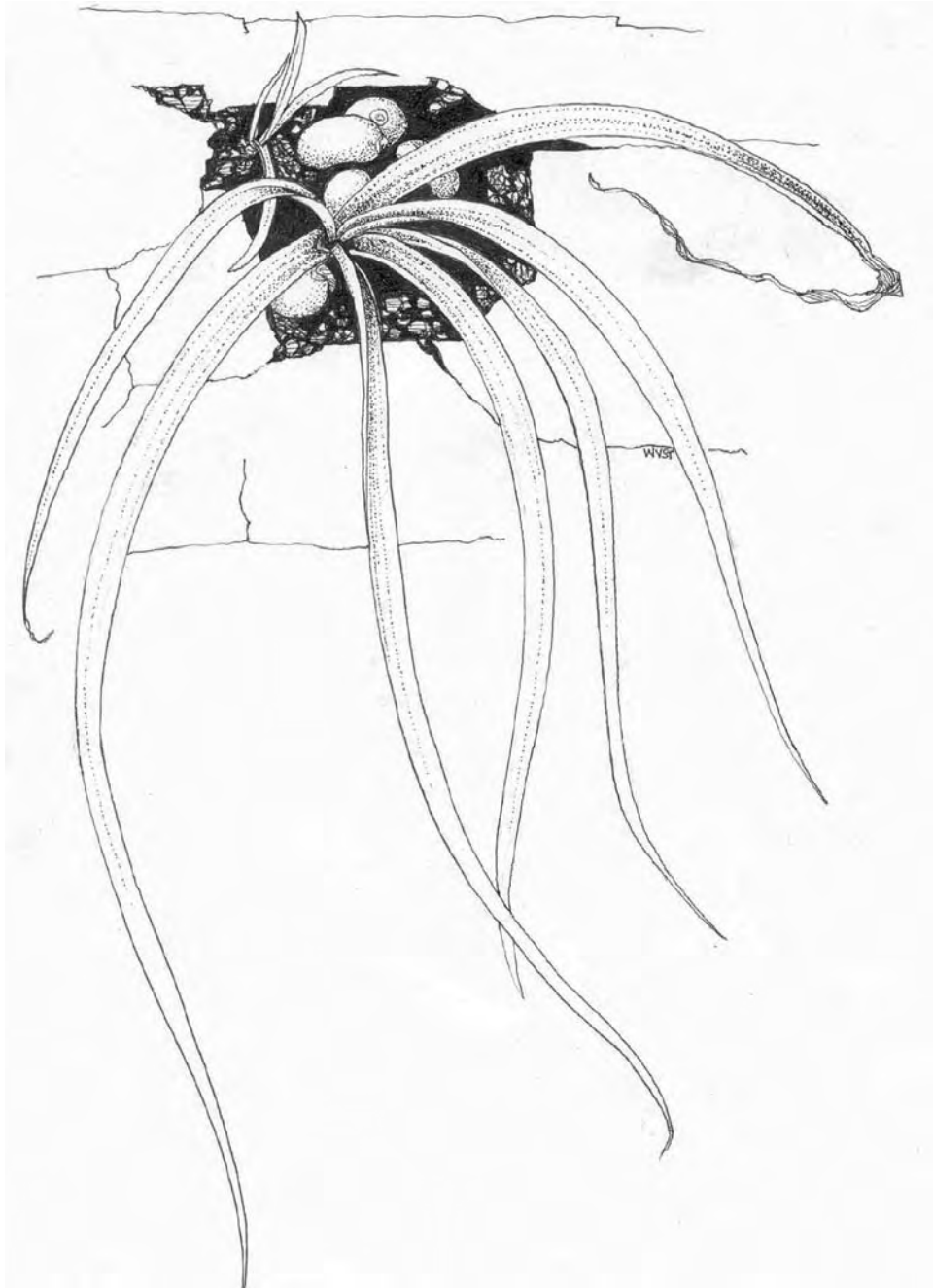


PLATE 69

Drimia cremnophila. Sketched from a plant grown at Kirstenbosch (from a shale cliff face along the Mzimvubu River, Transkei region of the Eastern Cape, Van Jaarsveld, Xaba & Harrower 97). Artist: Vicki Thomas.

71. *Drimia loedolffiae*



PLATE 71

Drimia loedolffiae. Drawn from a plant cultivated at Kirstenbosch (material from near the mouth of the Kei River, Eastern Cape, *Van Jaarsveld 17914*). Artist: Jeanette Loedolff.

72. *Drimia mzimvubuensis*



PLATE 72

Drimia mzimvubuensis (type plant). Drawn from plants collected on a shale cliff along the Mzimvubu River, Transkei region, Eastern Cape. Artist: Elbe Joubert.

73. *Drimia uniflora*

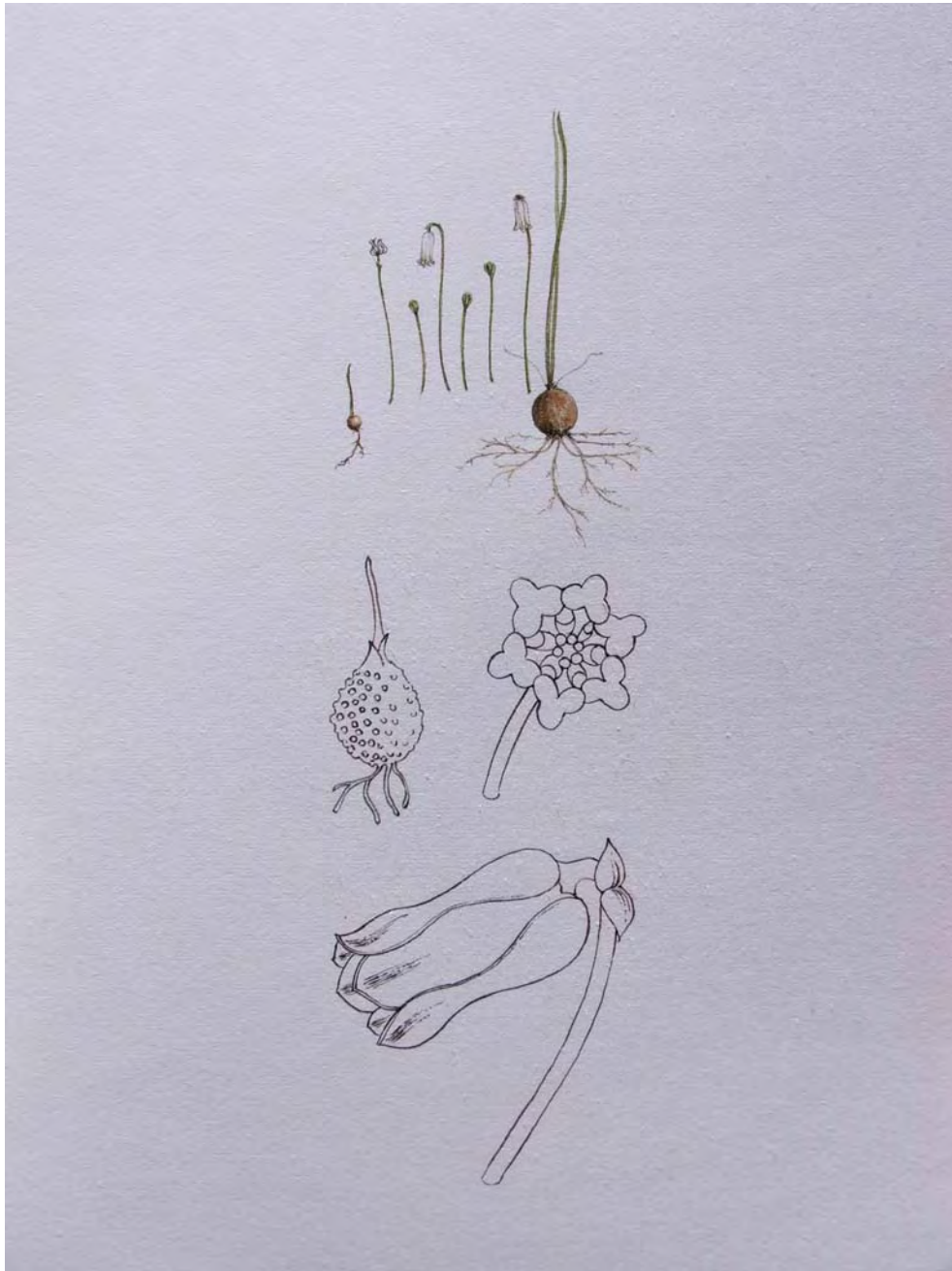


PLATE 73

Drimia uniflora (= *Litanthus pusillus*). Drawn from cultivated material at Kirstenbosch (from Aasvoëlberg cliffs, Willowmore, Eastern Cape, *Van Jaarsveld & Nordenstam 20041*). Artist: Lisa Strachan.

75. *Ledebouria cremnophila*



PLATE 75

Ledebouria cremnophila. In flower in its sandstone cliff-face habitat (Kaaprivierspoort, Mpumalanga, *Van Jaarsveld 19372*). Artist: Jeanette Loedolff.

76. *Ledebouria venterii*



PLATE 76

Ledebouria venterii (type plant). Flowering in cultivation at Kirstenbosch.
Artist: Jeanette Loedolff.

78. *Ornithogalum longibracteatum*



PLATE 78

Ornithogalum longibracteatum. In its cliff-face habitat at Tsolorha, Bashee River, Transkei region, Eastern Cape (*Van Jaarsveld 16896*). Note the production of bulbils at the base of the bulb (cloning). Artist: Jeanette Loedolff.

79. *Ornithogalum pendens*



PLATE 79

Ornithogalum pendens. Shown in its habitat, a sandstone cliff at Skaap-rivierspoort, Namaqualand, Northern Cape (drawn from the type collection).
Artist: Vicki Thomas.

82. *Lavrania haagnerae*



PLATE 82

Lavrania haagnerae. Depicted on a cliff west of Sesfontein (Van Jaarsveld 19879). Artist: Gerhard Marx.



85. *Kleinia galpinii*



PLATE 85

Kleinia galpinii. Grown in the Kirstenbosch cliff-plant collection. Plant collected on a cliff near Barberton, Mpumalanga. Artist: Vicki Thomas.

86. *Othonna armiana*



PLATE 86

Othonna armiana. Drawn from a plant growing in the Kirstenbosch cliff-plant collection (material from Rooiberg, Eksteenfontein, Richtersveld, Northern Cape, *Van Jaarsveld & Kuhn 8188*). Artist: Jeanette Loedolff.

87. *Othonna capensis*



PLATE 87

Othonna capensis. Drawn from a plant growing in the Kirstenbosch cliff-plant collection (material from Valley of Desolation, Graaff-Reinet, Eastern Cape, *Van Jaarsveld 16589*). Artist: Jeanette Loedolff.

88. *Othonna cremnophila*



PLATE 88

Othonna cremnophila. Drawn from a plant growing in the Kirstenbosch cliff-plant collection (material from Rosyntjieberg, Richtersveld, Northern Cape, Van Jaarsveld 19119). Artist. Lisa Strachan.

89. *Othonna triplinervia* (cremnophilous form)



PLATE 89

Othonna triplinervia. Painted from a plant growing in the Kirstenbosch cliff-plant collection (material from Enon, Eastern Cape, *Van Jaarsveld 17855*). Artist: Jeanette Loedolff.

90. *Senecio medley-woodii*



PLATE 90

Senecio medley-woodii. Drawn from a plant growing in the Kirstenbosch cliff-plant collection (material from Mzimvubu River, Transkei, Eastern Cape, *Van Jaarsveld, Harrower & Xaba 20*). Artist: Jeanette Loedolff.

92. *Senecio pondoensis*



PLATE 92

Senecio pondoensis. Drawn from a plant growing in the Kirstenbosch cliff-plant collection (material from Mzamba River, Transkei region, Eastern Cape, *Van Jaarsveld, Styles & Buring 19297*). Artist: Jeanette Loedolff.



97. *Adromischus cristatus* var. *schonlandii*



PLATE 97

Adromischus cristatus var. *schonlandii*. Drawn from a plant growing in the Kirstenbosch cliff-plant collection (material from the Kouga Dam, Eastern Cape, *Van Jaarsveld 17102*, collected 19 December 2001). Artist: Jeanette Loedolff.

100. *Adromischus fallax*



PLATE 100

Adromischus fallax. Drawn from a plant growing in the Karoo Desert National Botanical Garden. Artist: Elise Bodley.

101. *Adromischus leucophyllus*



PLATE 101

Adromischus leucophyllus. Painted from a plant in the Kirstenbosch cliff-plant collection (material from Keurkloof, De Doorns, Hex River Valley, Western Cape, *Van Jaarsveld 19556*). Artist: Vicki Thomas.

104. *Adromischus subdistichus*



PLATE 104

Adromischus subdistichus. Drawn from a plant growing in the growing in the Karoo Desert National Botanical Garden (material from Nuwekloof Pass, Baviaanskloof, Eastern Cape). Artist: Elise Bodley.

106. *Cotyledon barbeyi* var. A



PLATE 106

Cotyledon barbeyi var. A. Drawn from a plant in the Kirstenbosch cliff-plant collection (material from Wyllies Poort, Limpopo Province, *Van Jaarsveld 18035*). Artist: Vicki Thomas.

108. *Cotyledon pendens*



PLATE 108

Cotyledon pendens. Drawn from a plant growing in the Kirstenbosch cliff-plant collection (drawn from the type collection from Tsolorha, Bashee River, Transkei region, Eastern Cape). Artist: Lisa Strachan.

109. *Cotyledon tomentosa* subsp. *tomentosa*



PLATE 109

Cotyledon tomentosa subsp. *tomentosa*. Drawn from a plant growing in the Kirstenbosch cliff-plant collection (material from Kouga Dam, Eastern Cape, Van Jaarsveld 17180). Artist: Gillian Foster.

115. *Crassula capitella* subsp. *thyrsiflora* (cremnophilous form)



PLATE 115

Crassula capitella subsp. *thyrsiflora*. Drawn from plants in the Kirstenbosch cliff-plant collection (material from cliffs at Gertsmitkloof, Baviaanskloof, Eastern Cape, *Van Jaarsveld* 7234). Artist: Lisa Strachan.

116. *Crassula cremnophila*



PLATE 116

Crassula cremnophila. Drawn from plants in the Kirstenbosch cliff-plant collection (material from cliffs at Keurkloof, Kouga River, Eastern Cape, *Van Jaarsveld 17368*). Artist: Cora Jardine.



116a. *Crassula cremnophila*



PLATE 116a

Crassula cremnophila. Drawn from plants in the Kirstenbosch cliff-plant collection (material from cliffs at Keurkloof, Kouga River, Eastern Cape, *Van Jaarsveld 17368*). Artist: Lisa Strachan.

125. *Crassula montana* subsp. *montana*



PLATE 125

Crassula montana subsp. *montana*. Drawn from plants in the Kirstenbosch cliff-plant collection (material from cliffs at Badspoort near Calitzdorp, Western Cape, *Van Jaarsveld 14144*). Artist: Lisa Strachan.

131. *Crassula perforata* subsp. *kougaensis*



PLATE 131

Crassula perforata subsp. *kougaensis*. Drawn from plants in the Kirstenbosch cliff-plant collection (material from cliffs at Kouga Dam, Eastern Cape, *Van Jaarsveld* 9905). Artist: Gillian Foster.

142. *Crassula sladenii*



PLATE 142

Crassula sladenii. Drawn from plants growing in the Kirstenbosch cliff-plant collection (material from cliffs at Konsertnaberg, Ai-Ais Richtersveld Transfrontier National Park, southern Namibia, *Van Jaarsveld 21070*). Artist: Jeanette Loedolff.

143. *Crassula smithii*



PLATE 143

Crassula smithii. Drawn from plants in the Kirstenbosch cliff-plant collection (material from cliffs at Noodsberg, KwaZulu-Natal, collected by Gideon Smith). Artist: Vicki Thomas.

145. *Crassula streyi*



PLATE 145

Crassula streyi. Drawn from plants in the Kirstenbosch cliff-plant collection (material from Mzamba, northern Transkei region, Eastern Cape, *Van Jaarsveld 18258*). Artist: Jeanette Loedolff.



145a. *Crassula streyi*



PLATE 145a

Crassula streyi. Drawn from plants in the Kirstenbosch cliff-plant collection (material from Mtamvuna, southern KwaZulu-Natal). Artist: Jeanette Loedolff.

151. *Tylecodon bruynsii*



PLATE 151

Tylecodon bruynsii. Painted from a plant in the Kirstenbosch cliff-plant collection (material from south-facing cliffs, Kuamsibberg, Hunsberg, southern Namibia, *Van Jaarsveld 21088*). Artist: Vicki Thomas.

155. *Tylecodon ellaphieae*



PLATE 155

Tylecodon ellaphieae (type). Drawn from a plant in the Kirstenbosch collection (material from Rosyntjieberg, Richtersveld, Northern Cape). Artist: Ellaphie Ward-Hilhorst.

157. *Tylecodon petrophilus*



PLATE 157

Tylecodon petrophilus. Drawn from the type plant in the Kirstenbosch cliff-plant collection (material from south-facing cliffs in Skaaprivierspoort, Namaqualand, Northern Cape). Artist: Vicki Thomas.

159. *Tylecodon sulphureus* var. *armianus*



PLATE 159

Tylecodon sulphureus var. *armianus* (type). Painted from a plant in the Kirstenbosch collection (material from south-facing cliffs, Pellaberg, Northern Cape). Artist: Ellaphie Ward-Hilhorst.

164. *Streptocarpus kentaniensis*



PLATE 164

Streptocarpus kentaniensis. Drawn from a plant growing in the Kirstenbosch cliff-plant collection (material from Kei River, Eastern Cape, *Van Jaarsveld 17923*).
Artist: Vicki Thomas.

166. *Aeollanthus rydingianus*



PLATE 166

Aeollanthus rydingianus. Drawn from plants collected at Omavanda, Baynes Mountains, northern Namibia (type collection). Artist: Vicki Thomas.

168. *Plectranthus ernstii*



PLATE 168

Plectranthus ernstii (type collection). Painted from plants in the Kirstenbosch collection (material from south-facing cliffs, Oribi Gorge, southern KwaZulu-Natal). Artist: Lynne MacKenzie.

169. *Plectranthus mutabilis*



PLATE 169

Plectranthus mutabilis. Drawn from plants collected on dolomite cliffs at Sudwala Caves, Mpumalanga. Artist: Lynne MacKenzie.

170. *Plectranthus mzimvubuensis*

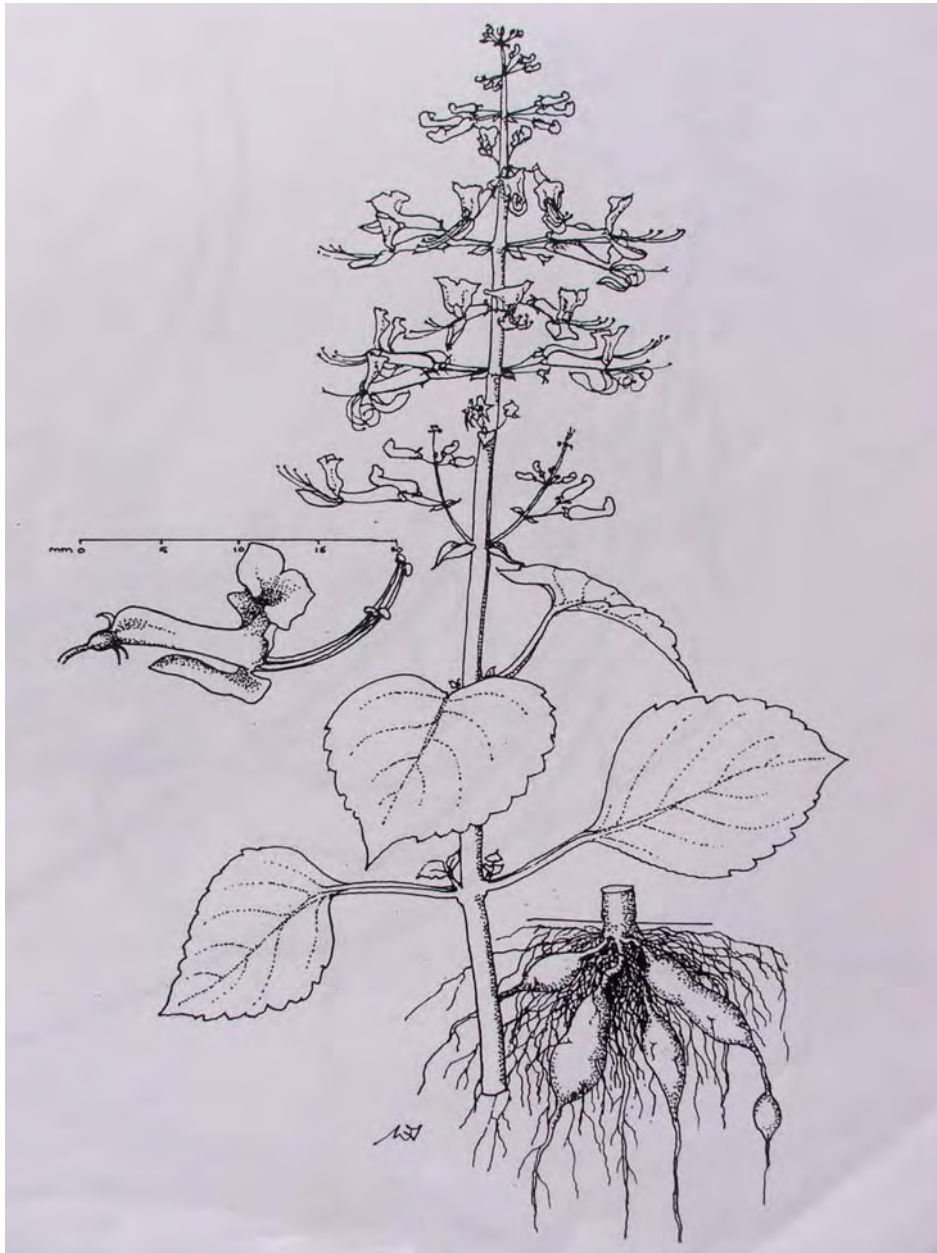


PLATE 170

Plectranthus mzimvubuensis. Drawn from plants (type collection) collected at the Mzimvubu River, Transkei region, Eastern Cape. Artist: Vicki Thomas.

170a. *Plectranthus mzimvubuensis*



PLATE 170a

Plectranthus mzimvubuensis. Painted from plants (type collection) collected along the Mzimvubu River, Transkei region, Eastern Cape. Artist: Vicki Thomas.

172. *Plectranthus saccatus* subsp. *pondoensis*



PLATE 172

Plectranthus saccatus subsp. *pondoensis*. Drawn from plants grown at the Kirstenbosch collection (material from sandstone cliffs at Oribi Gorge, type collection). Artist: Elise Bodley.

174. *Carruanthus peersii*



PLATE 174

Carruanthus peersii. Drawn from a plant grown in the Kirstenbosch cliff-plant collection (material from Toorwaterspoort, Groot Swartberg, Western Cape, *Van Jaarsveld 17412*). Artist: Jeanette Loedolff.



189. *Conophytum ricardianum* subsp. *ricardianum*

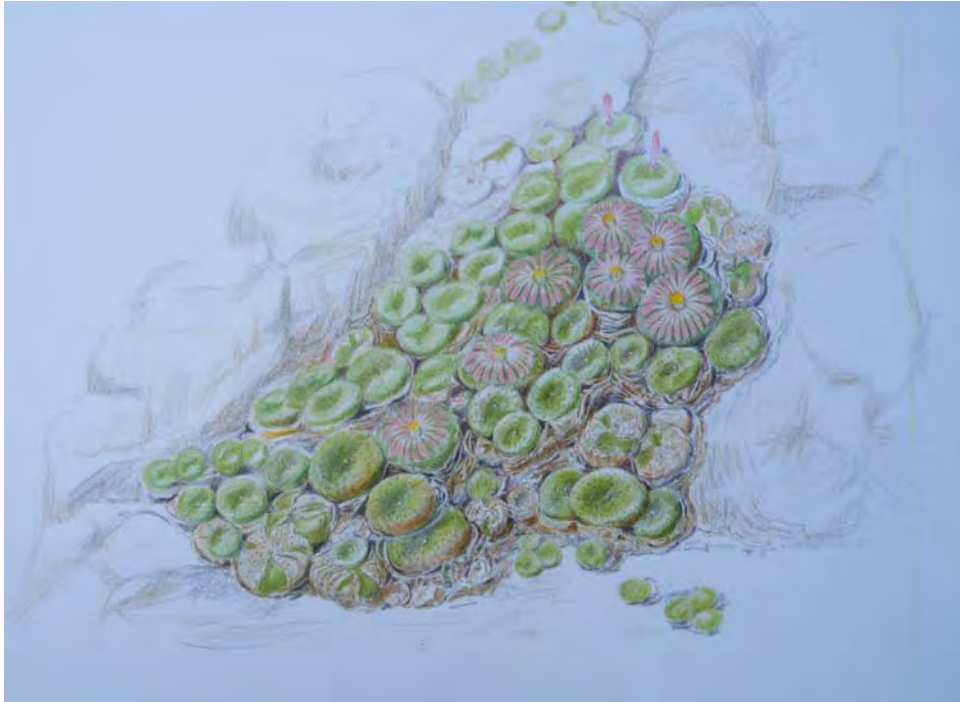


PLATE 189

Conophytum ricardianum subsp. *ricardianum*. Depicted in habitat on Kuamsib-berg, Hunsberg, southern Namibia (*Van Jaarsveld 21087*). Artist: Jeanette Loedolff.



190. *Conophytum stephanii* subsp. *stephanii*

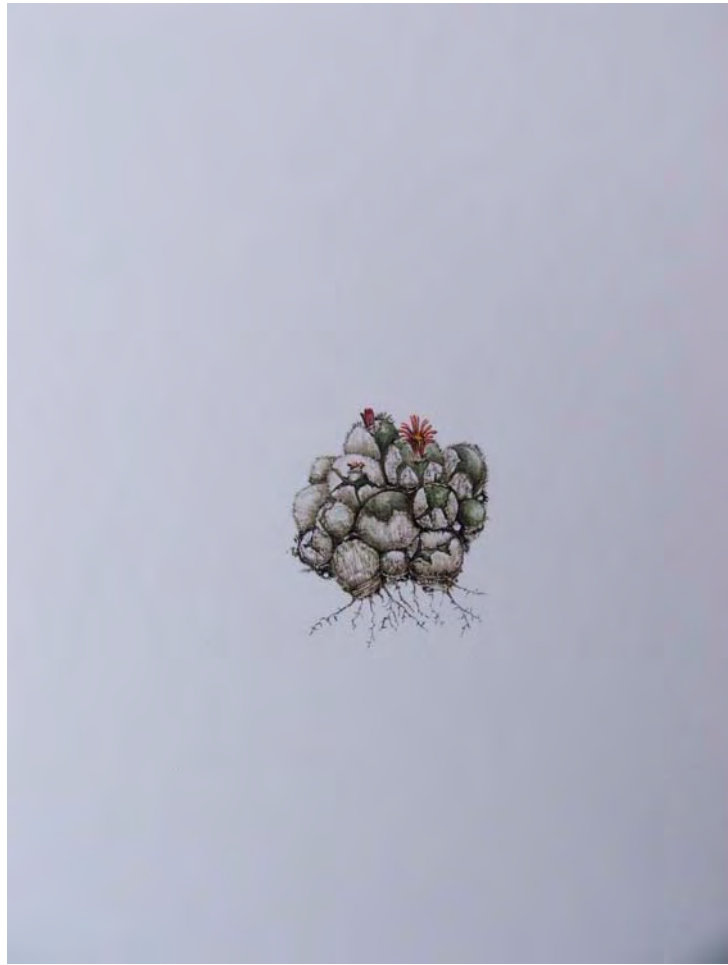


PLATE 190

Conophytum stephanii subsp. *stephanii*. Drawn from a plant collected on the Rosyntjieberg, Richtersveld, Northern Cape (*Van Jaarsveld 19130*). Artist: Lisa Strachan.

192. *Conophytum taylorianum* subsp. *ernianum*



PLATE 192

Conophytum taylorianum subsp. *ernianum*. Drawn from a plant collected on the Hohenzollern, Hunsberg, southern Namibia (*Van Jaarsveld 21032*). Artist: Lisa Strachan.

193. *Conophytum taylorianum* subsp. *rosynense*



PLATE 193

Conophytum taylorianum subsp. *rosynense*. Painted from a plant collected on the Rosyntjieberg, Richtersveld, Ai-Ais Richtersveld Transfrontier National Park, Northern Cape (*Van Jaarsveld* 22271, 580/09). Artist: Jeanette Loedolff.

196. *Delosperma esterhuyseniae*



PLATE 196

Delosperma esterhuyseniae. Drawn from a plant grown in the Kirstenbosch cliff-plant collection (material from Gertsmitskloof, Baviaanskloof, Eastern Cape, *Van Jaarsveld* 7245). Artist: Jeanette Loedolff.

202. *Delosperma tradescantioides*



PLATE 202

Delosperma tradescantioides. Drawn from a plant grown in the Kirstenbosch cliff-plant collection (material from cliffs along the Kei River, Eastern Cape, collected by Cameron MacMaster & Rhoda van Zijl). Artist: Jeanette Loedolff.

204. *Delosperma waterbergense*



PLATE 204

Delosperma waterbergense. Drawn from a plant grown in the Kirstenbosch cliff-plant collection (material from cliffs on the Waterberg, Marakele National Park, Limpopo Province, *Van Jaarsveld 17953*). Artist: Jeanette Loedolff.

207. *Drosanthemum expersum*



PLATE 207

Drosanthemum expersum. Drawn from a plant grown in the Kirstenbosch cliff-plant collection. Note the woody resprouting base and the young red fruiting capsules (material from cliffs on the Baviaansberg, Western Cape Province, *Van Jaarsveld 18621*). Artist: Jeanette Loedolff.

211. *Jensenobotrya lossowiana*



PLATE 211

Jensenobotrya lossowiana. Painted from a plant at Dolphin Head on the southern Namibian coast (*Van Jaarsveld 21145*). Artist: Jeanette Loedolff.

214. *Oscularia cremnophila*



PLATE 214

Oscularia cremnophila. Drawn from a plant grown at the Kirstenbosch cliff-plant collection (material from Steenbokfontein, near Elands Bay, Western Cape, from the type collection). Artist: Lisa Strachan.

221. *Dewinteria petrophila*



PLATE 221

Dewinteria petrophila. Painted from a plant grown at the Kirstenbosch cliff-plant collection (material from Otjihipa Mountains, Kaokoveld, Namibia). Artist: Vicki Thomas.

1. *Pyrrosia schimperiana*



FIGURE 1a. *Pyrrosia schimperiana* on a sandstone cliff face at Blyderivierspoort (Van Jaarsveld 17246, 28 February 2002). Plants proliferate from stolons, occupying crevices (vegetative proliferation as backup strategy).



FIGURE 1b. Blyderivierspoort, the habitat of *Pyrrrosia schimperiana* (28 February 2002).



FIGURE 1c. *Pyrrrosia schimperiana* growing on cliffs along to the Blyde River (Van Jaarsveld 17246, 28 February 2002).

2. Cyrtanthus falcatus



FIGURE 2a & 2b. *Cyrtanthus falcatus* in habitat at the Mzinga Waterfall (KwaZulu-Natal Drakensberg). Note the drooping, sickle-shaped (falcate) leaves (Van Jaarsveld 18266, 11 October 2003).



FIGURE 2c. Mzinga Waterfall, habitat of *Cyrtanthus falcatus* (11 October 2003).



FIGURE 2d. Inflorescence of *Cyrtanthus falcatus*. Note the U-bend and the dark inner portion of the perianth.

3. *Cyrtanthus flammosus*



FIGURE 3a. *Cyrtanthus flammosus* in habitat on a ledge at the Kouga Dam. Note the bulb half exposed. Associated cremnophytes include *Adromischus sphenophyllus*, *Aloe pictifolia*, *Crassula muscosa* and *Haworthia viscosa*.

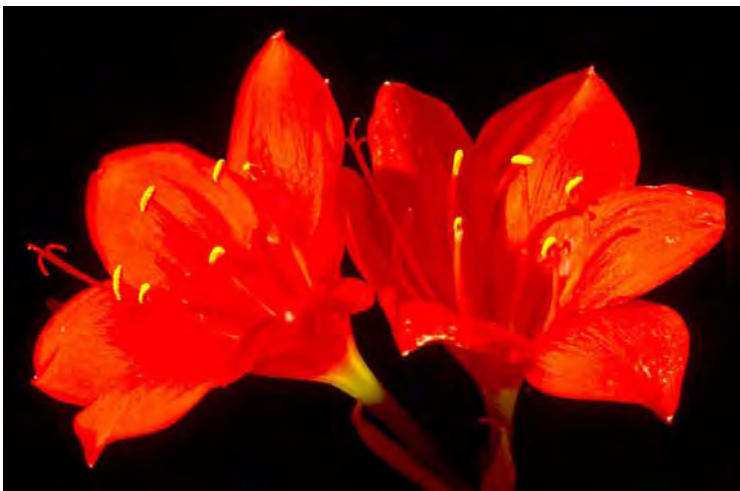


FIGURE 3b. Flowers of *Cyrtanthus flammosus*, an example of rich flowering on the cliff face.

4. *Cyrtanthus flanagani*



FIGURE 4a. *Cyrtanthus flanagani* in habitat on the Sentinel, KwaZulu-Natal Drakensberg (Van Jaarsveld 16989, 14 December 2001).



FIGURE 4b. Habitat of *Cyrtanthus flanagani*, the Sentinel in the background.

5. *Cyrtanthus herrei*



FIGURE 5a. *Cyrtanthus herrei* on Harasberg cliffs.



FIGURE 5b. *Cyrtanthus herrei* growing on a cliff on the Kuamsibberg (Hunsberg), southern Namibia.



FIGURE 5c. Inflorescence of *Cyrtanthus herrei* (cultivated at Kirstenbosch). Flowers pollinated by sunbirds.



FIGURE 5d. Fruit of *Cyrtanthus herrei*. Seed winged, wind-dispersed.

6. *Cyrtanthus inaequalis*



FIGURE 6a. *Cyrtanthus inaequalis* in flower at Kirstenbosch (from Eastern Cape material). Note the curved perianth tube. Flowers pollinated by sunbirds. Seed winged, wind-dispersed.



FIGURE 6b. *Cyrtanthus inaequalis* in habitat at Toorwaterspoort, Eastern Cape.



FIGURE 6c. Cliffs at Toorwaterspoort, habitat of *Cyrtanthus inaequalis*.



FIGURE 6d. Bulbils of *Cyrtanthus inaequalis* on a cliff face at Buffelspoort, Western Cape (vegetative backup).

7. Cyrtanthus junodii



FIGURE 7a. *Cyrtanthus junodii* in flower at Kirstenbosch (from Wolkberg material collected by E.J. van Jaarsveld).

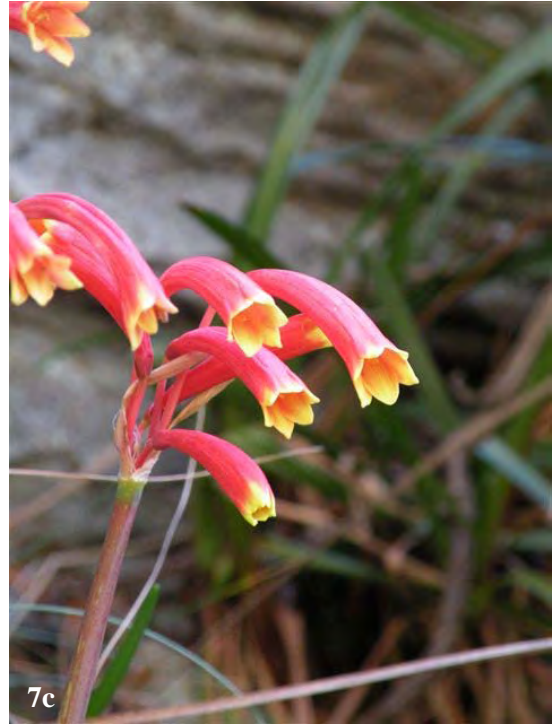


FIGURE 7b & 7c. *Cyrtanthus junodii* in habitat on the Wolkberg, Limpopo Province. Photograph: Wessel Swanepoel.



FIGURE 7d. Dolomite cliffs of the Wolkberg, habitat of *Cyrtanthus junodii*. Photograph: Wessel Swanepoel.

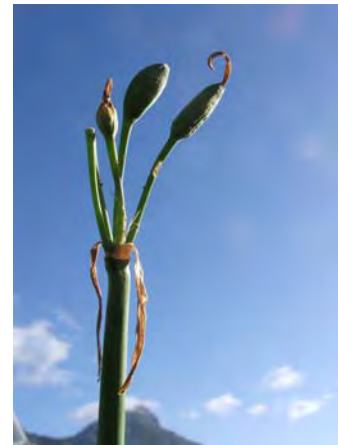


FIGURE 7e. *Cyrtanthus junodii* in fruit. Seed winged, wind-dispersed.

8. *Cyrtanthus labiatus*



FIGURE 8a. *Cyrtanthus labiatus* grown at Kirstenbosch, pollinated by sunbirds in its native habitat. Seeds winged and wind-dispersed.



FIGURE 8b. *Cyrtanthus labiatus* in flower on a cliff face at Kouga Dam, sharing its habitat with *Aloe pictifolia*, another cremnophyte.



FIGURE 8c. Bulbils of *Cyrtanthus labiatus*, a vegetative propagation backup strategy in its cliff-face habitat.

9. *Cyrtanthus montanus*



FIGURE 9a. *Cyrtanthus montanus* is endemic to the southeastern Cape and is pollinated by butterflies (*Meneris tulbaghia*). Seed winged, wind-dispersed.



FIGURE 9b. *Cyrtanthus montanus* growing on a ledge in habitat at Keurkloof, Kouga. Note the formation of vegetative bulbils so characteristic of many cremnophilous succulent and bulbous plants.



FIGURE 9c. Baviaanskloof, the cliff-face habitat of *Cyrtanthus montanus*.



FIGURE 9d. *Cyrtanthus montanus* occupying rock crevices at Grootrivierspoort in the Eastern Cape.

10. *Haemanthus albiflos*



FIGURE 10a. *Haemanthus albiflos* in its cliff-face habitat along the Mzimvubu River in the Transkei region of the Eastern Cape.



FIGURE 10b. *Haemanthus albiflos* in flower and fruit at Kirstenbosch in the summer of 2009.



FIGURE 10c. *Haemanthus albiflos* in fruit at Kirstenbosch in autumn. The fleshy berries turn red when ripe and are dispersed by birds.

11. *Haemanthus humilis* subsp. *humilis*



FIGURE 11a & 11b. *Haemanthus humilis* subsp. *humilis* (from Tandyberg, Graaff-Reinet).



FIGURE 11c. *Haemanthus humilis* subsp. *humilis* in its cliff-face habitat.

12. *Haemanthus paucifolius*



FIGURE 12a. *Haemanthus paucifolius* in fruit (cultivated from material from Barberton). Note the vegetative spread of young bulbs at the base of the plant.



FIGURE 12b. *Haemanthus paucifolius* in its native habitat, cliffs near Barberton.

13. *Aloe arborescens* subsp. *mzimnyati*



FIGURE 13a. *Aloe arborescens* subsp. *mzimnyati* on a scree below the cliff face along the Mzimnyati River, KwaZulu-Natal.



FIGURE 13b. *Aloe arborescens* subsp. *mzimnyati* on a cliff face at the Mzimnyati River, KwaZulu-Natal.



FIGURE 13c. Note the short flowers of *Aloe arborescens* subsp. *mzimnyati*, from the Mzimnyati River, KwaZulu-Natal.



FIGURE 13d. *Aloe arborescens* subsp. *mzimnyati* in flower at the Mzimnyati River in KwaZulu-Natal. Pollinated by sunbirds.

14. *Aloe catengiana*



FIGURE 14a. *Aloe catengiana* in flower at Kirstenbosch.



FIGURE 14b. The habitat of *Aloe catengiana*, the sheer cliff faces of Omavanda in the Kaokoveld of Namibia.



FIGURE 14c. A juvenile of *Aloe catengiana* in a rock crevice at Omavanda, Kaokoveld, Namibia. Plants are pollinated by sunbirds, the seeds dispersed by wind.

15. *Aloe challisii*



FIGURE 15a. *Aloe challisii* in its habitat on Steenkampsberg in Mpumalanga.



FIGURE 15b. Steenkampsberg, cliff-face habitat of *Aloe challsii*.



FIGURE 15c. *Aloe challsii* in fruit at Steenkampsberg in Mpumalanga.

16. *Aloe corallina*



FIGURE 16a. *Aloe corallina* in its habitat at Otjiboronbongo in the Cunene Valley in the northern Baynes Mountains in Namibia.



FIGURE 16b. Inflorescence of *Aloe corallina*. The flowers are pollinated by sunbirds.



FIGURE 16c. Cunene Valley in the Baynes Mountains where *Aloe corallina* is found in its native habitat.

17. *Aloe dabenorisana*



FIGURE 17a. *Aloe dabenorisana* in flower (from Dabenorisberg, Bushmanland).



FIGURE 17b. *Aloe dabenorisana* in habitat on the shady south-facing slopes of Pellaberg.



FIGURE 17c. The inflorescence of *Aloe dabenorisana*.



FIGURE 17d. *Aloe dabenorisana* in habitat on Dabenorisberg, Bushmanland. Plants grow in drooping clusters.

18. *Aloe dewinteri*



FIGURE 18a. *Aloe dewinteri* growing on a dolomite cliff face at Khowarib, Sesfontein, Kaokoveld.



FIGURE 18b. Dolomitic mountains east of Sesfontein, the habitat of *Aloe dewinteri*.



FIGURE 18c. *Aloe dewinteri* growing on a dolomite cliff face, east of Sesfontein in the Kaokoveld.

19. *Aloe haemanthifolia*



FIGURE 19a. *Aloe haemanthifolia* growing on a ledge on the Skurweberg in the Western Cape.



FIGURE 19b. *Aloe haemanthifolia* growing on a ledge on the Skurweberg in the Western Cape.



FIGURE 19c. *Aloe haemanthifolia* sharing its habitat with *Crassula atropurpurea* var. *anomala* on the Skurweberg.



FIGURE 19d. Clusters of *Aloe haemanthifolia* in accessible places near the cliffs are heavily grazed. Note the fibrous leaves.

20. *Aloe hardyi*



FIGURE 20a. *Aloe hardyi* in flower at Kirstenbosch (material from Kromellenboog, Olifants River, Mpumalanga). The flowers are pollinated by sunbirds.



FIGURE 20b. Dolomite cliffs at Kromellenboog, habitat of *Aloe hardyi*—some plants visible in the background.



FIGURE 20c. *Aloe hardyi* sharing its habitat with *Sarcostemma viminale* at Kromellenboog, Olifants River, Mpumalanga.

21. *Aloe kouebokkeveldensis*



FIGURE 21a. *Aloe kouebokkeveldensis* here in its habitat, Teerivierskloof, near Citrusdal in the Western Cape. Plants grow solitary.



FIGURE 21b. Fynbos cliff-face habitat of *Aloe kouebokkeveldensis* at Teerivierskloof south of Citrusdal.



FIGURE 21c. *Aloe kouebokkeveldensis* at Teerivierskloof.

22. *Aloe meyeri*



FIGURE 22a. *Aloe meyeri* in habitat on the Rosyntjieberg in January 1980.



FIGURE 22b. *Aloe meyeri* in habitat on a cliff at the Rosyntjieberg together with *Tylecodon kritzingeri*.



FIGURE 22c. *Aloe meyeri* growing on the shady south-facing slopes of the Rosyntjieberg.

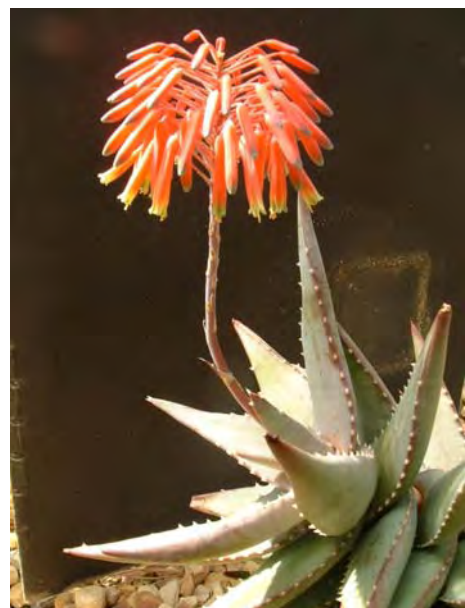


FIGURE 22d. *Aloe meyeri* in flower at Kirstenbosch.

23. *Aloe mutabilis*



FIGURE 23a. The habitat of *Aloe mutabilis* at Chuniespoort.



FIGURE 23b. *Aloe mutabilis* growing on cliffs at Chuniespoort, Limpopo Province.

24. *Aloe nubigena*



FIGURE 24a. *Aloe nubigena* in habitat at God's Window, Graskop.



FIGURE 24b. Cliff-face habitat of *Aloe nubigena*.



FIGURE 24c. Moist Afro-temperate Forest at Graskop, habitat of *Aloe nubigena*.



FIGURE 24d. *Aloe nubigena* in flower and fruit at God's Window near Graskop.

25. *Aloe omavandae*



FIGURE 25a. *Aloe omavandae* on an Omavanda cliff face of the Baynes Mountains in the Kaokoveld, Namibia.



FIGURE 25b. *Aloe omavandae* growing on a cliff at Omavanda, Baynes Mountains, together with *Cotyledon orbiculata* and *Sarcostemma viminale*.

26. *Aloe pavelkae*



FIGURE 26a. *Aloe pavelkae* at Kuamsibberg on the Hunsberg in the Orange River Valley in southern Namibia. Note the functional leaves confined to the stem apices. Plants grow on sandstone cliffs on shady, south-facing slopes.



FIGURE 26b. *Aloe pavelkae* in seed. Plants flower from late April to May, the seeds ripening in winter. Seed capsules are always presented ascending or ascending-spreading.



FIGURE 26c. Upper sandstone cliff face of Kuamsibberg, habitat of *Aloe pavelkae* on the Hunsberg in southern Namibia.



FIGURE 26d. *Aloe pavelkae* in flower at Kirstenbosch in May 2008.
Note the long, slender pedicels (shorter in *A. meyeri* and *A. dabenorisana*).
Pollinated by sunbirds.

27. *Aloe pictifolia*



FIGURE 27a. *Aloe pictifolia* growing on a sandstone cliff at the Kouga Dam in the Eastern Cape.



FIGURE 27b. *Aloe pictifolia* in habitat at the Kouga Dam in the Eastern Cape.



FIGURE 27c. *Aloe pictifolia* in flower.



FIGURE 27d. Sheer cliff faces of the Kouga Dam in the Eastern Cape, home of *Aloe pictifolia*.

28. *Aloe reynoldsii*



FIGURE 28a. *Aloe reynoldsii* in its native habitat along the Bashee River at Tsolorha in the Transkei region of the Eastern Cape.



FIGURE 28b. *Aloe reynoldsii* growing on mudstone cliffs at Tsolorha in the Transkei region of the Eastern Cape.



FIGURE 28c. A young plant of *Aloe reynoldsii* growing on mudstone cliffs together with *Portulacaria afra*.

29. *Aloe soutpansbergensis*



FIGURE 29a. *Aloe soutpansbergensis* growing among *Selaginella* ferns on a cliff on a southeastern slope of the Soutpansberg. The leaves are soft and fragile.



FIGURE 29b. The cliff-face habitat of *Aloe soutpansbergensis* on some upper south-facing slopes of the Soutpansberg.



FIGURE 29c. *Aloe soutpansbergensis* in its native habitat on the Soutpansberg.

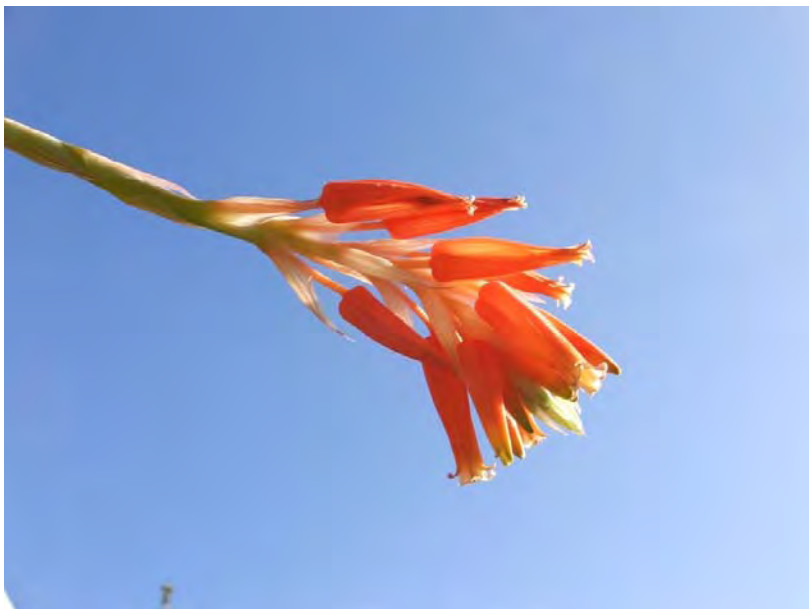


FIGURE 29d. Inflorescence of *Aloe soutpansbergensis*. It does not curve upwards. The flowers remain projected forwardly, a unique way of presentation in *Aloe*, especially compared to closely related species such as *A. nubigena*.

30. *Aloe thompsoniae*



FIGURE 30a. *Aloe thompsoniae* in flower at Kirstenbosch.



FIGURE 30b. *Aloe thompsoniae* growing in a hanging basket at Kirstenbosch.



FIGURE 30c. The Wolkberg in Limpopo Province, the habitat of *Aloe thompsoniae*.



FIGURE 30d. *Aloe thompsoniae* on a sandstone cliff face on the Soutpansberg.



FIGURE 30e. *Aloe thompsoniae* in a container at Kirstenbosch.

31. *Bulbine cremnophila*



FIGURE 31a. *Bulbine cremnophila* at Gertsmitzkloof in the Baviaanskloof growing on a shady cliff face together with *Crassula pellucida* subsp. *marginalis*.



FIGURE 31b. *Bulbine cremnophila* growing in Gertsmitkloof in the Baviaanskloof.



FIGURE 31c. *Bulbine cremnophila* flowering at Kirstenbosch—flowers during daytime.

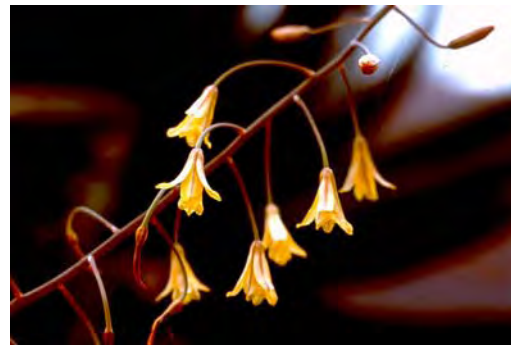


FIGURE 31d. *Bulbine cremnophila* flowering at Kirstenbosch—flowers at night.

32. *Bulbine latifolia* var. *curvata*



FIGURE 32a. *Bulbine latifolia* var. *curvata* flowering at Kirstenbosch, material from the Kouga Dam, Eastern Cape.



FIGURE 32b & 32c. *Bulbine latifolia* var. *curvata* on a cliff at the Kouga Dam in the Eastern Cape. Note the pendent, almost terete leaves.

33. *Bulbine meiringii*



FIGURE 33a. *Bulbine meiringii* in its native habitat at Meiringspoort in the Klein Karoo, Western Cape.



FIGURE 33b. *Bulbine meiringii* in flower at Kirstenbosch.



FIGURE 33c. *Bulbine meiringii* growing in its native habitat at Meiringspoort.

34. *Bulbine natalensis*



FIGURE 34a. *Bulbine natalensis* growing on a cliff face at the Bashee River at Collywobbles in the Transkei region of the Eastern Cape.



FIGURE 34b. *Bulbine natalensis* on a cliff face. The leaves are very soft and fragile.

35. *Bulbine pendens*



FIGURE 35a. *Bulbine pendens* in fruit on a cliff at the Skaaprivierspoort growing together with *Rhadamanthus montanus*.



FIGURE 35b. *Bulbine pendens* at the Skaaprivierspoort.

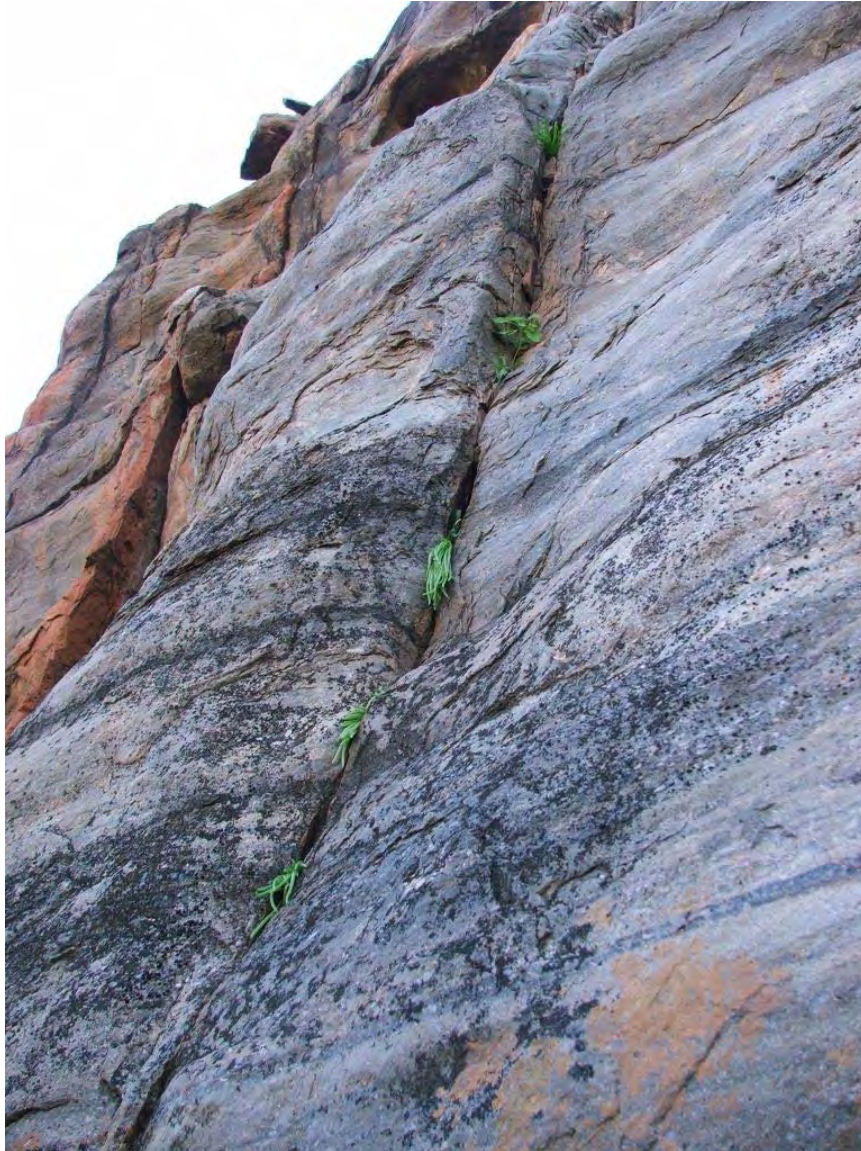


FIGURE 35c. *Bulbine pendens* growing on a sheer south-facing cliff at the Skaaprivierspoort.



FIGURE 35d. Red iron-rich sandstone at the Skaaprivierspoort, the habitat of *Bulbine pendens*, *Ornithogalum pendens* and *Tylecodon petrophilus*.

36. *Bulbine ramosa*



FIGURE 36a. *Bulbine ramosa* in habitat at Badspoort (Calitzdorp).



FIGURE 36b. *Bulbine ramosa* in flower at Kirstenbosch.

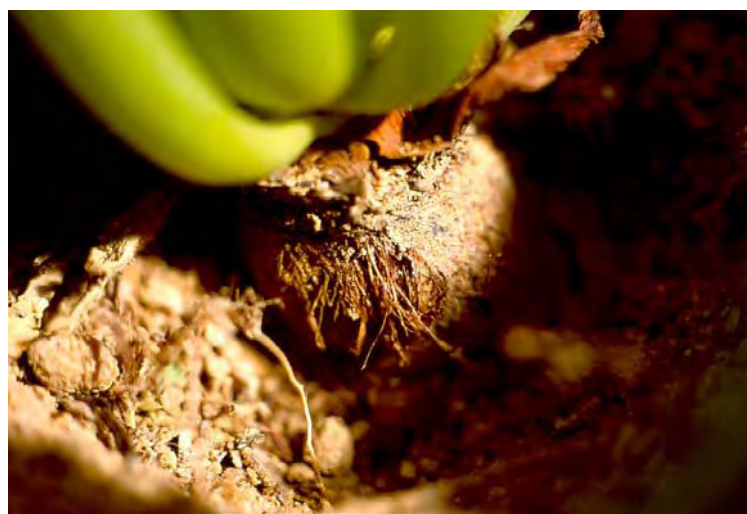


FIGURE 36c. Tuber of *Bulbine ramosa*, from Badspoor, Calitzdorp.

37. *Bulbine retinens*



FIGURE 37a. *Bulbine retinens* of the Kouga River (Hoeree) where it grows on sandstone cliffs.



FIGURE 37b. *Bulbine retinens* growing with *Adromischus sphenophyllus* on a sandstone cliff face at Hoeree.



FIGURE 37c. The habitat of *Bulbine meiringii* at Hoeree on the Kouga River.

38. *Bulbine rupicola*



FIGURE 38a. *Bulbine rupicola* growing below Guernakop, Kouga River.



FIGURE 38b. *Bulbine rupicola* growing in dense mats below Guernakop, Kouga River.



FIGURE 38c. Cliffs along the Kouga River, near Keurboskloof, the habitat of *Bulbine rupicola*.

39. *Bulbine suurbergensis*



FIGURE 39a. *Bulbine suurbergensis* in its native habitat along the banks of the Witte-rivier in the Suurberg, Eastern Cape.



FIGURE 39b. *Bulbine suurbergensis* in its native habitat along the banks of the Witterivier in the Suurberg, Eastern Cape.



FIGURE 39c. *Bulbine suurbergensis* in its native habitat along the banks of the Witterivier in the Suurberg, Eastern Cape.

40. *Bulbine thomasiae*



FIGURE 40a. *Bulbine thomasiae* in its resting phase on upper south-facing cliffs along the Bashee River at Collywobbles in the Transkei region.



FIGURE 40b. *Bulbine thomasiae* in the rainy season on south-facing cliffs along the Bashee River at Tsolorha in the Transkei region of the Eastern Cape.



FIGURE 40c. *Bulbine thomasiae* in flower where it grows on south-facing cliffs along the Bashee River at Tsolorha in the Transkei region.

41. *Gasteria batesiana* var. *batesiana*



FIGURE 41a. *Gasteria batesiana* var. *batesiana* on a cliff at Klipwal Goldmine, along the Pongola River in KwaZulu-Natal where it shares the habitat with another cremnophyte, *Schizobasis intricata*.



FIGURE 41b. Cliffs above the Pongola River, habitat of *Gasteria batesiana* var. *batesiana*.



FIGURE 41c. *Gasteria batesiana* var. *batesiana* on banks of the White Mfolozi in the Mkuze Game Reserve. A narrow-leaved form. Photograph: Dave Gwen-Evans.



FIGURE 41d. Flowers of *Gasteria batesiana* var. *batesiana*, pollinated by sunbirds.



FIGURE 41e. Young plants of *Gasteria batesiana* have proliferated from fallen leaves.

42. *Gasteria batesiana* var. *dolomitica*



FIGURE 42a. *Gasteria batesiana* var. *dolomitica* growing on a dolomite cliff face on the farm Ostend at Penge in the Olifants River Valley in Limpopo Province.



FIGURE 42b. Inflorescence of *Gasteria batesiana* var. *dolomitica* at Kirstenbosch, a large inflorescence compared to the relatively small plants—an example of rich flowering (material from Penge, Limpopo Province). The flowers are pollinated by sunbirds.



FIGURE 42c. *Gasteria batesiana* var. *dolomitica* on a cliff face at Penge. Note the dense clusters and vegetative output. Leaves often proliferate where they touch the ground or if they become detached.

43. *Gasteria croucheri* subsp. *pendulifolia*



FIGURE 43a. *Gasteria croucheri* subsp. *pendulifolia* growing on a cliff face at Mamba Valley along the Umgeni River.



FIGURE 43b. *Gasteria croucheri* subsp. *pendulifolia* growing on a cliff face at Mamba Valley along the Umgeni River. The plants proliferate from the base to form dense groups. Detached leaves proliferate and form new plants.



FIGURE 43c. Inflorescence of *Gasteria croucheri* subsp. *pendulifolia* (material from Mamba Valley, Umgeni River). Flowers are pollinated by sunbirds.

44. *Gasteria doreeniae*



FIGURE 44a. *Gasteria doreeniae* growing on a ledge in Swartwaterspoort in the Eastern Cape. Plants proliferate, forming dense groups. Detached leaves will also proliferate.



FIGURE 44b. *Gasteria doreeniae* growing in a container at Kirstenbosch (material from Swartwaterspoort, Eastern Cape). Plants proliferate, forming dense groups.



FIGURE 44c. Swartwaterspoort, habitat of *Gasteria doreeniae*.

45. *Gasteria glauca*



FIGURE 45a. *Gasteria glauca* growing on a shady ledge below Guernakop, Kouga River. Plants proliferate from the base, forming dense groups.



FIGURE 45b. *Gasteria glauca* growing on an exposed ledge below Guernakop, Kouga River. Plants proliferate from the base, forming dense groups.



FIGURE 45c. *Gasteria glauca* in flower at Kirstenbosch.



FIGURE 45d. The Kouga River where *Gasteria glauca* inhabits the sheer east-facing cliffs.

46. *Gasteria glomerata*



FIGURE 46a. *Gasteria glomerata* growing on a sheer cliff face at Kouga Dam. Plants proliferate, forming dense groups. Detached leaves landing in crevices can also root, forming new plants.



FIGURE 46b. *Gasteria glomerata* flowering at Kirstenbosch. The perianth is large and conspicuous compared to the body size of the plants (rich flowering). Flowers are pollinated by sunbirds.



FIGURE 46c. *Gasteria glomerata* sharing the habitat with *Streptocarpus meyeri* at the Kouga Dam in the Eastern Cape.

47. *Gasteria pillansii* var. *ernesti-ruschii*



FIGURE 47a. *Gasteria pillansii* var. *ernesti-ruschii* on Kuamsibberg, Hunsberg, Namibia. Plants proliferate, forming dense groups. Detached leaves landing up in crevices can also root, forming new plants.



FIGURE 47b. *Gasteria pillansii* var. *ernesti-ruschii* on a quartz cliff face of the Kuamsibberg, Hunsberg.

48. *Gasteria rawlinsonii*



FIGURE 48a. *Gasteria rawlinsonii* grown at Kirstenbosch (material from Gertsmit-skloof, Baviaanskloof, Eastern Cape). The flowers are pollinated by sunbirds.



FIGURE 48b. *Gasteria rawlinsonii* in its habitat at Gertsmitaskloof in the Baviaanskloof, Eastern Cape.

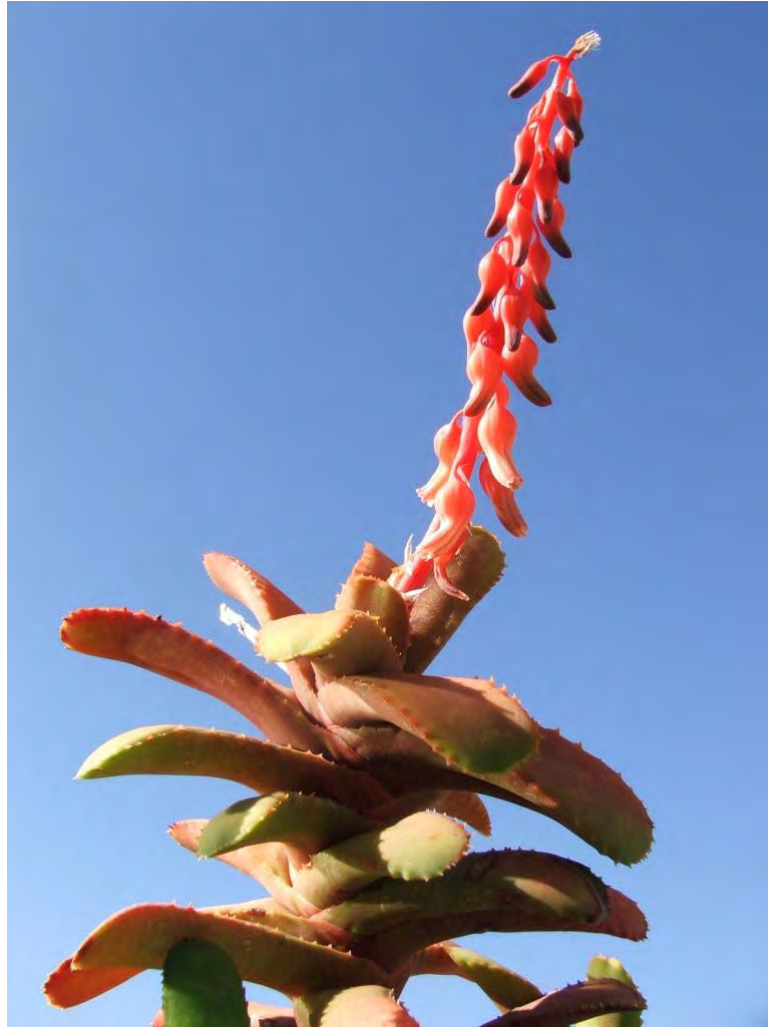


FIGURE 48c. *Gasteria rawlinsonii* grown at Kirstenbosch (material from Geelhoutboskloof, Baviaanskloof, Eastern Cape). The flowers are pollinated by sunbirds.

49. *Gasteria tukhelensis*



FIGURE 49a. *Gasteria tukhelensis* on a cliff face sharing its habitat with *Bulbine natalensis* at Shongweni on the Thukela River in KwaZulu-Natal.

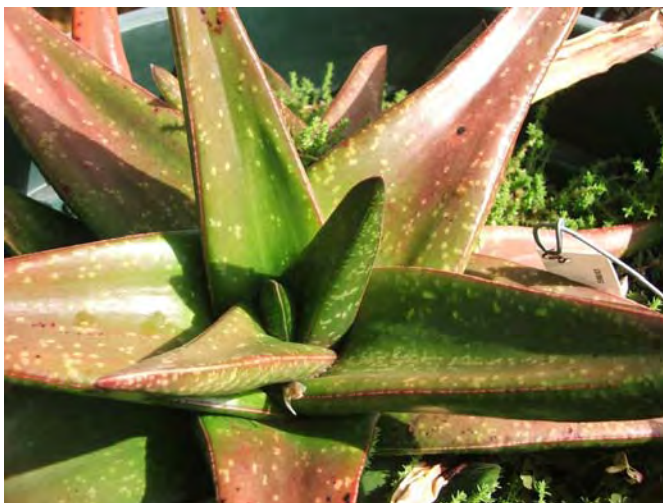


FIGURE 49b. *Gasteria tukhelensis* in cultivation at Kirstenbosch (material from Shongweni on the Thukela River in KwaZulu-Natal).



FIGURE 49c. *Gasteria tukhelensis* in flower at Kirstenbosch (material from Shongweni on the Thukela River in KwaZulu-Natal). Flowers are pollinated by sunbirds. Note the long, slender pedicles.



FIGURE 49d. The cliff habitat of *Gasteria tukhelensis* along the Thukela River in KwaZulu-Natal.



FIGURE 49e. *Gasteria tukhelensis* on a cliff face at Shongweni, Thukela River, KwaZulu-Natal.

50. *Haworthia angustifolia* var. *baylissii*



FIGURE 50a. A plant of *Haworthia angustifolia* var. *baylissii* in its shady habitat on a cliff in the Suurberg (Witterivier Poort). *Crassula cordata* in the background. Note the recurving leaves exposed to the maximum light.



FIGURE 50b. *Haworthia angustifolia* var. *baylissii* in its shady habitat on a cliff in the Suurberg (Witterivier Poort). *Crassula cordata* in the background.

51. *Haworthia attenuata* var. *attenuata* (Enon cliff form)



FIGURE 51a. *Haworthia attenuata* var. *attenuata* (Enon cliff-face form).



FIGURE 51b. *Haworthia attenuata* var. *attenuata* on an Enon conglomerate cliff face at Enon in the Eastern Cape.



FIGURE 51c. Enon conglomerate cliff face at Enon in the Eastern Cape.

52. *Haworthia cymbiformis* var. *ramosa*



FIGURE 52a. *Haworthia cymbiformis* var. *ramosa* at Wooldridge in the Eastern Cape.



FIGURE 52b. Cliff face at Wooldridge, the habitat of *Haworthia cymbiformis* var. *ramosa*.

53. *Haworthia cymbiformis* var. *setulifera*



FIGURE 53a. *Haworthia cymbiformis* var. *setulifera* sharing its shady, south-facing cliff habitat with *Crassula orbicularis* and *Senecio ficoides* at Collywobbles on the Bashee River in the Transkei region of the Eastern Cape.



53b



53c

FIGURE 53b & 53c. *Crassula cymbiformis* var. *setulosa* on a shady south-facing cliff at Collywobbles on the Bashee River in the Transkei region of the Eastern Cape.

54. *Haworthia glabrata*



FIGURE 54a. *Haworthia glabrata* in habitat on an exposed north-facing slope at Collywobbles in the Transkei region of the Eastern Cape.



FIGURE 54b. *Haworthia glabrata* on an exposed north-facing slope along the Bashee River at Collywobbles in the Transkei region of the Eastern Cape.

55. *Haworthia gracilis* var. *picturata*



FIGURE 55a. *Haworthia gracilis* var. *picturata* at the Kouga Dam in the Eastern Cape. Plants grow on shady cliff faces. Note the translucent windows.



FIGURE 55b. *Haworthia gracilis* var. *picturata* sharing its habitat with *Adromischus sphenophyllus* and *Cotyledon tomentosa* var. *tomentosa* at the Kouga Dam, Gamtoos River, Eastern Cape.

56. *Haworthia marumiana* var. *batesiana*



FIGURE 56a. *Haworthia marumiana* var. *batesiana* flowering on cliffs at the Valley of Desolation near Graaff-Reinet.

57. *Haworthia marumiana* var. *marumiana*



FIGURE 57a. *Haworthia marumiana* var. *marumiana* growing on the upper southern cliff face of Aasvoëlberg near Willowmore.



FIGURE 57b. The south-facing cliffs of Aasvoëlberg west of Willowmore, habitat of *Haworthia marumiana* var. *marumiana*.

58. *Haworthia mirabilis* var. *consanguinea*



FIGURE 58a. *Haworthia mirabilis* subsp. *consanguinea* growing on a cliff in Boesmanspoort near Greyton in the Western Cape. The reddish colour of the plants is due to the production of anthocyanins during the dry season.



FIGURE 58b. Boesmanspoort near Greyton in the Western Cape, the cliff-face habitat of *Haworthia mirabilis* subsp. *consanguinea*.



FIGURE 58c. *Haworthia mirabilis* subsp. *consanguinea* growing on a cliff in Boesmanspoort near Greyton in the Western Cape. Production of anthocyanins causes the reddish colour of the plants in the dry season.

59. *Haworthia scabra* var. *starkiana*



FIGURE 59a. *Haworthia scabra* var. *starkiana* in Schoemanskloof near the Cango Caves where the plants grow on exposed, sunny, northern slopes.



FIGURE 59b. *Haworthia scabra* var. *starkiana* growing on the cliffs of Schoemanskloof near the Cango Caves.

60. *Haworthia turgida* var. *turgida*



FIGURE 60a. *Haworthia turgida* on an east-facing sandstone cliff in the Tradouw Pass south of Barrydale.



FIGURE 60b. *Haworthia turgida* habitat on a west-facing sandstone cliff in the Tradouw Pass south of Barrydale.



FIGURE 60c. Cliff-face form of *Haworthia turgida* var. *turgida* in cultivation (material from the Tradouw Pass, Barrydale).

61. *Haworthia zantneriana*



FIGURE 61a. *Haworthia zantneriana* at Campher's Poort in the Eastern Cape. Plants grow on south-facing sandstone cliffs.



FIGURE 61b. *Haworthia zantneriana* at Campher's Poort.



FIGURE 61c. Campher's Poort, habitat of *Haworthia zantneriana*.

62. *Trachyandra tabularis*



FIGURE 62a. *Trachyandra tabularis* growing in its habitat on the upper shady south-facing cliffs of the back table of Table Mountain.



FIGURE 62b. *Trachyandra tabularis* in flower on the shady upper south-facing cliffs of the back table of Table Mountain.

63. *Albuca batteniana*



FIGURE 63a. *Albuca batteniana* on a cliff face near Morgan's Bay in the Eastern Cape. Note the *Agama atra atra* sharing its cliff habitat.



FIGURE 63b. *Albuca batteniana* growing on shale cliffs at Collywobbles in the former Transkei region of the Eastern Cape.



FIGURE 63c. Coastal cliffs near Morgan's Bay, habitat of *Albuca batteniana*.



FIGURE 63d. *Albuca batteniana* in flower at Kirstenbosch (material from Collywobbles, Transkei region, Eastern Cape).

64. *Albuca cremnophila*



FIGURE 64a. *Albuca cremnophila* in its cliff-face habitat at the Kouga Dam in the Eastern Cape.

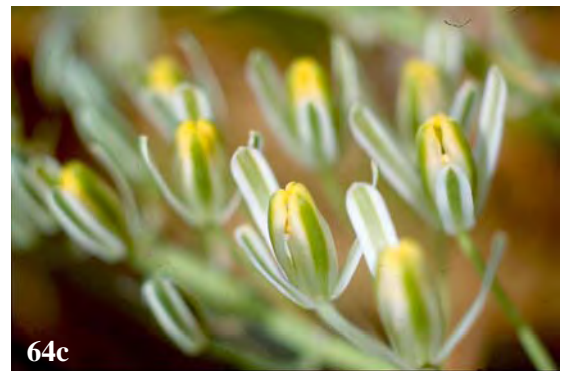


FIGURE 64b & 64c. *Albuca cremnophila* in flower at Kirstenbosch. Note the yellow tips of the tepals.



FIGURE 64c. Leaves of *Albuca cremnophila* in cultivation in the Botanical Society Conservatory at Kirstenbosch. Note the translucent inner window (white portion).

65. *Albuca crudenii*



FIGURE 65a. *Albuca crudenii* in flower at Kirstenbosch (material from Collywobbles, Transkei region, Eastern Cape).



FIGURE 65b. *Albuca crudenii* growing on a sheer shale cliff at Alicedale Poort in the Eastern Cape. Note the *O. longibracteatum* below the cliffs.

66. *Albuca kirstenii*



FIGURE 66a. *Albuca kirstenii* bulbs sprouting below the Gourits Bridge in autumn.



FIGURE 66b. Cliffs on the Gourits River in the Western Cape where *Albuca kirstenii* grows.

67. *Albuca shawii*



FIGURE 67a. *Albuca shawii* on a sandstone cliff at the White Mfolozi River in KwaZulu-Natal.



FIGURE 67b. *Albuca shawii* in flower at Kirstenbosch (material from White Mfolozi River, KwaZulu-Natal).



FIGURE 67c. The sandstone cliffs at the White Mfolozi River, the habitat of *Albuca shawii*.

68. *Albuca thermarum*



FIGURE 68a. *Albuca thermarum* in its natural habitat on a cliff face at Badspoort near Calitzdorp in the Western Cape.



FIGURE 68b. *Albuca thermarum* growing at Badspoort near Calitzdorp.



FIGURE 68c. *Albuca thermarum* thriving in the Botanical Society Conservatory at Kirstenbosch (material from Badspoor, Calitzdorp, Western Cape).



FIGURE 68d. A bulb of *Albuca thermanum* in the Botanical Society Conservatory at Kirstenbosch (material from Badspoort, Calitzdorp, Western Cape).



FIGURE 68e. *Albuca thermanum* flowering at Kirstenbosch (material from Badspoort, Calitzdorp, Western Cape).

69. *Drimia cremnophila*



FIGURE 69a. *Drimia cremnophila* on a shale cliff face along the Mzimvubu River in the Transkei region of the Eastern Cape. Plants proliferate, forming dense clusters and occupying crevices (vegetative proliferation backup). The plant here shares its habitat with *Crassula cordata*.



FIGURE 69b. *Drimia cremnophila* on shale cliffs, sharing its habitat with *Bulbine natalensis* in the former Transkei region of the Eastern Cape.



FIGURE 69c. *Drimia cremnophila* in flower at Kirstenbosch (from material collected at the Mzimvubu River, Transkei region of the Eastern Cape). Pollen is released only by insect vibration.

70. *Drimia flagellaris*



FIGURE 70a. *Drimia flagellaris* on a sandstone cliff face at Molweni, Durban, KwaZulu-Natal. Plants proliferate, forming dense clusters and occupying crevices (vegetative proliferation backup).



FIGURE 70b. Molweni at Durban in KwaZulu-Natal, habitat of *Drimia flagellaris*.



FIGURE 70c. *Drimia flagellaris* on a sandstone cliff face at Molweni, Durban, KwaZulu-Natal.



FIGURE 70d. *Drimia flagellaris* flowering at Kirstenbosch (material from cliff face at Molweni, Durban, KwaZulu-Natal).



70e



70f

FIGURE 70e & 70f. *Drimia flagellaris* at Kirstenbosch, the infructescence (70e) remains functional (photosynthetically active) after the seeds have been released (material from cliff face at Molweni, Durban).

71. *Drimia loedolffiae*



FIGURE 71a. *Drimia loedolffiae* on a shale cliff face at Bolo at the Kei River in the Eastern Cape.



FIGURE 71b & 71c. The habitat of *Drimia loedolffiae* along the Kei River in the Eastern Cape.



FIGURE 71d. *Drimia loedolffiae* in flower at Kirstenbosch (material from a cliff face at Molweni, Durban, KwaZulu-Natal).



FIGURE 71e. *Drimia loedolffiae* in fruit at Kirstenbosch. The inflorescence rapidly desiccates after fruiting (material from a cliff face at Molweni, Durban, KwaZulu-Natal).

72. *Drimia mzimvubuensis*



FIGURE 72a. *Drimia mzimvubuensis* on a shale cliff along the Mzimvubu River in the Transkei region of the Eastern Cape.



FIGURE 72b. *Drimia mzimvubuensis* in flower at Kirstenbosch (material from the Mzimvubu River, Transkei region, Eastern Cape). Pollen is released only by insect vibration.



FIGURE 72c. *Drimia mzimvubuensis* on a shale cliff along the Mzimvubu River in the Transkei region of the Eastern Cape. Note the fleshy bulb scales that are exposed.

73. *Drimia uniflora*



FIGURE 73a. The small, solitary, tubular flowers of *Drimia uniflora* (*Litanthus pusillus*) where it grows near Leeukloofberg in the Eastern Cape. Note *Crassula nemorosa*, another geophytic cremnophyte.



FIGURE 73b. *Drimia uniflora* in fruit at Kirstenbosch. Note the erect open capsules. The seeds are dispersed by wind.



FIGURE 73c. *Drimia uniflora* in habitat near Daniëlskuil in the Northern Cape, growing on banded ironstone cliffs together with *Adromischus trigynus*.



FIGURE 73d. *Drimia uniflora* in cultivation at Kirstenbosch (material from Aasvoëlberg cliffs near Willowmore in the Eastern Cape).

143. *Crassula smithii*



FIGURE 143a. Cliffs at Ozwatini on Noodsberg, the habitat of *Crassula smithii*.
Photograph: David Styles.



FIGURE 143b. A closer look at *Crassula smithii* on cliffs at Ozwatini on Noodsberg. Photograph: David Styles.

144. *Crassula socialis*



FIGURE 144a. *Crassula socialis* growing on shale cliffs along the Great Fish River north of Grahamstown in the Eastern Cape.



FIGURE 144b. *Crassula socialis* growing on the sandstone cliffs of Aasvoëlberg near Willowmore in the Eastern Cape.



FIGURE 144c. Aasvoëlberg near Willowmore in the Eastern Cape. The upper south-facing sandstone cliffs are the habitat of *Crassula socialis*.



FIGURE 144d. *Crassula socialis* growing in Kirstenbosch cliff house nursery (material from the Great Fish River, north of Grahamstown, Eastern Cape).

145. *Crassula streyi*



FIGURE 145a *Crassula streyi* grown at Kirstenbosch (material from Mtamvuna, southern KwaZulu-Natal).



FIGURE 145b. Cliffs of the Mtamvuna River Gorge in southern KwaZulu-Natal, habitat of *Crassula streyi*.



FIGURE 145c. *Crassula streyi* in flower at Kirstenbosch (material from Mtamvuna, southern KwaZulu-Natal).



FIGURE 145d. *Crassula streyi* on a sheer cliff in habitat at the Mazmba River in the Eastern Cape.

146. *Crassula tabularis*



FIGURE 146a. *Crassula tabularis* on the Auasberg in southern Namibia.



FIGURE 146b. South-facing cliffs on the Auasberg in southern Namibia, the habitat of *Crassula tabularis*.



FIGURE 146c. Plants of *Crassula tabularis* proliferating and forming small clusters on the Auasberg in southern Namibia.

147. *Crassula tomentosa* var. *glabrifolia*



FIGURE 147a. *Crassula tomentosa* var. *glabrifolia* growing on cliff ledges on the Gifberg on the farm Waterval in the Western Cape.



FIGURE 147b. South-facing cliffs of the Gifberg on the farm Waterval in the Western Cape, habitat of *Crassula tomentosa* var. *glabrifolia*.



FIGURE 147c. *Crassula tomentosa* var. *glabrifolia* on cliff ledges on the Gifberg on the farm Waterval in the Western Cape.



FIGURE 147d. South-facing cliffs of the Gifberg in the Western Cape, the habitat of *Crassula tomentosa* var. *glabrifolia*.

149. *Tylecodon bleckiae*



FIGURE 149a. *Tylecodon bleckiae* growing at Spitskloof in the Northern Cape.



FIGURE 149b. Cliffs in the southern Hunsberg in southern Namibia, habitat of the type plant of *Tylecodon bleckiae*.



FIGURE 149c. *Tylecodon bleckiae* flowering in the cliff-plant collection at Kirstenbosch.

150. *Tylecodon bodleyae*



FIGURE 150a. *Tylecodon bodleyae* at Gemsbokvlei. The habitat is sheer south-facing sandstone cliffs.



FIGURE 150b. *Tylecodon bodleyae* growing on sheer south-facing sandstone cliffs at Gemsbokvlei. The lichens on the rocks are the result of the regular fog.



FIGURE 150c. *Tylecodon bodleyae* in its habitat of sheer south-facing sandstone cliffs at Gemsbokvlei.



FIGURE 150d. *Tylecodon bodleyae* flowering in cultivation at Kirstenbosch.



FIGURE 150e. Gemsbokvlei, where many succulent species grow, the south-facing cliffs the habitat of *Tylecodon bodleyae*.

151. *Tylecodon bruynsii*

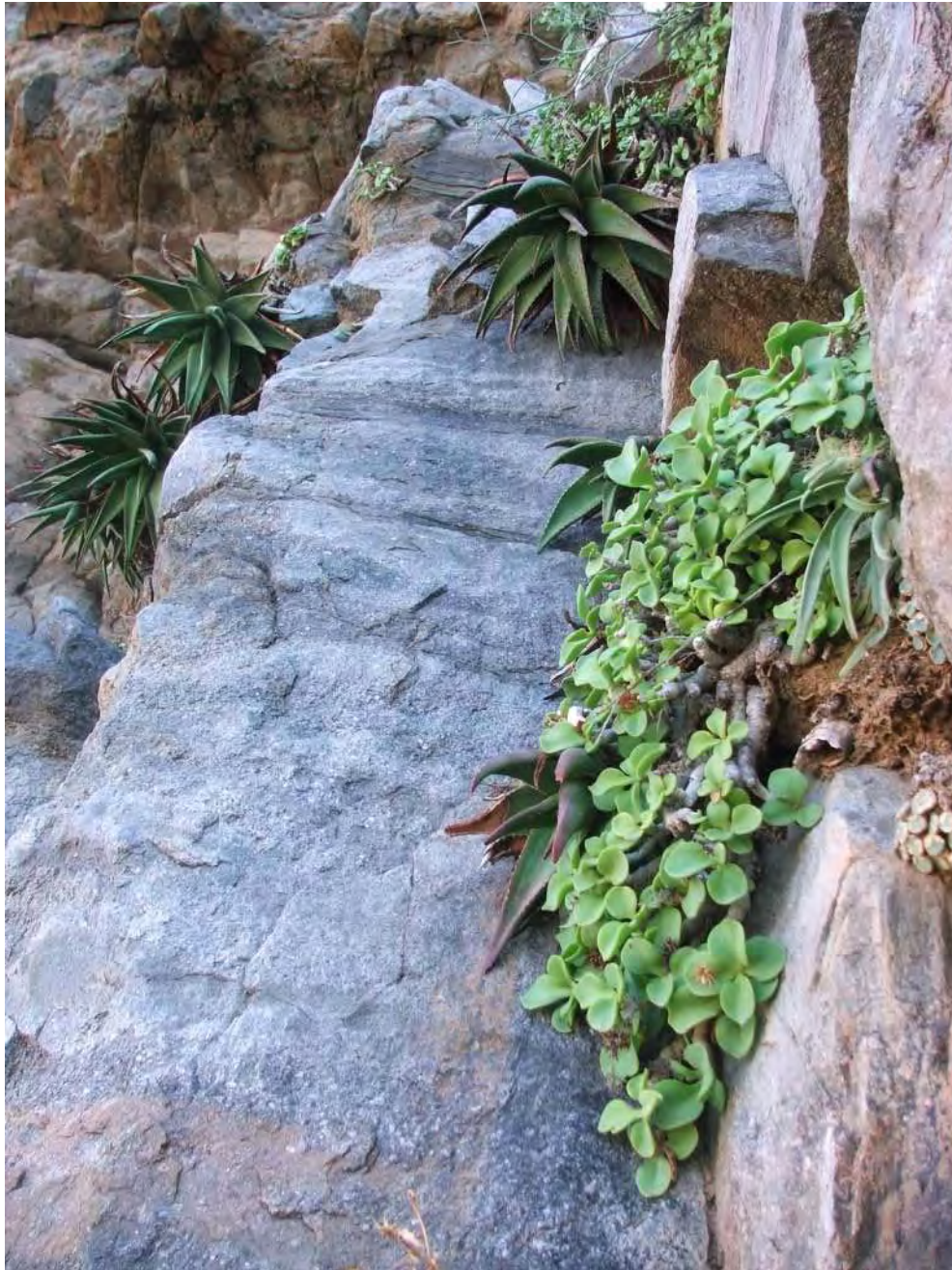


FIGURE 151a. *Tylecodon bruynsii*, on an upper south-facing cliff on Kuamsibberg in the Hunsberg in southern Namibia, here sharing its habitat with *Aloe pavelkae* and *Conophytum ricardianum*.



FIGURE 151b. *Tylecodon bruynsii*, on an upper south-facing cliff on Kuamsibberg in the Hunsberg in southern Namibia.



FIGURE 151c. *Tylecodon bruynsii* grows on the cliffs in the distance, where a cloud and fog are settling on Kuamsibberg in the Hunsberg in southern Namibia.

152. *Tylecodon buchholzianus* var. *fasciculatus*



FIGURE 152a. *Tylecodon buchholzianus* var. *fasciculatus* on the shady south-facing cliffs of Vyftienmyl se Berge at Oograbies Mountain in the Richtersveld.



FIGURE 152b. *Tylecodon buchholzianus* var. *fasciculatus* flowering at Kirstenbosch (material from shady south-facing cliffs of Vyftienmyl se Berge, Oograbies Mountain, Richtersveld).



FIGURE 152c. Vyftienmyl se Berge at Oograbies Mountain in the Richtersveld, the habitat of *Tylecodon buchholzianus* var. *fasciculatus* on the shady south-facing cliffs.



FIGURE 152d. *Tylecodon buchholzianus* var. *fasciculatus* on the shady south-facing cliffs of Vyftienmyl se Berge at Oograbies Mountain in the Richtersveld.

153. *Tylecodon cordiformis*



FIGURE 153a. *Tylecodon cordiformis* growing on shady south-facing cliffs of the Harasberg in northern Namaqualand.



FIGURE 153b. The shady south-facing cliffs of the Harasberg in northern Namaqualand where *Tylecodon cordiformis* grows.



FIGURE 153c. South-facing cliffs of the Harasberg, the habitat of *Tylecodon cordiformis* in northern Namaqualand.



FIGURE 153d. *Tylecodon cordiformis* on shady south-facing cliffs of the Harasberg, here sharing its habitat with another cremnophyte, *Crassula pseudohemisphaerica*.



FIGURE 153e. *Tylecodon cordiformis* in flower at Kirstenbosch.

154. *Tylecodon decipiens*



FIGURE 154a. Cliff hugger *Tylecodon decipiens* growing on cliffs in the Buffelsrivier at Grootmis near Kleinsee.



FIGURE 154b. *Tylecodon decipiens* on cliffs in the Buffelsrivier at Grootmis near Kleinsee.

155. *Tylecodon ellaphieae*



FIGURE 155a. Cliff hugger *Tylecodon ellaphieae* growing in crevices on cliffs of the Rosyntjieberg in the Richtersveld in the Northern Cape.



FIGURE 155b. *Tylecodon ellaphieae* hugging the sheer south-facing cliffs of the Rosyntjieberg in the Richtersveld in the Northern Cape.



FIGURE 155c. Sheer south-facing cliffs of the Rosyntjieberg in the Richtersveld in the Northern Cape, habitat of *Tylecodon ellaphieae*.



FIGURE 155d. *Tylecodon ellaphieae*, a cliff hugger, in flower at Kirstenbosch (material from Rosyntjieberg, Richtersveld).

156. *Tylecodon longipes*



FIGURE 156a. *Tylecodon longipes* growing on a south-facing cliff at Spitskloof in the Richtersveld in the Northern Cape.



FIGURE 156b. Spitskloof in the Richtersveld in the Northern Cape where *Tylecodon longipes* grows.



FIGURE 156c. A close look at a plant of *Tylecodon longipes* at Kirstenbosch.



FIGURE 156d. *Tylecodon longipes* in flower at Kirstenbosch.

157. *Tylecodon petrophilus*

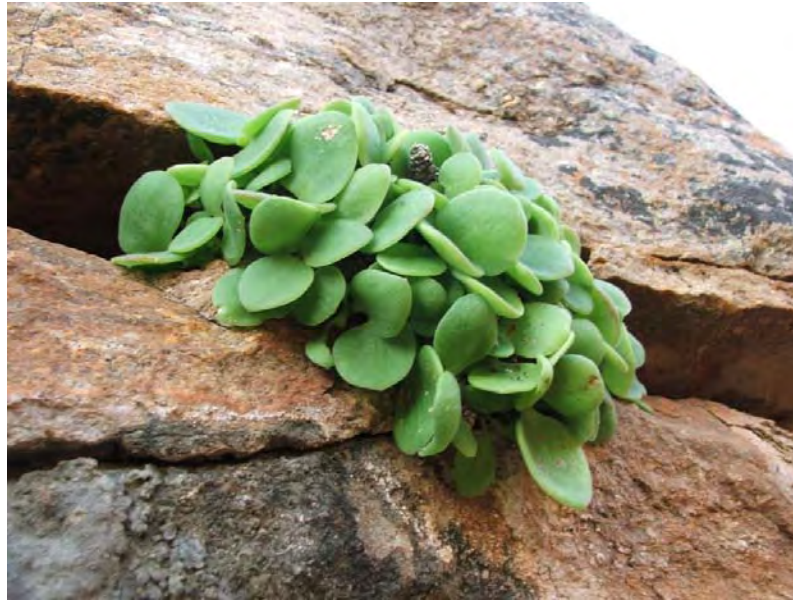


FIGURE 157a. *Tylecodon petrophilus* on a sheer south-facing cliff face in the Skaaprivierspoort in Namaqualand in the Northern Cape.



FIGURE 157b. A sheer south-facing cliff face in the Skaaprivierspoort in Namaqualand in the Northern Cape, habitat of *Tylecodon petrophilus*.

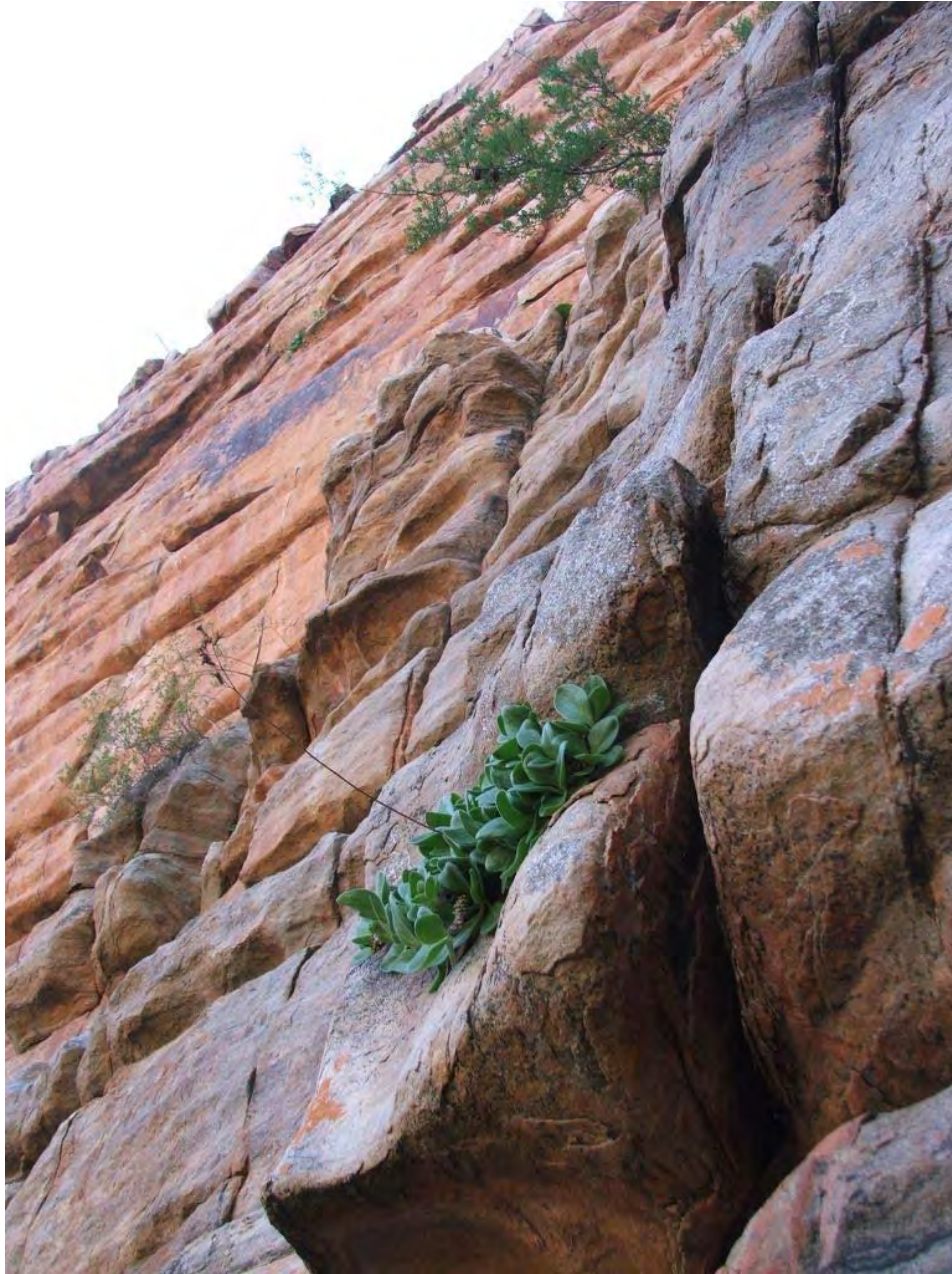


FIGURE 157c. *Tylecodon petrophilus* on a sheer south-facing cliff face in the Skaaprivierspoort in Namaqualand.

158. *Tylecodon singularis*



FIGURE 158a. *Tylecodon singularis* in cultivation at Kirstenbosch. The hairy leaves and channelled petioles guide moisture to the base of the plants, in nature growing in the fog zone of the lower Orange River Valley.



FIGURE 158b. *Tylecodon singularis* on a cliff in the Sonberg in the Hunsberg in southern Namibia.



FIGURE 158c. Konsertinaberg in southern Namibia, habitat of *Tylecodon singularis*.



FIGURE 158d & 158e. *Tylecodon singularis* on a cliff on Konsertinaberg in the Hunsberg in southern Namibia.

159. *Tylecodon sulphureus* var. *armianus*



FIGURE 159a & 159b. *Tylecodon sulphureus* var. *armianus* on a sheer south-facing cliff face at Pellaberg.



FIGURE 159c. The Dabenorisberg, south-facing cliffs, habitat of *Tylecodon sulphureus* var. *armianus*.



FIGURE 159d & 159e. *Tylecodon sulphureus* var. *armianus* during a good rainy season (May 2011) on south-facing cliffs of the Dabenorisberg. Note the old inflorescence in Figure 159e.

160. *Tylecodon torulosus*



FIGURE 160a. *Tylecodon torulosus* in its winter phase on a sheer, lichen-covered, south-facing cliff face at Karrachabpoort at Lekkersing in the Richtersveld in the Northern Cape.



FIGURE 160b. Winter phase of *Tylecodon torulosus* on a sheer south-facing cliff face at Karrachabpoort at Lekkersing in the Richtersveld.



FIGURE 160c. *Tylecodon torulosus* in the cliff-plant collection at Kirstenbosch (material from Lekkersing, Richtersveld). The torulose stems are in their summer phase.

161. *Tylecodon viridiflorus*



FIGURE 161a. *Tylecodon viridiflorus* flowering at Kirstenbosch.



FIGURE 161b. *Tylecodon viridiflorus* at Skouerfontein in the Richtersveld, the plant here sharing its habitat with *Crassula sericea* var. *sericea* and *Adromischus alstonii*.

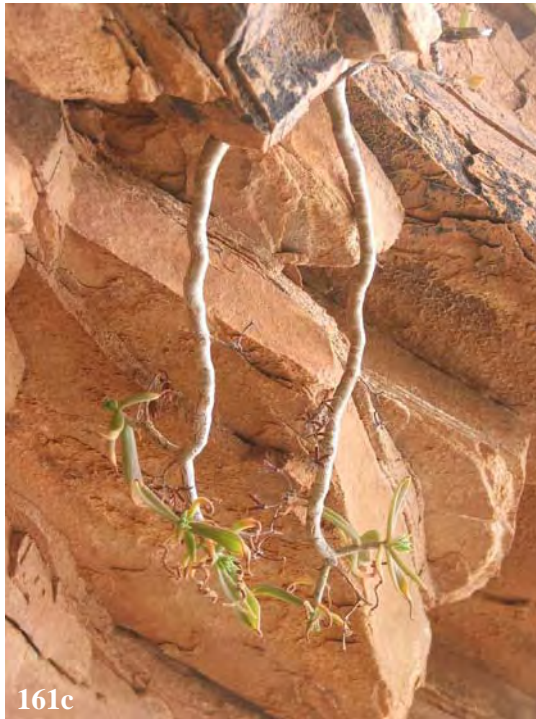


FIGURE 161c & 161d. *Tylecodon viridiflorus* and its cliff habitat at Skouerfontein in the Richtersveld.



FIGURE 161e & 161f. *Tylecodon viridiflorus* in habitat at Skouerfontein in the Richtersveld.

162. *Pelargonium mutans*



FIGURE 162a. *Pelargonium mutans* at Kirstenbosch (material from cliff face at Pongola River, Klipwal Gold Mine, Mpumalanga).



FIGURE 162b. *Pelargonium mutans* in flower at Kirstenbosch (material from cliff face at Pongola River, Klipwal Gold Mine, Mpumalanga).



FIGURE 162c. *Pelargonium mutans* at Kirstenbosch (material from cliff face at Pongola River, Klipwal Gold Mine, Mpumalanga).



FIGURE 162d. Sheer cliffs at Kranskop in KwaZulu-Natal, the habitat of *Pelargonium mutans*.

163. *Pelargonium vanderwaltii*



FIGURE 163a. *Pelargonium vanderwaltii* on a cliff face on the upper south-facing slope of Otjihipa Peak in the Kaokoveld east of Otjihungwa in Namibia.



FIGURE 163b. Otjihipa Peak in the Kaokoveld east of Otjihungwa in Namibia, the habitat of *Pelargonium vanderwaltii*.

164. *Streptocarpus kentaniensis*



FIGURE 164a. *Streptocarpus kentaniensis* growing on sandstone cliffs in the lower Kei River Valley in the Eastern Cape, here together with *Stenoglottis fimbriatus*.

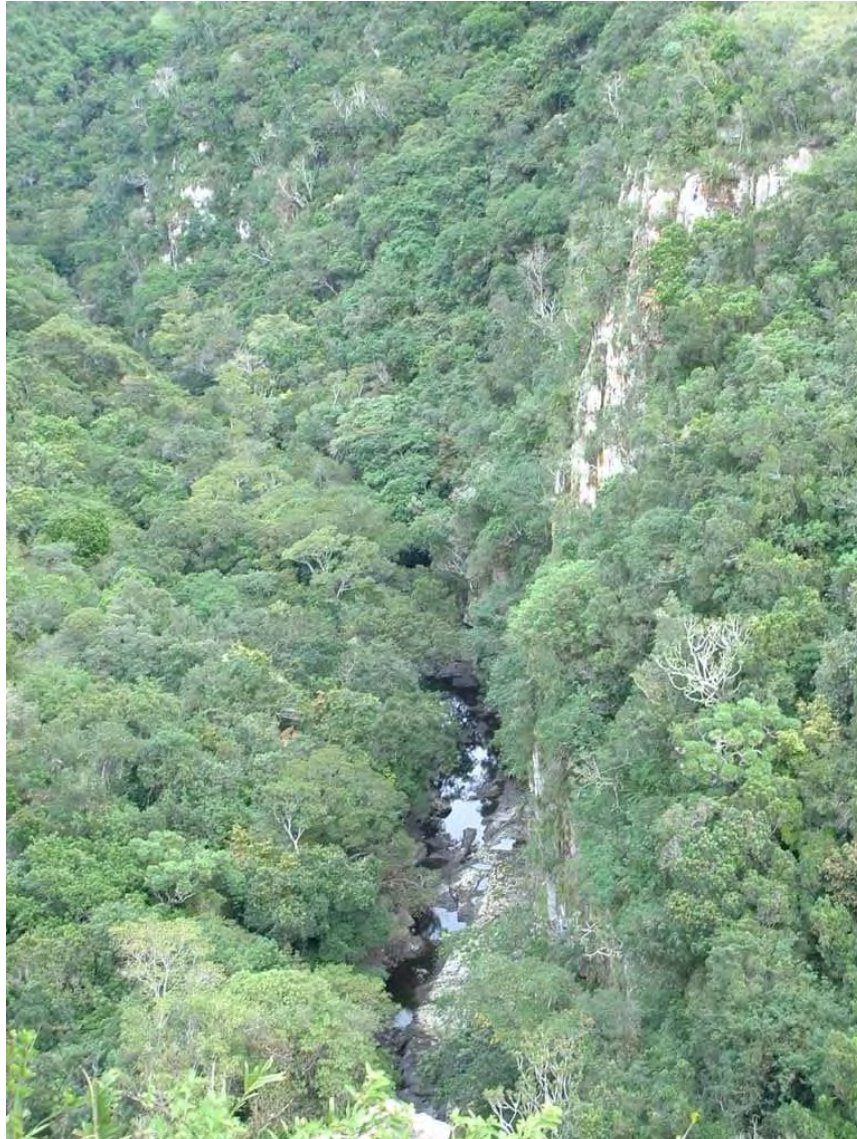


FIGURE 164b. Lower Kei River Valley in the Eastern Cape, a tributary with sheer sandstone cliffs, the habitat of *Streptocarpus kentaniensis*.

165. *Aeollanthus haumannii*



FIGURE 165a. *Aeollanthus haumannii* on a sheer cliff face at Otjihipa in the Kaokoveld in Namibia.

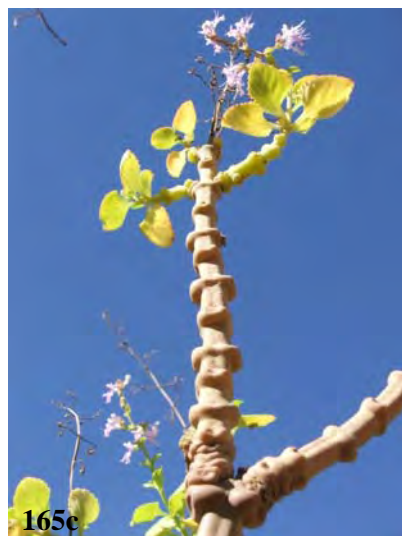
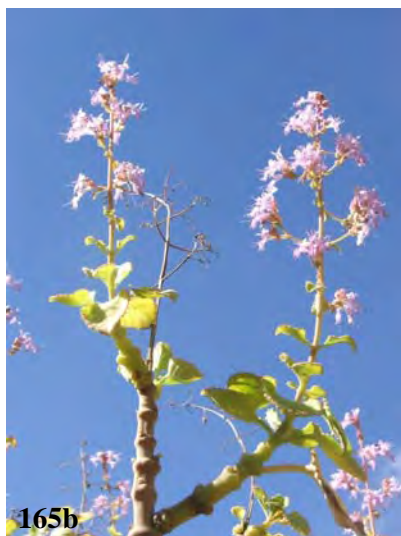


FIGURE 165b & 165c. *Aeollanthus haumannii* flowering at Kirstenbosch.

166. *Aeollanthus rydingianus*



FIGURE 166a. *Aeollanthus rydingianus* in flower on a sheer south-facing cliff at Omavanda on the Baynes Mountains in the Kaokoveld in Namibia.



FIGURE 166b. *Aeollanthus rydingianus* at Omavanda on the Baynes Mountains in the Kaokoveld in Namibia, here growing with an *Adiantum* fern.



FIGURE 166c. *Aeollanthus rydingianus* habitat, sheer south-facing cliff at Omavanda on the Baynes Mountains in the Kaokoveld in Namibia.



FIGURE 166d. Plant of *Aeollanthus rydingianus* in flower at Kirstenbosch (material from Omavanda, Baynes Mountains, Kaokoveld, Namibia).

167. *Plectranthus dolomiticus*



FIGURE 167a. *Plectranthus dolomiticus* in flower at Kirstenbosch.



FIGURE 167b. *Plectranthus dolomiticus* on a dolomite cliff at Penge in Limpopo Province.



FIGURE 167c. Olifants River near Penge in Limpopo Province, habitat of *Plectranthus dolomiticus*.

168. *Plectranthus ernstii*



FIGURE 168a. *Plectranthus ernstii* on a cliff at Mtamvuna in southern KwaZulu-Natal, here growing with the lithophytic orchid *Rangaeris muscicola*.



FIGURE 168b. Oribi Gorge in southern KwaZulu-Natal, the habitat of *Plectranthus ernstii*.



FIGURE 168c. *Plectranthus ernstii* planted on a vertical rock crevice in cultivation at Kirstenbosch.



FIGURE 168d. *Plectranthus ernstii* in habitat on a south-facing sandstone cliff at Oribi Gorge in southern KwaZulu-Natal.



FIGURE 168e. *Plectranthus ernstii* on a cliff at Mtamvuna in southern KwaZulu-Natal, growing with the epiphytic orchid *Rangaeris muscicola* (bottom).

169. *Plectranthus mutabilis*



FIGURE 169a. *Plectranthus mutabilis* on a dolomite cliff at the Sudwala Caves in Mpumalanga.



FIGURE 169b. *Plectranthus mutabilis* on a dry stone wall in cultivation at Kirstenbosch.



FIGURE 169c. Dolomite cliffs above Pilgrim's Rest in Mpumalanga, habitat of *Plectranthus mutabilis* and here growing together with *Aloe spicata*.



FIGURE 169d. *Plectranthus mutabilis* on a dolomite cliff above Pilgrim's Rest in Mpumalanga.

170. *Plectranthus mzimvubuensis*



FIGURE 170a. *Plectranthus mzimvubuensis* in flower at Kirstenbosch.



FIGURE 170b. *Plectranthus mzimvubuensis* on a shale cliff above the Mzimvubu River in the Eastern Cape. Note the thickened stem base.



FIGURE 170c. The habitat of *Plectranthus mzimvubuensis*, cliffs above the Mzimvubu River in the Eastern Cape.



FIGURE 170d. *Plectranthus mzimvubuensis* in cultivation at Kirstenbosch.

171. *Plectranthus purpuratus* subsp. *purpuratus*



FIGURE 171a. *Plectranthus purpuratus* subsp. *purpuratus* here in cultivation at Kirstenbosch. Note the compact, imbricate leaves (material from Shongweni Dam, KwaZulu-Natal).



FIGURE 171b. *Plectranthus purpuratus* subsp. *purpuratus* in habitat on a south-facing cliff at Molweni, Durban. Note the compact, imbricate leaves.



FIGURE 171c. South-facing cliff face at Molweni near Durban in KwaZulu-Natal, the habitat of *Plectranthus purpuratus* subsp. *purpuratus*.



FIGURE 171d. *Plectranthus purpuratus* subsp. *purpuratus* growing in the cliff-plant collection at Kirstenbosch.



FIGURE 171e. Habitat of *Plectranthus purpuratus* subsp. *purpuratus*, a south-facing cliff face at Tafelberg near Pietermaritzburg in KwaZulu-Natal.

172. *Plectranthus saccatus* subsp. *pondoensis*



FIGURE 172a. *Plectranthus saccatus* subsp. *pondoensis* on a south-facing cliff face at Isikuba in the Eastern Cape.



FIGURE 172b. Habitat of *Plectranthus saccatus* subsp. *pondoensis* at Isikuba in the Eastern Cape.

173. *Tetradenia kaokoensis*



FIGURE 173a. Male plant of *Tetradenia kaokoensis* (Lamiaceae) in flower on a sandstone cliff in its habitat at Omavanda.



FIGURE 173b. A close look at *Tetradenia kaokoensis* at Omavanda.



FIGURE 173c. Omavanda cliffs, habitat of *Tetradenia kaokoensis*.

174. *Carruanthus peersii*



FIGURE 174a. *Carruanthus peersii* on a cliff face at Toorwaterspoort in the Western Cape.



FIGURE 174b. *Carruanthus peersii* on a cliff face at Toorwaterspoort in the Western Cape.



FIGURE 174c. *Carruanthus peersii* in flower in the cliff house at Kirstenbosch.

175. *Conophytum auriflorum* subsp. *turbiniforme*



FIGURE 175a. *Conophytum auriflorum* subsp. *turbiniforme* in its sandstone cliff-face habitat at the Spektakelpas in Namaqualand in the Northern Cape.



FIGURE 175b. Spektakelpas in Namaqualand in the Northern Cape, cliff-face habitat of *Conophytum auriflorum* subsp. *turbiniforme*.

176. *Conophytum bolusiae* subsp. *bolusiae*



FIGURE 176a & 176b. The sheer cliffs of Vyftienmyl se Berge on Oograbiesberg at Gemsbokvlei where *Conophytum bolusiae* subsp. *bolusiae* grows.



FIGURE 176c & 176d. *Conophytum bolusiae* subsp. *bolusiae* in habitat and in flower at Vyftienmyl se Berge on Oograbiesberg at Gemsbokvlei.

177. *Conophytum carpianum*



FIGURE 177a. *Conophytum carpianum* growing on a west-facing granite cliff on the upper western slope of the Ploegberg.



FIGURE 177b. *Conophytum carpianum* growing among numerous lichens on a west-facing granite cliff on the upper western slope of the Ploegberg.



FIGURE 177c. West-facing granite cliffs on the upper slopes of the Ploegberg in the Northern Cape, habitat of *Conophytum carpianum*.

179. *Conophytum ernstii*



FIGURE 179a. *Conophytum ernstii* in flower in the succulent nursery at Kirstenbosch (material from Sandrivier, Richtersveld, Northern Cape).



FIGURE 179b. *Conophytum ernstii* in the succulent nursery at Kirstenbosch (material from Sandrivier, Richtersveld, Northern Cape).

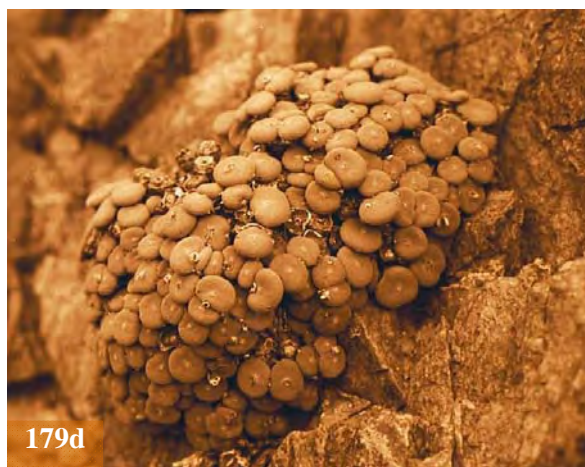


FIGURE 179c & 179d. *Conophytum ernstii* on Sandberg in the AiAis-Richtersveld Transfrontier National Park in the Northern Cape.



FIGURE 179e. Habitat of *Conophytum ernstii* at Sandberg in the AiAis-Richtersveld Transfrontier National Park in the Northern Cape.

180. *Conophytum francoiseae*



FIGURE 180a. Oograbies Wes, habitat of *Conophytum francoiseae*.



FIGURE 180b *Conophytum francoiseae* growing on a ledge in its native habitat at Oograbies Wes in the Richtersveld.



FIGURE 180c & 180d. Getting close to *Conophytum francoiseae* on a ledge in the Richtersveld.

181. *Conophytum fulleri*



FIGURE 181a. *Conophytum fulleri* on a quartz cliff at Aggeneys in Bushmanland in the Western Cape.



FIGURE 181b. *Conophytum fulleri* on a quartz cliff at Gamsberg in Bushmanland in the Western Cape.



FIGURE 181c. *Conophytum fulleri* on a quartz cliff at Aggeneys in Bushmanland.

182. *Conophytum hanae*



FIGURE 182a. *Conophytum hanae* on a granite cliff in southern Namaqualand in the Western Cape.



FIGURE 182b. Granite cliffs in southern Namaqualand in the Western Cape, the habitat of *Conophytum hanae*.



FIGURE 182c. *Conophytum hanae* on a granite cliff in southern Namaqualand in the Western Cape.



FIGURE 182d. *Conophytum hanae* on a granite cliff in southern Namaqualand.

183. *Conophytum luckhoffii*



FIGURE 183a. *Conophytum luckhoffii* on a sandstone cliff at the Piekenierskloof Pass in the Western Cape.



FIGURE 183b. Getting close to a plant of *Conophytum luckhoffii* on a sandstone cliff at the Piekenierskloof Pass, here growing with *Crassula montana* subsp. *montana* and *C. rupestris*.



FIGURE 183c & 183d. *Conophytum luckhoffii* flowering in the Piekenierskloof Pass in May.



FIGURE 183e. *Conophytum luckhoffii* here flowering among lichens in the Piekenierskloof Pass in May.

184. *Conophytum marginatum* subsp. *haramoepense*



FIGURE 184a. *Conophytum marginatum* subsp. *haramoepense* in flower in the Kirstenbosch succulent nursery (material from Naip se Berg, Northern Cape).



FIGURE 184b. Winter-active growth of *Conophytum marginatum* subsp. *haramoepense* in the Kirstenbosch succulent nursery (material from Naip se Berg, Northern Cape).



FIGURE 184c. Winter-active growth of *Conophytum marginatum* subsp. *haramoepense* in its native habitat at Dabenorisberg in the Northern Cape.

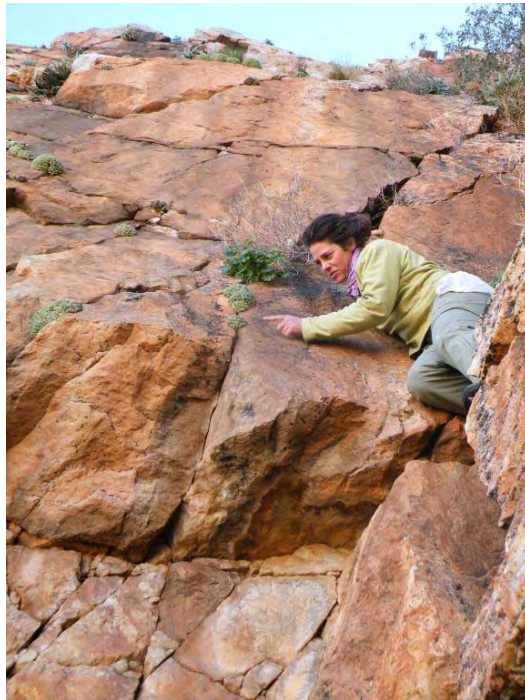


FIGURE 184d. *Conophytum marginatum* subsp. *haramoepense* where it grows at Dabenorisberg. Natanya Mulholland looking at the plant on the cliff face.

188. *Conophytum quaesitum* subsp. *quaesitum* var. *rostratum*



FIGURE 188a. *Conophytum quaesitum* subsp. *quaesitum* var. *rostratum* in habitat on Rooiberg in the AiAis-Richtersveld Transfrontier National Park.



FIGURE 188b. *Conophytum quaesitum* subsp. *quaesitum* var. *rostratum* in habitat on Rooiberg in the AiAis-Richtersveld Transfrontier National Park.

189. *Conophytum ricardianum* subsp. *ricardianum*



FIGURE 189a. *Conophytum ricardianum* subsp. *ricardianum* in its cliff-face habitat on the Sonberg on the Hunsberge in southern Namibia, here together with *Tylecodon bruynsii*.



FIGURE 189b. *Conophytum ricardianum* subsp. *ricardianum* growing on Kuamsibberg, Hunsberge, in southern Namibia in summer, the young leaves covered with remains of the present year's leaves.



FIGURE 189c. *Conophytum ricardianum* subsp. *ricardianum* in its cliff-face habitat on the Sonberg on the Hunsberge in southern Namibia.

190. *Conophytum stephanii*



FIGURE 190a. *Conophytum stephanii* in its cliff habitat at Gemsbokvlei at Oograbiesberg in Namaqualand in the Northern Cape.



FIGURE 190b. *Conophytum stephanii* in its cliff habitat at Gemsbokvlei at Oograbiesberg in Namaqualand in the Northern Cape.



FIGURE 190c. Gemsbokvlei at Oograbiesberg, the habitat of *Conophytum stephanii* in Namaqualand in the Northern Cape.



FIGURE 190d & 190e. *Conophytum stephanii* in flower at Kirstenbosch (material from Gemsbokvlei, Namaqualand, Northern Cape).



191. *Conophytum tantillum* subsp. *amicorum*



FIGURE 191a & 191b. *Conophytum tantillum* subsp. *amicorum* in its south-facing quartz cliff habitat south of Steinkopf in the Northern Cape. Photographs: Andy Young.

192. *Conophytum taylorianum* subsp. *ernianum*



FIGURE 192a & 192b. *Conophytum taylorianum* subsp. *ernianum* in its cliff habitat at Hohenzollern on the Hunsberg in southern Namibia.



FIGURE 192c. Hohenzollern on the Hunsberg where the upper cliff face is the habitat of *Conophytum taylorianum* subsp. *ernianum*.



FIGURE 192d. *Conophytum taylorianum* subsp. *ernianum* in cultivation at Kirstenbosch (material from Hohenzollern, Hunsberg, southern Namibia).

193. *Conophytum taylorianum* subsp. *rosynense*



FIGURE 193a. *Conophytum taylorianum* subsp. *rosynense* here in its quartz cliff habitat on the Rosyntjieberg in the Richtersveld in the Northern Cape.



FIGURE 193b. *Conophytum taylorianum* subsp. *rosynense* in its sandstone cliff habitat on the Rosyntjieberg in the Richtersveld in the Northern Cape.



FIGURE 193c. *Conophytum taylorianum* subsp. *rosynense* in its sandstone cliff habitat on the Rosyntjieberg in the Richtersveld in the Northern Cape.



FIGURE 193d. Rosyntjieberg quartz cliff habitat of *Conophytum taylorianum* subsp. *rosynense* in the Richtersveld in the Northern Cape. The plants here share the habitat with other cremnophytes such as *Aloe meyeri*, *Bulbine pendens*, *Conophytum stephanii*, *Othonna cremnophila* and *Tylecodon ellaphieae*.



FIGURE 193e. *Conophytum taylorianum* subsp. *rosynense* in cultivation at Kirstenbosch (material from Richtersveld, Northern Cape).

194. *Delosperma* sp. A



FIGURE 194a. *Delosperma* sp. A at Banana Point, Mtamvuna in KwaZulu-Natal.



FIGURE 194b. *Delosperma* sp. A here growing on cliffs at Banana Point, Mtamvuna in KwaZulu-Natal.



FIGURE 194c. Banana Point cliffs at Mtamvuna, habitat of *Delosperma* sp. A in KwaZulu-Natal.

195. *Delosperma* sp. B



FIGURE 195a. *Delosperma* sp. B on a sandstone cliff face at Waterfall Bluff on the Eastern Cape coast.



FIGURE 195b. *Delosperma* sp. B on a sandstone cliff face at Waterfall Bluff on the Eastern Cape coast.



FIGURE 195c. *Delosperma* sp. **B** on a sandstone cliff face at Waterfall Bluff on the Eastern Cape coast.



FIGURE 195d. Cliff face at Waterfall Bluff on the Eastern Cape coast where *Delosperma* sp. **B** grows.

196. *Delosperma esterhuyseniae*

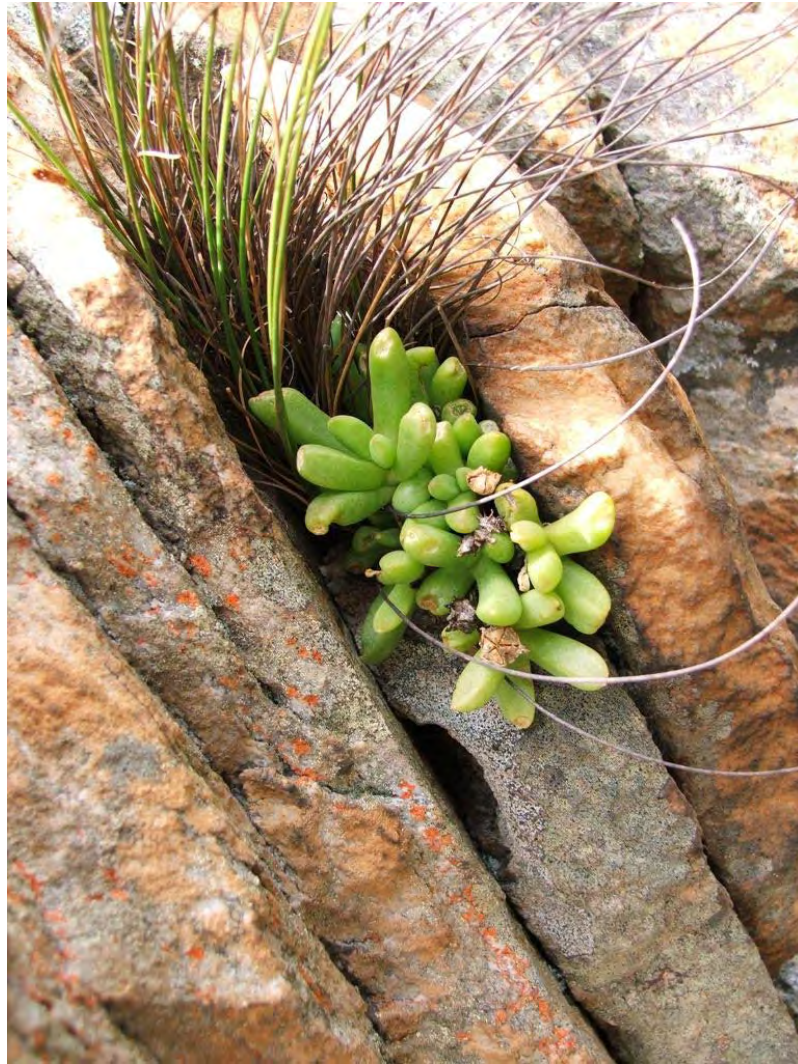


FIGURE 196a. *Delosperma esterhuyseniae* on a sandstone cliff on the Cockscomb Mountain in the Eastern Cape.



FIGURE 196b. Cliffs of the Cockscomb Mountain in the Eastern Cape, habitat of *Delosperma esterhuyseniae*. Werner Voigt standing in the foreground.



FIGURE 196c & 196d. *Delosperma esterhuyseniae* on sandstone cliffs in Gertsmitzkloof in the Baviaanskloof Mountains in the Eastern Cape, sharing its habitat with *Bulbine cremnophila*.

197. *Delosperma knox-daviesii*



FIGURE 197a. *Delosperma knox-daviesii* flowering on a sandstone cliff face at Blyderivierspoort in Mpumalanga.



FIGURE 197b. Cliff face at Blyderivierspoort in Mpumalanga, habitat of *Delosperma knox-daviesii*.

198. *Delosperma laxipetalum*



FIGURE 198a. *Delosperma laxipetalum* hanging down a sandstone cliff face at Swartwaterspoort in the Eastern Cape.



FIGURE 198b. *Delosperma laxipetalum* growing on a sandstone cliff face at Swartwaterspoort in the Eastern Cape.



FIGURE 198c. Cliff face at Swartwaterspoort in the Eastern Cape, habitat of *Delosperma laxipetalum*.

199. *Delosperma nubigenum*



FIGURE 199a. *Delosperma nubigenum* in cultivation at the Denver Botanical Garden in Denver, Colorado, USA.



FIGURE 199b. *Delosperma nubigenum* in its habitat at Mont-aux-Sources in the Drakensberg in KwaZulu-Natal.



FIGURE 199c. *Delosperma nubigenum* in cultivation at Denver Botanical Garden in Denver, Colorado, USA.



FIGURE 199d. *Delosperma nubigenum* in habitat near Sani, drooping from a cliff face.



FIGURE 199e. Drakensberg habitat of *Delosperma nubigenum* in KwaZulu-Natal, with Mont-aux-Sources in the background.

200. *Delosperma saxicola*



FIGURE 200a. *Delosperma saxicola* in habitat in the Tsitsikamma National Park in the Western Cape.



FIGURE 200b. *Delosperma saxicola* in the Tsitsikamma National Park.



FIGURE 200c. The habitat of *Delosperma saxicola* in the Tsitsikamma National Park in the Western Cape.



FIGURE 200d. *Delosperma saxicola* in habitat in the Tsitsikamma National Park in the Western Cape.

201. *Delosperma subpetiolatum*



FIGURE 201a. *Delosperma subpetiolatum* growing on a sandstone cliff near Maclear in the Eastern Cape.



FIGURE 201b. *Delosperma subpetiolatum* in flower on a sandstone cliff near Maclear in the Eastern Cape.



FIGURE 201c. Sandstone cliff near Maclear in the Eastern Cape, habitat of *Delosperma subpetiolatum*.

202. *Delosperma tradescantioides*



FIGURE 202a. *Delosperma tradescantioides* flowering at Kirstenbosch (material from a cliff in the Kei River, Eastern Cape, collected by Cameron and Rhoda Macmaster).

203. *Delosperma velutinum*



FIGURE 203a. *Delosperma velutinum* flowering on the cliffs of Die Kop at Kranskop in the Thukela region in KwaZulu-Natal, here sharing its habitat with *Aeollanthus parvifolius*, *Crassula lanceolata* and *C. perfoliata*.



FIGURE 203b. Cliff habitat of *Delosperma velutinum* at Die Kop, Kranskop in KwaZulu-Natal, the Thukela River in the background.



FIGURE 203c. *Delosperma velutinum* on cliffs at Die Kop, here growing with *Aeollanthus parvifolius*, *Crassula lanceolata* and *C. perfoliata*.

204. *Delosperma waterbergense*



FIGURE 204a. *Delosperma waterbergense* on a sandstone cliff on the Kransberg in the Marakele National Park where the plants grow in a shady kloof.



FIGURE 204b. Sandstone cliff faces on the Kransberg in the Marakele National Park, habitat of *Delosperma waterbergense* and *Crassula cymbiformis*, both endemic to the Kransberg in Limpopo Province.



FIGURE 204c. Flower of *Delosperma waterbergense* at Kirstenbosch.

205. *Delosperma zoutpansbergense*



FIGURE 205a. *Delosperma zoutpansbergense* in habitat on upper south-facing cliffs at Hanglip in Limpopo Province, growing together with *Plectranthus mutabilis*.



FIGURE 205b. A close look at *Delosperma zoutpansbergense* on cliffs at Hanglip in Limpopo Province.



FIGURE 205c. Upper south-facing cliffs, the habitat of *Delosperma zoutpansbergense* at Hanglip in Limpopo Province.

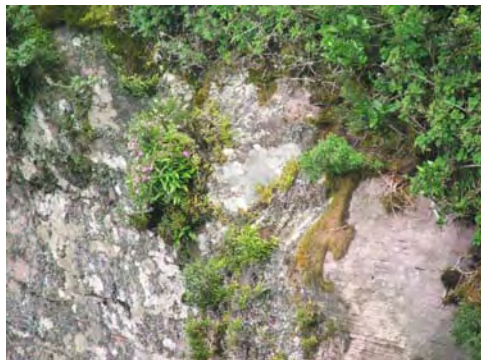


FIGURE 205d. Pink-flowering *Delosperma zoutpansbergense* on cliffs at Hanglip, Limpopo Province.

206. *Drosanthemum anemophilum*



FIGURE 206a. *Drosanthemum anemophilum* in flower in the Kirstenbosch Conservatory.



FIGURE 206b. *Drosanthemum anemophilum* in habitat on a cliff at Rooinek Pass.



FIGURE 206c. *Drosanthemum anemophilum* in flower in habitat. Note the pollinator (Rooinek Pass).



FIGURE 206d. Habitat of *Drosanthemum anemophilum* at Rooinek Pass.

207. *Drosanthemum expersum*



FIGURE 207a. *Drosanthemum expersum* on a sandstone cliff on the Waboomsberg near Ceres in the Western Cape.



FIGURE 207b. *Drosanthemum expersum* on a sandstone cliff at Conical Peak of the Matroosberg near Ceres in November 2009.



FIGURE 207c & 207d. *Drosanthemum expersum* on a shale cliff at Conical Peak on the Matroosberg near Ceres in the Western Cape in November 2009.





FIGURE 207e. *Drosanthemum expersum* on a sandstone cliff on Tafelberg north of Ceres in the Western Cape.



FIGURE 207f. *Drosanthemum expersum* on a sandstone cliff on Waboomsberg north of Ceres in the Western Cape.



FIGURE 207g. *Drosanthemum expersum* in flower on a sandstone cliff on Rooiberg on the Matroosberg in the Western Cape.



FIGURE 207h. South-facing sandstone cliff on Waboomsberg north of Ceres, the habitat of *Drosanthemum expersum*.



FIGURE 207i. *Drosanthemum expersum* on a sandstone cliff on Baviaansberg northeast of Ceres in the Western Cape.

208. *Drosanthemum inornatum*



FIGURE 208a. *Drosanthemum inornatum* growing on a south-facing dolomite cliff face at Konsertinaberg on the Hunsberg in southern Namibia.



FIGURE 208b. South-facing dolomite cliff face at Konsertinaberg on the Hunsberg in southern Namibia, habitat of *Drosanthemum inornatum*.

209. *Erepsia heteropetala*



FIGURE 209a. *Erepsia heteropetala* on a south-facing sandstone cliff on the Witteberg at Du Toitskloof in the Western Cape.



FIGURE 209b. South-facing sandstone cliffs on the Witteberg, Du Toitskloof, habitat of *Erepsia heteropetala* and *Esterhuyseniae stokoei*.



FIGURE 209c. Young plant of *Erepsia heteropetala* on a south-facing sandstone cliff on the Witteberg at Du Toitskloof in the Western Cape.



FIGURE 209d & 209e. *Erepsia heteropetala* hanging from a south-facing sandstone cliff on the Witteberg at Du Toitskloof in the Western Cape. The plant on the right here in flower in November 2009.

210. *Esterhuysenia stokoei*



FIGURE 210a. *Esterhuysenia stokoei* on a south-facing sandstone cliff on the Witteberg at Du Toitskloof in the Western Cape.



FIGURE 210b & 210c. *Esterhuysenia stokoei* on the Witteberg at Du Toitskloof in the Western Cape. The plant on the left was in fruit in March and the one on the right in flower in December 2009.



FIGURE 210d. *Esterhuysenia stokoei* growing sympatrically with *Erepisia heteropetala* on a south-facing sandstone cliff on the Witteberg at Du Toitskloof in the Western Cape.



FIGURE 210e. South-facing sandstone cliffs on the Witteberg at Du Toitskloof in the Western Cape, habitat of *Esterhuysenia stokoei* and *Erepisia heteropetala*.



FIGURE 210f. *Esterhuysenia stokoei* flowering on a south-facing sandstone cliff on the Witteberg at Du Toitskloof in the Western Cape in November 2009.

211. *Jensenobotrya lossowiana*



FIGURE 211a. *Jensenobotrya lossowiana* growing in the Namib Desert on a south-facing sandstone cliff at Dolphin Head on the coast in southern Namibia.



FIGURE 211b. Namib Desert habitat of *Jensenobotrya lossowiana*. It grows on a south-facing sandstone cliff at Dolphin Head in the background.



FIGURE 211c & 211d. *Jensenobotrya lossowiana* growing on a south-facing sandstone cliff at Dolphin Head on the southern Namibian coast. The plant on the left was photographed in 2007. On the right is the same plant photographed by Willi Giess in 1974.



FIGURE 211e. *Jensenobotrya lossowiana* growing in the Namib Desert on a south-facing sandstone cliff at Dolphin Head on the southern Namibian coast. Note the condensation of fog on the leaves.



FIGURE 211f. *Jensenobotrya lossowiana* in flower in the Namib Desert where it grows on a sheer south-facing sandstone cliff at Dolphin Head on the southern Namibian coast.

212. *Lampranthus affinis*



FIGURE 112a. *Lampranthus affinis* in flower in cultivation (material from Baviaanskloof, Eastern Cape).



FIGURE 212b. *Lampranthus affinis* in flower on a dry stone wall (material from Baviaanskloof, Eastern Cape).



FIGURE 212c. *Lampranthus affinis* in flower, growing on a sandstone cliff at the Seweweekspoort near Ladismith in the Western Cape.



FIGURE 212d. A white-flowering form of *Lampranthus affinis* from the Kouga Dam in the Eastern Cape.

213. *Machairophyllum brevifolium*



FIGURE 213a. A close look at *Machairophyllum brevifolium* in flower at Skuinsklip in the Western Cape.



FIGURE 213b. *Machairophyllum brevifolium* in habitat at Skuinsklip in the Western Cape.

214. *Oscularia cremnophila*



FIGURE 214a & 214b. *Oscularia cremnophila* on a south-facing sandstone cliff at Steenbokfontein near Elands Bay in the Western Cape.



FIGURE 214c. Getting close to *Oscularia cremnophila* in flower on a south-facing sandstone cliff at Steenbokfontein near Elands Bay in the Western Cape.



FIGURE 214d. Lower stem of *Oscularia cremnophila* on a south-facing sandstone cliff at Steenbokfontein near Elands Bay. Note the fissured bark.



FIGURE 214e. Young plant of *Oscularia cremnophila* in a fissure of a south-facing quartzitic sandstone cliff at Steenbokfontein near Elands Bay in the Western Cape.

215. *Ruschia knysnana*



FIGURE 215a. *Ruschia knysnana* in flower on a south-facing conglomerate cliff north of the Lake at Knysna. Growing with it are a young *Aloe ferox*, *Crassula biplanata*, *C. perforata* subsp. *perforata* and *Senecio crassulaefolius*.



FIGURE 215b. A young plant of *Ruschia knysnana* growing on a cliff north of the Lake at Knysna. Note the extended flowering stalks. Associated cliff dwellers in the background (non-obligatory) are *Crassula rubricaulis* and *Senecio crassulaefolius*.

216. *Ruschia promontorii*



FIGURE 216a. A close look at *Ruschia promontorii* in flower on a sandstone cliff face near the lighthouse at Cape Point Nature Reserve in the Western Cape.



FIGURE 216b. *Ruschia promontorii* growing on a sandstone cliff face in the Cape Point Nature Reserve.



FIGURE 216c. *Ruschia promontorii* growing on a sandstone cliff face near the lighthouse in the Cape Point Nature Reserve in the Western Cape.

217. *Scopelogenia bruynsii*



FIGURE 217a. *Scopelogenia bruynsii* in flower on a cliff face on Rooiberg on the Knersvlakte in the Western Cape.

218. *Scopelogenia verruculata*



FIGURE 218a. *Scopelogenia verruculata* hanging from a cliff face near Riviersonderend.



FIGURE 218b. *Scopelogenia verruculata* in flower on a cliff face near Riviersonderend.



FIGURE 218c. *Scopelogenia verruculata* on a cliff on the southern face of Lion's Head at Cape Town in the Western Cape.



FIGURE 218d. Southern cliff faces of Lion's Head where *Scopelogenia verruculata* grows near Cape Town in the Western Cape.

219. *Oxalis pocockiae*



FIGURE 219a. *Oxalis pocockiae* in its sandstone cliff-face habitat at Keurkloof in the Hex River Valley in the Western Cape. Note the infructescence bending towards the cliff face.



FIGURE 219b. *Oxalis pocockiae* on a cliff face at Keurkloof in the Hex River Valley near De Doorns in the Western Cape. Note the winged vegetative bulbils at the stem tip.



FIGURE 219c. *Oxalis pocockiae* taken from a crevice in a cliff face at Keurkloof in the Hex River Valley near De Doorns in the Western Cape, showing the production of winged bulbils, which are dispersed by wind to other crevices on the cliff (cloning).



FIGURE 219d. *Oxalis pocockiae* in a crevice at Keurkloof near De Doorns.

220. *Anacampseros scopata*



FIGURE 220a. *Anacampseros scopata* on a quartz cliff face at Gemsbokvlei in the Richtersveld in Namaqualand in the Northern Cape. The white hairs on the plant heads act as a fog trap. Low fog clouds are characteristic of this region.



FIGURE 220b. Oograbiesberg at Gemsbokvlei in the Richtersveld, habitat of *Anacampseros scopata*. Low fog clouds are characteristic of this region.



FIGURE 220c. *Anacampteros scopata* on a quartz cliff face at Gemsbokvlei in the Richtersveld in Namaqualand in the Northern Cape.

221. *Dewinteria petrophila*



FIGURE 221a. *Dewinteria petrophila* hanging from an ledge on the Otjihipa Mountains above the Cunene River.



FIGURE 221b. *Dewinteria petrophila* hanging from the Otjihipa Mountains above the Cunene River. Note the filiform basal branches entering crevices where they produce capsules and cloned seed.



FIGURE 221c. Young plant of *Dewinteria petrophila* on the Otjihipa Mountains in northern Namibia.



FIGURE 221d. *Dewinteria petrophila* growing on a steep south-facing cliff in northern Namibia.



FIGURE 221e. *Dewinteria petrophila* in flower on the Otjihipa Mountains, a pollinator visiting a flower early in the morning.

222. *Stemodiopsis rivae*



FIGURE 222a. *Stemodiopsis rivae* in flower on a sandstone cliff face on a southern slope of a cliff on the farm Little Leigh in the Soutpansberg. Plants grow in crevices, the inflorescence growing into the crevices after flowering. The lower plant is *Crassula expansa* subsp. *fragilis*.



FIGURE 222b. *Stemodiopsis rivae* in flower on a sandstone cliff face on a southern slope on the farm Little Leigh in the Soutpansberg. The plants grow in crevices, the inflorescence growing into the crevices after flowering.



FIGURE 222c. *Stemodiopsis rivae* growing below an overhang on a southern slope of a sandstone cliff face on the farm Little Leigh in the Soutpansberg.

74. *Ledebouria concolor*



FIGURE 74a. *Ledebouria concolor* in flower in its sandstone cliff-face habitat at the Witterivier in the Suurberg in the Eastern Cape.



FIGURE 74b. *Ledebouria concolor* (*Litanthus pusillus*) on cliffs at the Witterivier in the Suurberg in the Eastern Cape.



FIGURE 74c. *Ledebouria concolor* in cultivation and flowering at Kirstenbosch.

75. *Ledebouria cremnophila*



FIGURE 75a. *Ledebouria cremnophila* in flower in its sandstone cliff-face habitat at Kaaprivierspoort in Mpumalanga.



FIGURE 75b. *Ledebouria cremnophila* in flower at Kirstenbosch.



FIGURE 75c. *Ledebouria cremnophila* on a sandstone cliff face at Kaap-rivierspoort, Mpumalanga, sharing the habitat with *Aloe spicata* and *Cyanotis speciosa*.

76. *Ledebouria venterii*



FIGURE 76a. *Ledebouria venterii* in cultivation, flowering at Kirstenbosch.

77. *Ornithogalum juncifolium* var. *emsii*



FIGURE 77a. *Ornithogalum juncifolium* var. *emsii* on shale cliffs along the Fish River north of Grahamstown, here sharing its habitat with *Crassula socialis*, another cremnophyte.



FIGURE 77b. *Ornithogalum juncifolium* var. *emsii* at in cultivation at Kirstenbosch (material from the Fish River north of Grahamstown). Note the darker bulbs in the foreground, *Drimia uniflora*.

78. *Ornithogalum longibracteatum*



FIGURE 78a. *Ornithogalum longibracteatum* on a cliff at Tsolorha on the Bashee River in the Transkei region of the Eastern Cape.



FIGURE 78b. *Ornithogalum longibracteatum* bulbils (cloning). Bulbils spill over, often becoming wedged in crevices and then forming new colonies.



FIGURE 78c. *Ornithogalum longibracteatum* on a cliff at the Gourits River in the Western Cape.

79. *Ornithogalum pendens*



FIGURE 79a. *Ornithogalum pendens* on a sandstone cliff at Skaaprivierspoort in Namaqualand in the Northern Cape.



FIGURE 79b. *Ornithogalum pendens* removed from a sandstone cliff at Skaaprivierspoort in Namaqualand in the Northern Cape. Note the proliferation of bulbils (backup cloning).

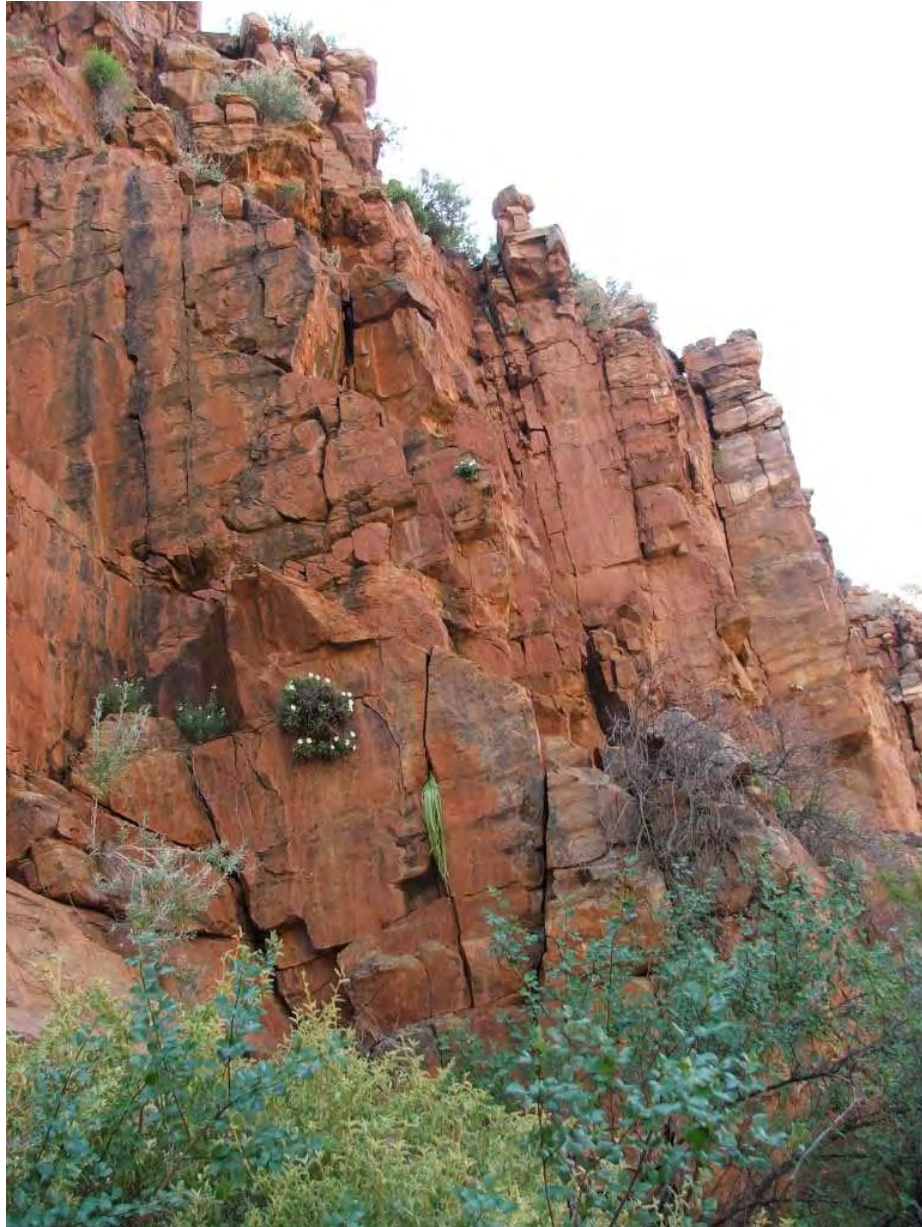


FIGURE 79c. The red sandstone cliffs at Skaaprivierspoort, the habitat of *Ornithogalum pendens*.

80. *Schizobasis intricata*



FIGURE 80a. *Schizobasis intricata* where it grows on a sandstone cliff along the Mzimnyati River in KwaZulu-Natal.



FIGURE 80b. *Schizobasis intricata* sharing its habitat on a cliff face at the Kouga Dam in the Eastern Cape with *Adromischus cristatus* var. *schonlandii* and *Crassula perforata* subsp. *kougaensis*.



FIGURE 80c. *Schizobasis intricata* growing on a sandstone cliff along the Pongola River at Klipwal Gold Mine in KwaZulu-Natal.

81. *Huernia pendula*

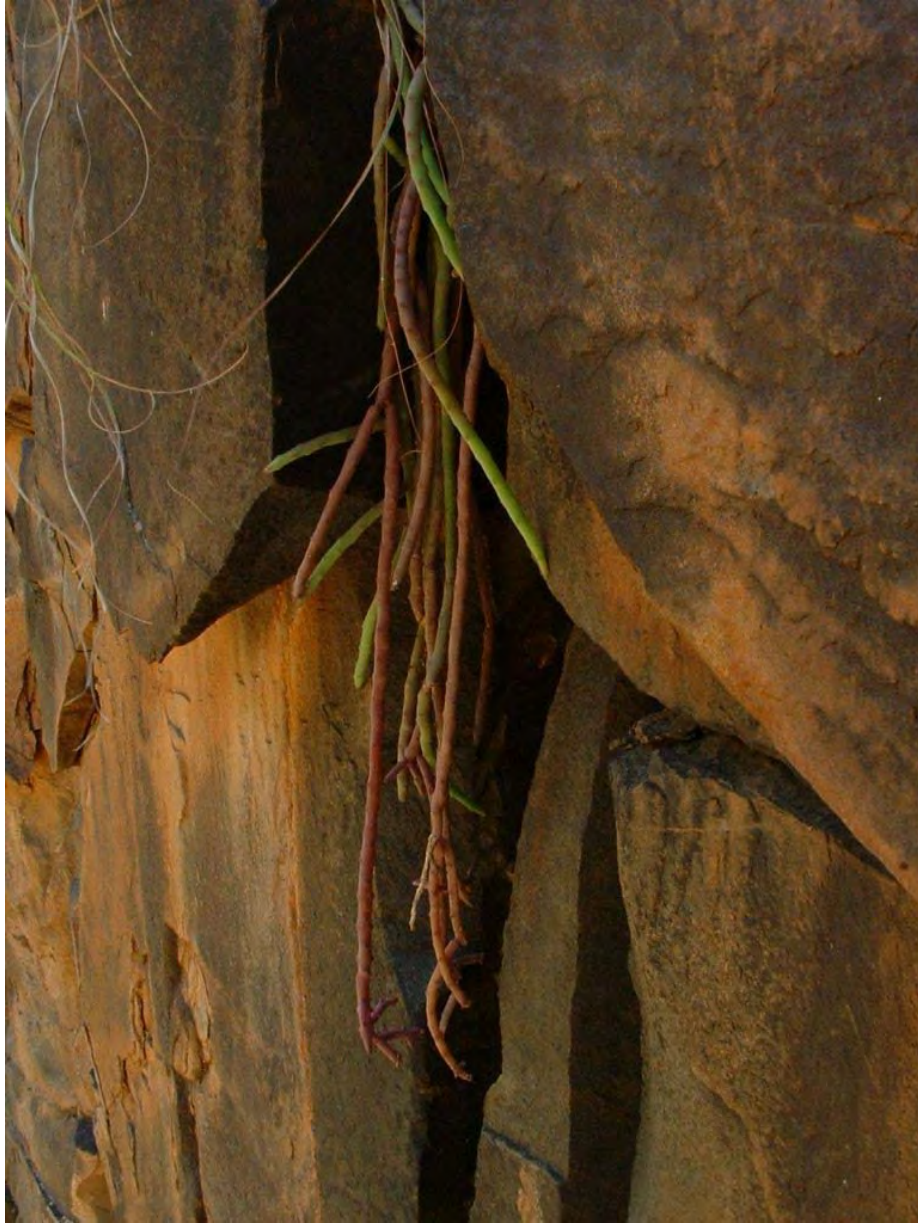


FIGURE 81a. *Huernia pendula* on a shale cliff face along the Kei River near Bolo Head in the Eastern Cape. Plants proliferate from stems that grow and occupy new crevices (vegetative proliferation backup).



FIGURE 81b. *Huernia pendula* in habitat on a shale cliff face along the Kei River near Bolo Head in the Eastern Cape.



FIGURE 81c. Cliffs along the Kei River near Bolo Head, habitat of *Huernia pendula*.



FIGURE 81d. *Huernia pendula* in flower.



FIGURE 81e. *Huernia pendula* in flower at Kirstenbosch.

82. *Lavrania haagnerae*



FIGURE 82a. *Lavrania haagnerae* on a dolomite cliff face east of Sesfontein in Damaraland, Namibia. Plants proliferate, forming dense clusters and occupying new crevices (vegetative proliferation backup).



FIGURE 82b. Dolomite cliff-face habitat of *Lavrania haagnerae* east of Sesfontein in Damaraland, Namibia.



FIGURE 82c. *Lavrania haagnerae* in flower at Kirstenbosch in October 2007.

83. *Tromotriche baylissii*



FIGURE 83a. *Tromotriche baylissii* in flower at Kirstenbosch in April 2007.



FIGURE 83b. Cliffs above the Kouga Dam in the Eastern Cape where *Tromotriche baylissii* grows.



FIGURE 83c. Plant of *Tromotriche baylissii* on a cliff together with *Crassula cordata*.



FIGURE 83d. *Tromotriche baylissii* in habitat at the Kouga Dam in the Eastern Cape.



FIGURE 83e. *Tromotriche baylissii* in habitat at Geelhoutboskloof in the Eastern Cape.

84. *Tromotriche choanantha*



FIGURE 84a. *Tromotriche choanantha* in habitat on a sandstone cliff at Badspoort near Calitzdorp in the Western Cape in August 2009.



FIGURE 84b. Cliffs at Badspoort, habitat of *Tromotriche choanantha*.

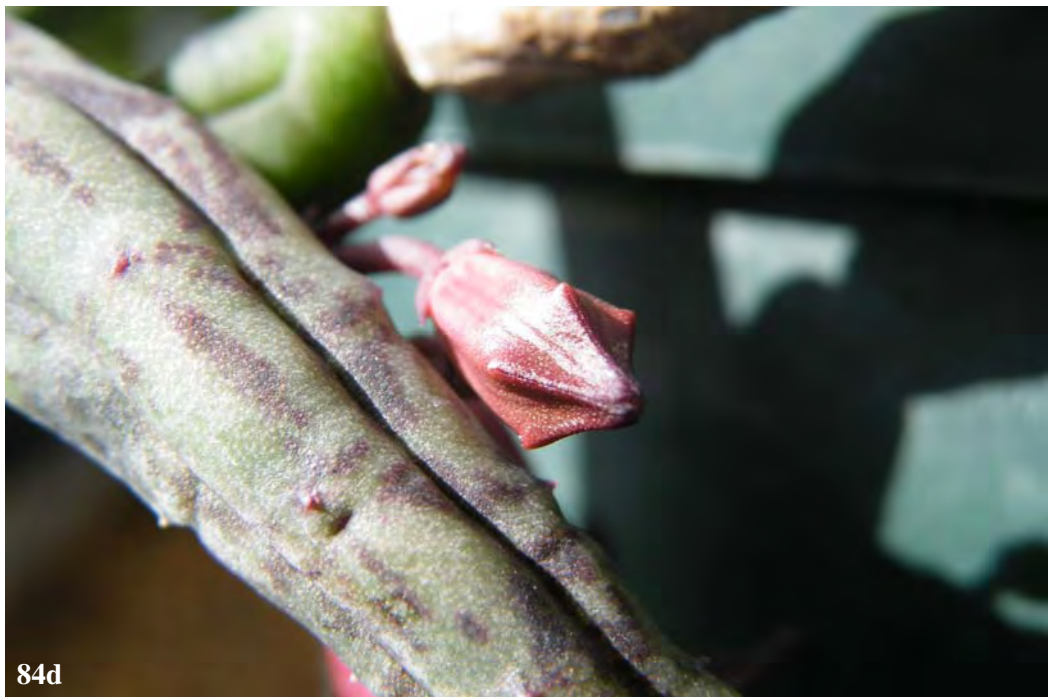


FIGURE 84c & 84d. *Tromotriche choanantha* in flower (material from Badspoort, Calitzdorp, Western Cape). Flowers are produced at the base of the stems.

85. *Kleinia galpinii*



FIGURE 85a. *Kleinia galpinii* on cliffs near Barberton in Mpumalanga. Plants stoloniferous, forming clusters. Here it shares the habitat with *Aloe spicata*.



FIGURE 85b. Cliffs near Barberton in Mpumalanga where *Kleinia galpinii* grows



FIGURE 85c. A dense cluster of *Kleinia galpinii* plants sharing the habitat with *Crassula sarcocaulis*.



FIGURE 85d. Flowers of *Kleinia galpinii* at Kirstenbosch.

86. *Othonna armiana*



FIGURE 86a. *Othonna armiana* flowering in cultivation at Kirstenbosch.



FIGURE 86b. *Othonna armiana* on Rooiberg near Eksteenfontein in the Richtersveld.

87. *Othonna capensis*



FIGURE 87a. Cliff hanger *Othonna capensis* on Tandjiesberg, near Graaff-Reinet in the Eastern Cape.



FIGURE 87b. Tandjiesberg near Graaff-Reinet, the habitat of *Othonna capensis*.



FIGURE 87c. *Othonna capensis* hanging from cliffs in its native habitat at Horee at the Kouga River in the Eastern Cape.

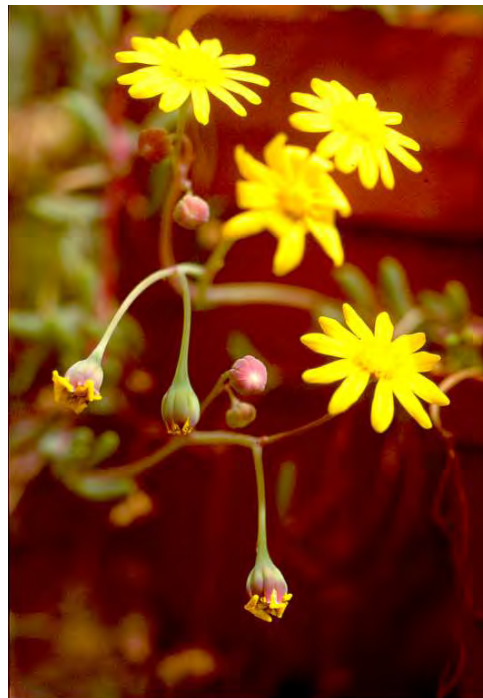


FIGURE 87d. *Othonna capensis* flowers at Kirstenbosch.

88. *Othonna cremnophila*



FIGURE 88a. Cliff squatter *Othonna cremnophila* confined to quartz crevices on south-facing slopes on the Rosyntjieberg.



FIGURE 88b. *Othonna cremnophila* growing on a cliff on the Rosyntjieberg in the Richtersveld in the Northern Cape.



FIGURE 88c. The Rosyntjieberg in the Richtersveld where south-facing cliffs are the habitat of *Othonna cremnophila*.

89. *Othonna triplinervia*



FIGURE 89a. *Othonna triplinervia* on a quartz cliff along the Grootrivierspoort in the Eastern Cape.



FIGURE 89b. Sandstone cliffs of Grootrivierspoort, habitat of *Othonna triplinervia*.



FIGURE 89c. The flowers of *Othonna triplinervia*.



FIGURE 89d. Young plant of *Othonna triplinervia* in a quartz cliff at the Kouga Dam in the Eastern Cape.



FIGURE 89e. *Othonna triplinervia* at the Kouga Dam.

90. *Senecio medley-woodii*



FIGURE 90a. *Senecio medley-woodii* in habitat on a shale cliff along the Mzimvubu River in the Transkei region of the Eastern Cape.



FIGURE 90b. Shale-cliff habitat of *Senecio medley-woodii* along the Mzimvubu River in the Transkei region of the Eastern Cape. Associated plants include *Crassula foveata*, *Euphorbia triangularis* and *Portulacaria afra*.



FIGURE 90c. *Senecio medley-woodii* in habitat on a sandstone cliff along the Mgeni River in KwaZulu-Natal. Associated plants include *Gasteria croucheri* subsp. *pendulifolia*, *Portulacaria afra* and *Rhipsalis baccifera*.

91. *Senecio muiirii*



FIGURE 91a. *Senecio muiirii* in its habitat on a cliff face above Calitzdorp in the mountains of the Huis River Pass.

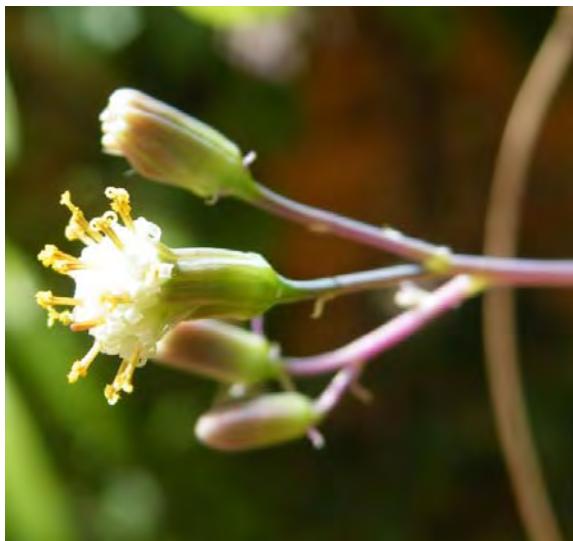


FIGURE 91b. *Senecio muiirii* in flower at Kirstenbosch.



FIGURE 91c. *Senecio muiirii* in cultivation at Kirstenbosch. Note the translucent veins allowing efficient penetration of light. The adventitious roots forming on the stem enable the plant to occupy new crevices (cloning).



FIGURE 91d. *Senecio muirii* growing on a shale cliff face at Valsriviermond farm along the Gourits River near Calitzdorp in the Western Cape.



FIGURE 91e. *Senecio muirii* growing on a sandstone cliff face at Badspoort near Calitzdorp in the Western Cape.

92. *Senecio pondoensis*



FIGURE 92a. *Senecio pondoensis* in cultivation at Kirstenbosch. The broad translucent central part on the adaxial side for the leaf ensures efficient penetration of light on the shady south-facing cliffs. Stems form adventitious roots, enabling the plants to occupy new crevices (cloning).



FIGURE 92b. South-facing cliffs in Pondoland in the Eastern Cape where *Senecio pondoensis* grows.

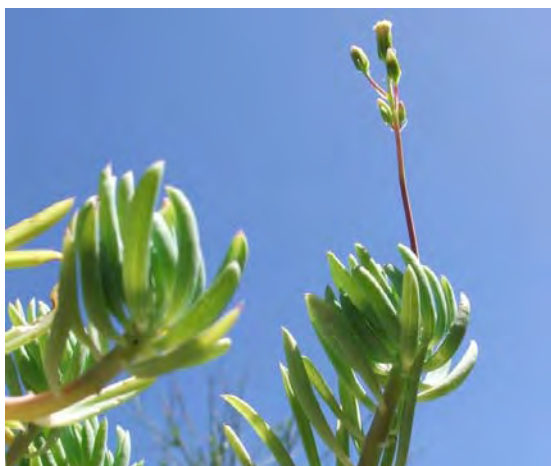


FIGURE 92c. *Senecio pondoensis* in flower at Kirstenbosch.

93. *Senecio serpens*



FIGURE 93a. *Senecio serpens* in habitat at Cape Point Nature Reserve, growing on an east-facing cliff of quartzitic sandstone rock.



FIGURE 93b. Getting closer to *Senecio serpens* at Cape Point Nature Reserve.



FIGURE 93c. Cliffs at Cape Point Nature Reserve in December 2007, habitat of *Senecio serpens*.



FIGURE 93d. *Senecio serpens* on a cliff face at Cape Point Nature Reserve in the Western Cape.

94. *Senecio talinoides* subsp. *talinoides*



FIGURE 94a. *Senecio talinoides* cultivated at Kirstenbosch (material from Collywobbles, Bashee River, Eastern Cape).



FIGURE 94b. *Senecio talinoides* in flower, grown at Kirstenbosch (material from Collywobbles, Bashee River, Eastern Cape).

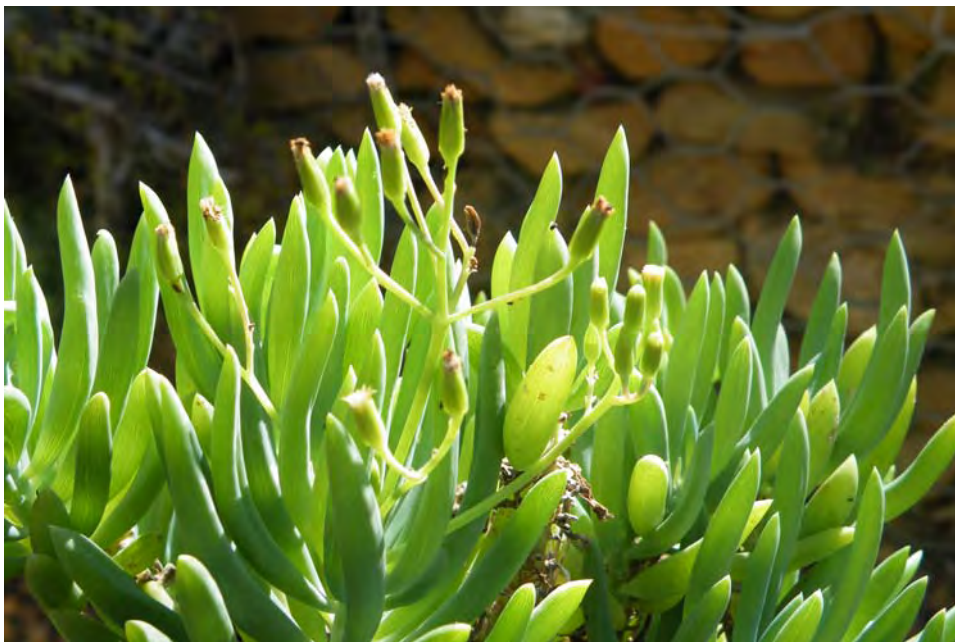


FIGURE 94c. *Senecio talinoides* flowering at Kirstenbosch (material from Collywobbles, Bashee River, Eastern Cape).

95. *Rhipsalis baccifera*



FIGURE 95a. *Rhipsalis baccifera* on a cliff face at Molweni in KwaZulu-Natal. It is a typical cliff hanger, with terete stems becoming pendent on the cliff face.



FIGURE 95b. *Rhipsalis baccifera* on a cliff face at Oribi Gorge in KwaZulu-Natal.

96. *Adromischus cristatus* var. *mzimvubuensis*



FIGURE 96a. *Adromischus cristatus* var. *mzimvubuensis* where it grows on a shale cliff along the Mzimvubu River in the Transkei region of the Eastern Cape.



FIGURE 96b. Cliff hugger *Adromischus cristatus* var. *mzimvubuensis* growing on a shale cliff along the Mzimvubu River in the Eastern Cape. Note the detached leaves spilling over the cliffs, rooting and filling new crevices. Here it grows together with *Crassula foveata* subsp. *foveata* and *C. perforata* subsp. *perforata*.



FIGURE 96c. Kudikela, cliff habitat of *Adromischus cristatus* subsp. *mzimvubuensis* along the Mzimvubu River in the Transkei region of the Eastern Cape.



FIGURE 96d. *Adromischus cristatus* var. *mzimvubuensis* in flower at Kirstenbosch.

97. *Adromischus cristatus* var. *schonlandii*



FIGURE 97a. Cliff hugger *Adromischus cristatus* var. *schonlandii* growing on a sheer sandstone cliff face at the Kouga Dam in the Eastern Cape.



FIGURE 97b. Cliff hugger *Adromischus cristatus* var. *schonlandii* on a sheer sandstone cliff face at the Kouga Dam, sharing the habitat with *Aloe pictifolia* and *Crassula perforata* subsp. *kougaensis*.



FIGURE 97c. *Adromischus cristatus* var. *schonlandii* in flower at Kirstenbosch.



FIGURE 97d. *Adromischus cristatus* var. *schonlandii* on a sheer sandstone cliff face at the Kouga Dam.

98. *Adromischus cristatus* var. *zeyheri*



FIGURE 98a. *Adromischus cristatus* var. *schonlandii* on a sheer sandstone cliff face at the Kouga Dam.



FIGURE 98b. Sheer sandstone cliffs above the Kouga Dam in the Eastern Cape where *Adromischus cristatus* var. *schonlandii* grows.



FIGURE 98c. *Adromischus cristatus* var. *zeyheri* growing on sheer cliffs at the Kouga Dam in the Eastern Cape. The leaves are brittle and when they become detached, they will root in new crevices (cloning backup).

99. *Adromischus diabolicus*



FIGURE 99a. *Adromischus diabolicus* on a sheer south-facing quartzitic sandstone cliff face on Dabenorisberg in the Northern Cape.



FIGURE 99b. Dabenorisberg in the Northern Cape, the habitat of *Adromischus diabolicus*.



FIGURE 99c. *Adromischus diabolicus* on a sheer south-facing quartzitic sandstone cliff face near Aggeneys in the Northern Cape.

100. *Adromischus fallax*



FIGURE 100a. *Adromischus fallax*, a cliff hugger on the Tandjiesberg near Graaff-Reinet.



FIGURE 100b. Tandjiesberg near Graaff-Reinet, habitat of *Adromischus fallax*.



FIGURE 100c. A close look at *Adromischus fallax* on a cliff on the Tadjiesberg.

101. *Adromischus leucophyllus*



FIGURE 101a. *Adromischus leucophyllus* growing in Buffelspoort west of Ladismith in the Western Cape.



FIGURE 101b. Buffelspoort, the habitat of *Adromischus leucophyllus*.



FIGURE 101c. *Adromischus leucophyllus*, a cliff hugger at Buffelspoort. When the brittle leaves become detached, they will start to grow and occupy new crevices.



FIGURE 101d. *Adromischus leucophyllus* hugging the cliffs at Waterkloof in the Hex River Valley in the Western Cape, the brittle leaves forming new plants if they should break off and land in a new crevice (cloning backup).

102. *Adromischus liebenbergii* subsp. *orientalis*



FIGURE 102a. Cliff hugger *Adromischus liebenbergii* subsp. *orientalis* growing on shale cliffs at Tsolorha at the Bashee River in the Transkei region of the Eastern Cape.

103. *Adromischus schuldianus* subsp. *brandbergensis*



FIGURE 103a. Orabeswand (cliff in background), Brandberg in northern Namibia, habitat of *Adromischus schuldianus* subsp. *brandbergensis*.



FIGURE 103b. *Adromischus schuldianus* subsp. *brandbergensis* growing on cliffs of Orabeswand in northern Namibia. Leaves are brittle and grooved, with an adaxial translucent window. Detached leaves will root and grow in new crevices (cloning backup).



FIGURE 103c. *Adromischus schuldianus* subsp. *brandbergensis* growing at Kirstenbosch. Leaves are grooved, with an adaxial translucent window.

104. *Adromischus subdistichus*



FIGURE 104a. *Adromischus subdistichus* at Toorwaterspoort in the Groot Swartberge, west of Willowmore. Leaves are brittle and when they become detached, they will root in new crevices (cloning backup).

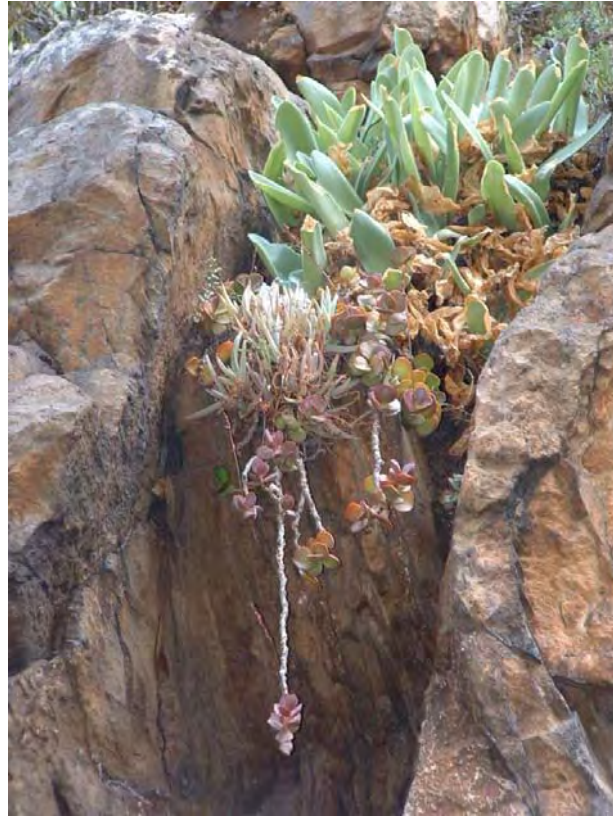


FIGURE 104b. *Adromischus subdistichus* at Toorwaterspoort in the Groot Swartberge west of Willowmore. Here growing with *Bulbine frutescens* and *Haemanthus albiflos*.



FIGURE 104c. Toorwaterspoort in the eastern Swartberg in the Western Cape, habitat of *Adromischus subdistichus* and many other succulent cremnophytes.



FIGURE 104d. *Adromischus subdistichus* growing on and in cliffs at Aasvoëlberg near Willowmore.

105. *Adromischus umbraticola* subsp. *ramosus*



FIGURE 105a. *Adromischus umbraticola* subsp. *ramosus* growing at Chuniespoort in Limpopo Province. The brittle leaves will root in new crevices if they become detached (cloning backup).



FIGURE 105b. Getting close to *Adromischus umbraticola* subsp. *ramosus* at Chuniespoort in Limpopo Province.



FIGURE 105c. Chuniespoort habitat of *Adromischus umbraticola* subsp. *ramosus* in Limpopo Province. Note the conspicuous *Aloe mutabilis* and *Sarcostemma viminale* drooping from the cliff face.

106. *Cotyledon barbeyi* var. A



FIGURE 106a. *Cotyledon barbeyi* var. A flowering at Kirstenbosch (material from Wyllies Poort, Limpopo Province).



FIGURE 106b. The leaves of *Cotyledon barbeyi* var. A in cultivation at Kirstenbosch (material from Wyllies Poort, Limpopo Province).

107. *Cotyledon elisae*



FIGURE 107a. *Cotyledon elisae* growing on a sandstone cliff in the Gourits River in the Western Cape.

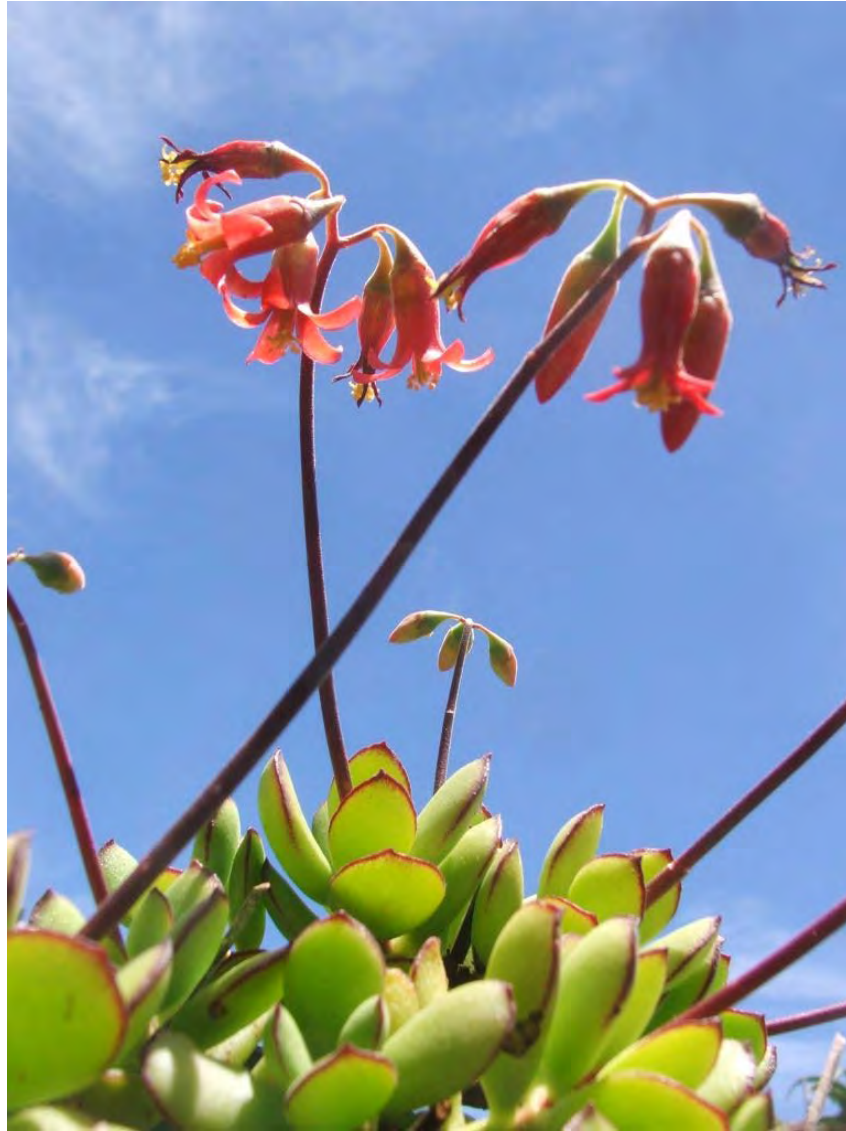


FIGURE 107b. *Cotyledon elisae* in cultivation at Kirstenbosch.

108. *Cotyledon pendens*



FIGURE 108a. *Cotyledon pendens* growing at Kirstenbosch. Branches will root if they find new crevices. Detached leaves will also root, forming new plantlets, a distinct and unique clonal backup.



FIGURE 108b. The inflorescence of *Cotyledon pendens*.



FIGURE 108c. Shale cliffs along the Bashee River in the Eastern Cape where *Cotyledon pendens* grows.

109. *Cotyledon tomentosa* subsp. *tomentosa*



FIGURE 109a. *Cotyledon tomentosa* subsp. *tomentosa* on a sandstone cliff face in the Huis River Pass.

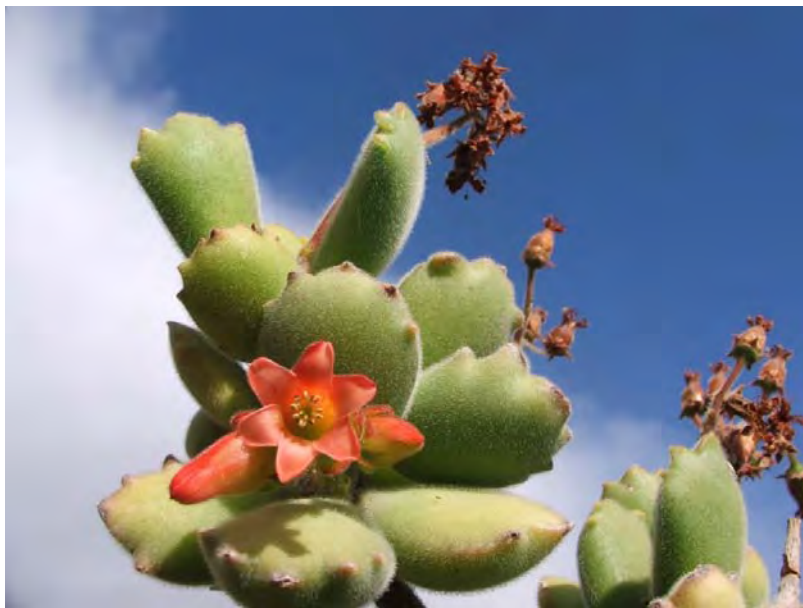


FIGURE 109b. *Cotyledon tomentosa* subsp. *tomentosa* in flower at Kirstenbosch.



FIGURE 109c. *Cotyledon tomentosa* subsp. *tomentosa* on a cliff face at the Kouga Dam in the Eastern Cape.

110. *Crassula alba* var. *pallida*



FIGURE 110a. *Crassula alba* var. *pallida* growing on a dolomite cliff face at the Abel Erasmus Pass in Mpumalanga.

111. *Crassula atropurpurea* var. *anomala*



FIGURE 111a. *Crassula atropurpurea* subsp. *anomala* growing on a sandstone cliff face in Du Toitskloof in the Witteberg in the Western Cape.



FIGURE 111b. Witteberg, habitat of *Crassula atropurpurea* var. *anomala*.



FIGURE 111c. *Crassula atropurpurea* subsp. *anomala* on a sandstone cliff face in Du Toitskloof. The seeds germinate on lichen- and moss-covered cliffs.



FIGURE 111d. *Crassula atropurpurea* subsp. *anomala* on a sandstone cliff face at Dwarsrivierspoort in the Western Cape.

113. *Crassula badspoortense*



FIGURE 113a. *Crassula badspoortense* growing at Badspoort south of Calitzdorp in the Western Cape.



FIGURE 113b. *Crassula badspoortense* in flower at Kirstenbosch.



FIGURE 113c. *Crassula badspoortense* in habitat. The inflorescence initially curves down, a distinct character.



FIGURE 113d. *Crassula badspoortense* drooping from a cliff face at Waterkloof in the Hex River Valley.

114. *Crassula brachystachya*



FIGURE 114a. *Crassula brachystachya* on a cliff near Touws River.



FIGURE 114b. *Crassula brachystachya* growing on cliffs near Touws River.



FIGURE 114c. *Crassula brachystachya* at Bosluiskloof near Die Hel in the Western Cape.



FIGURE 114d. *Crassula brachystachya* growing below an overhang at Bosluiskloof.

115. *Crassula capitella* subsp. *thyrsoflora*



FIGURE 115a & 115b. Cliff-face form of *Crassula capitella* subsp. *thyrsoflora* at Gertsmitkloof. The plants form dense clusters and branches falling into new crevices will soon root.



FIGURE 115c. Cliff-face form of *Crassula capitella* subsp. *thyrsiflora* grown at Kirstenbosch (material from Gertsmitzkloof).



FIGURE 115d. Cliff-face form of *Crassula capitella* subsp. *thyrsiflora* from Mistkraal, here in cultivation at Kirstenbosch.



FIGURE 115e. Cliff-face form of *Crassula capitella* subsp. *thyrsoflora* at the Kouga Dam, growing in dense clusters. Branches that fall into crevices will soon root there.



FIGURE 115f. *Crassula capitella* subsp. *thyrsoflora*, the cliff-face form on the farm Valsriviermond at the Gourits River in the Western Cape. Plants here grow on shale.



FIGURE 115g. *Crassula capitella* subsp. *thyrsoflora* at Grootrivierspoort in the Eastern Cape on quartz cliffs. The Grootrivier is a tributary of the Gamtoos River.



FIGURE 115h. The common non-cliff form of *Crassula capitella* subsp. *thyrsoflora* at the Grootrivierspoort in the Eastern Cape. The two forms grow sympatrically. The non-cliff-face form above is not as compact and this growth is retained in cultivation.

116. *Crassula cremnophila*



FIGURE 116a. *Crassula cremnophila* at the Kouga River on the farm Keurkloof where it grows on sandstone rock among lichens and moss. Plants are found on south-facing cliffs, the clusters solitary or dividing. Note the old infructescence.



FIGURE 116b. *Crassula cremnophila* on the farm Keurkloof, growing among moss on sandstone rock. Note the old infructescence.

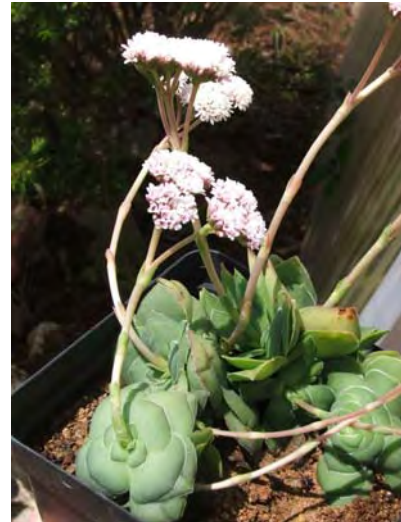


FIGURE 116c. *Crassula cremnophila* flowering in cultivation at Kirstenbosch (material from Keurkloof).



FIGURE 116d. The cliffs at Keurkloof, Kouga, habitat of *Crassula cremnophila*.

117. *Crassula cymbiformis*



FIGURE 117a. *Crassula cymbiformis* growing on cliffs of the Kransberg in the Marakele National Park in Limpopo Province. The plants grow among lichens on south-facing cliffs.



FIGURE 117b. *Crassula cymbiformis* in flower on a sandstone cliff on the Kransberg.



FIGURE 117c. The habitat of *Crassula cymbiformis* on the Kransberg in the Marakele National Park in Limpopo Province where the plants grow on cliffs higher than 1000 m above sea level.

118. *Crassula exilis* subsp. *cooperi*



FIGURE 118a. *Crassula exilis* subsp. *cooperi* on a sandstone cliff north of Graaff-Reinet and near the Kompasberg in the Northern Cape. Plants form dense clusters on shady cliffs.



FIGURE 118b. *Crassula exilis* subsp. *cooperi* in flower at Kirstenbosch.

119. *Crassula exilis* subsp. *exilis*



FIGURE 119a. *Crassula exilis* subsp. *exilis* growing on quartz rocks at Ratelpoort in Namaqualand in the Northern Cape. The plants form dense clusters on shady cliffs.



FIGURE 119b. A dense cluster of *Crassula exilis* subsp. *exilis* on shady quartz rocks at Ratelpoort.



FIGURE 119c. *Crassula exilis* subsp. *exilis* in full sun on quartz rocks of a cliff at Ratelpoort in the Northern Cape. The reddish colour of the leaves is due to the production of anthocyanins.



FIGURE 119d. Quartz cliff at Ratelpoort in the Northern Cape, habitat of *Crassula exilis* subsp. *exilis*.

120. *Crassula exilis* subsp. *sedifolia*



FIGURE 120a. *Crassula exilis* subsp. *sedifolia* (plant below the *Adromischus diabolicus*) growing on a shady south-facing cliff at Dabenorisberg in the Northern Cape.



FIGURE 120b. Dabenorisberg in the Northern Cape, habitat of *Crassula exilis* subsp. *sedifolia*. Plants grow on shady south-facing slopes. The Orange River is in the background.

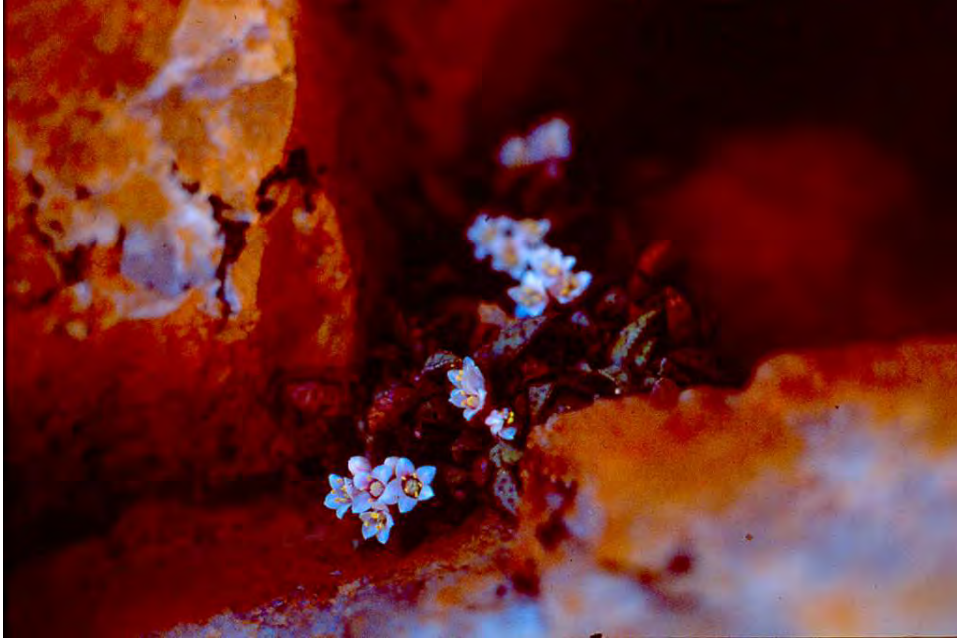


FIGURE 120c. *Crassula exilis* subsp. *sedifolia* flowering in a quartz crevice on Pellaberg.



FIGURE 120d. *Crassula exilis* subsp. *sedifolia* growing on Pellaberg.

121. *Crassula expansa* subsp. *fragilis*



FIGURE 121a. *Crassula expansa* subsp. *fragilis* growing on a dolomite cliff behind Pilgrim's Rest in Mpumalanga.



FIGURE 121b. *Crassula expansa* subsp. *fragilis* on cliffs at the White Mfolozi River in KwaZulu-Natal.

122. *Crassula foveata*



FIGURE 122a. *Crassula foveata* of Collywobbles in the Transkei region of the Eastern Cape. Propagules on the stem will root when becoming detached, forming new colonies (cloning).



FIGURE 122b. *Crassula foveata* from Collywobbles in flower at Kirstenbosch.

123. *Crassula intermedia*



FIGURE 123a. *Crassula intermedia* (Van Jaarsveld 16830) on a sandstone cliff at Wooldridge in the Eastern Cape), with *Haworthia cymbiformis* var. *ramosa* in the background.



FIGURE 123b. Cliff hugger *Crassula intermedia* growing on a shady south-facing sandstone cliff near Kirkwood in the Eastern Cape.



FIGURE 123c. *Crassula intermedia* on a sandstone cliff near Kirkwood, here sharing its habitat with *C. orbicularis* (on the left).

124. *Crassula lanuginosa* var. *lanuginosa*



FIGURE 124a. *Crassula lanuginosa* var. *lanuginosa* on a cliff at Leeukloofberg east of Graaff-Reinet in the Eastern Cape. A cliff hugger, here growing and acting as a hanger.



FIGURE 124b. *Crassula lanuginosa* var. *lanuginosa* in cultivation at Kirstenbosch.



FIGURE 124c. *Crassula lanuginosa* var. *lanuginosa* hugging a cliff at Leeukloofberg, east of Graaff-Reinet in the Eastern Cape.



FIGURE 124d. A close look at *Crassula lanuginosa* var. *lanuginosa* in cultivation at Kirstenbosch.

125. *Crassula montana* subsp. *montana*



FIGURE 125a. *Crassula montana* subsp. *montana* growing on a sandstone cliff above Skitterykloof in the Western Cape.



FIGURE 125b. *Crassula montana* subsp. *montana* on a sandstone cliff in the Doorn River Valley in the Western Cape.



FIGURE 125c. *Crassula montana* subsp. *montana* growing on a sandstone cliff on the Wolfberg in the Cedarberg in the Western Cape.



FIGURE 125d. The Doorn River Valley in the Western Cape, habitat of *Crassula montana* subsp. *montana*.



FIGURE 125e. *Crassula montana* subsp. *montana* at Blinkberg in the Western Cape.



FIGURE 125f. *Crassula montana* subsp. *montana* on a sandstone cliff on the Wolfberg of the Cedarberg in the Western Cape.



FIGURE 125g. *Crassula montana* subsp. *montana* on a sandstone cliff on the Wolfberg.

126. *Crassula montana* subsp. *quadrangularis*



FIGURE 126a. *Crassula montana* subsp. *quadrangularis* growing on a shale cliff in the Karoo in the vicinity of Koup Station near Laingsburg in the Western Cape.



FIGURE 126b. *Crassula montana* subsp. *quadrangularis* on a shale cliff near Koup Station close to Laingsburg in the Karoo.



FIGURE 126c. *Crassula montana* subsp. *quadrangularis* on a shale cliff near Koup Station near Laingsburg in the Karoo.

127. *Crassula nemorosa*



FIGURE 127a. *Crassula nemorosa* growing at Kirstenbosch (material from the vicinity of Kirkwood, Eastern Cape).



FIGURE 127b. *Crassula nemorosa* growing on shady south-facing dolomite cliffs above Konsertinakrans on the Hunsberg in southern Namibia. Plants are summer-deciduous from small tubers in the crevices.



FIGURE 127c. The habitat of *Crassula nemorosa* above Konsertinakrans on the Hunsberg in southern Namibia, Gregory Nicolson in the background.



FIGURE 127d. *Crassula nemorosa* growing on a cliff face in the Eastern Cape.

128. *Crassula orbicularis* (Luputana form)



FIGURE 128a. *Crassula orbicularis* (Luputana form) growing at Waterfall Bluff on the Eastern Cape coast just south of Luputana Gorge.



FIGURE 128b. Luputana form of *Crassula orbicularis* at Waterfall Bluff on the Eastern Cape coast just south of Luputana Gorge.



FIGURE 128c. Waterfall Bluff in the Eastern Cape, the habitat of *Crassula orbicularis*. The Lupatana form of the species is restricted to sheer cliff faces.

129. *Crassula peculiaris*



FIGURE 129a. *Crassula peculiaris* on a sandstone cliff at the top of the Groot Swartberg, Swartberg Pass in the Western Cape.



FIGURE 129b. Sandstone cliffs of the Groot Swartberg, the habitat of *Crassula peculiaris*.

130. *Crassula pellucida* subsp. *spongiosa*



FIGURE 130a. *Crassula pellucida* subsp. *spongiosa* among moss on a south-facing slope on Witteberg sandstone cliffs at Du Toitskloof in the Western Cape.



FIGURE 130b. Sheer south-facing cliffs of Witteberg, habitat of *Crassula pellucida* subsp. *spongiosa* at Du Toitskloof in the Western Cape.



FIGURE 130c. Witteberg, Du Toitskloof in the Western Cape, the habitat of *Crassula pellucida* subsp. *spongiosa*.



FIGURE 130d. *Crassula pellucida* subsp. *spongiosa* growing among moss on a south-facing sandstone slope of the Witteberg.



131. *Crassula perforata* subsp. *kougaensis*



FIGURE 131a. *Crassula perforata* subsp. *kougaensis* in habitat at the Kouga Dam in the Eastern Cape.



FIGURE 131b. *Crassula perforata* subsp. *kougaensis* in cultivation at Kirstenbosch (material from Kouga Dam, Eastern Cape).



FIGURE 131c. *Crassula perforata* subsp. *kougaensis* in cultivation at Kirstenbosch (material from Kouga Dam, Eastern Cape). Note the compact leaves.



FIGURE 131d. *Crassula perforata* subsp. *kougaensis* in its habitat at the Kouga Dam.



132. *Crassula perforata* subsp. *perforata*



FIGURE 132a. *Crassula perforata* subsp. *perforata* in cultivation at Kirstenbosch.



FIGURE 132b. Cliff-face form of *Crassula perforata* at the Mzimvubu River in the Transkei region, Eastern Cape.



FIGURE 132c. Shale cliffs along the Mzimvubu River in the Eastern Cape, the habitat of *Crassula perforata* subsp. *perforata*.

133. *Crassula pseudohemisphaerica*



FIGURE 133a. *Crassula pseudohemisphaerica* on a south-facing quartzitic sandstone cliff at Skouerfontein. Other plants include *Tylecodon paniculatus* (right), *T. viridiflorus* (back).



FIGURE 133b. *Crassula pseudohemisphaerica* growing on quartz cliffs at Gemsbokvlei, Vyftienmyl se Berge near Port Nolloth in the Richtersveld in the Northern Cape.



FIGURE 133c. The cliff-face habitat at Skouerfontein at Eksteenfontein in the Richtersveld, habitat of *Crassula pseudohemisphaerica*.



FIGURE 133d. *Crassula pseudohemisphaerica* growing on sandstone cliffs on Kuamsibberg at Hunsberg in southern Namibia.

134. *Crassula pubescens* subsp. *rattrayi*



FIGURE 134a. *Crassula pubescens* subsp. *rattrayi* growing at Kirstenbosch (material from Olievenhoutberg, Graaff-Reinet).



FIGURE 134b. *Crassula pubescens* subsp. *rattrayi* growing on Olievenhoutsberg near Graaff-Reinet.

135. *Crassula rupestris* subsp. *marnieriana*



FIGURE 135a. *Crassula rupestris* subsp. *marnieriana* growing on south-facing cliffs at Buffelspoort west of Ladismith in the Western Cape.



FIGURE 135b. Buffelspoort west of Ladismith in the Western Cape, habitat of *Crassula rupestris* subsp. *marnieriana*.



FIGURE 135c. *Crassula rupestris* subsp. *marnieriana* growing on the lower slopes of Touwsberg in the Western Cape.



FIGURE 135d. *Crassula rupestris* subsp. *marnieriana* here growing sympatrically with *C. rupestris* subsp. *rupestris* on cliffs above the Huis River Pass in the Western Cape.

136. *Crassula rupestris* subsp. *rupestris* (cliff-face form)



FIGURE 136a. Cliff-face form of *Crassula rupestris* subsp. *rupestris* growing on the northern cliff face of Table Mountain at Cape Town in the Western Cape.



FIGURE 136b. North-facing sandstone cliff face of Table Mountain in the Western Cape, the habitat of the cliff-face form of *Crassula rupestris* subsp. *rupestris*.

137. *Crassula sediflora* var. *sediflora*



FIGURE 137a. *Crassula sediflora* var. *sediflora* where it grows on a steep granite slope near Cliffendale, Durban in KwaZulu-Natal.



FIGURE 137b. *Crassula sediflora* var. *sediflora* on a granite cliff near Cliffendale, Durban in KwaZulu-Natal.

138. *Crassula sericea* var. *sericea*



FIGURE 138a. *Crassula sericea* var. *sericea* on sandstone cliffs in the Gannakouriep in the Richtersveld in the Northern Cape. The leaves are brittle and will root when they become detached.



FIGURE 138b. *Crassula sericea* var. *sericea* growing on cliffs at Jenkinskop in the Richtersveld in the Northern Cape.



FIGURE 138c. Cliffs at Vandersterberg in the Richtersveld in the Northern Cape, the habitat of *Crassula sericea* var. *sericea*.

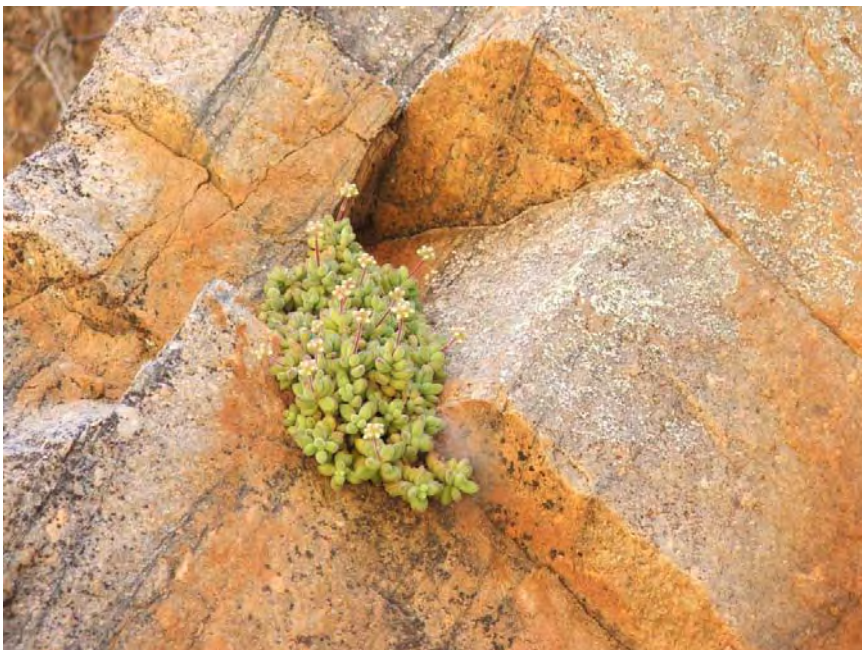


FIGURE 138d. *Crassula sericea* var. *sericea* growing on sheer sandstone cliffs at Vandersterberg in the Richtersveld in the Northern Cape.

139. *Crassula setulosa* var. *jenkinsii*



FIGURE 139a. *Crassula setulosa* var. *jenkinsii* growing on cliffs at Fairlands near Roodepoort in Gauteng.



FIGURE 139b. Cliffs at Chuniespoort, habitat of *Crassula setulosa* var. *jenkinsii*.



FIGURE 139c & 139d. *Crassula setulosa* var. *jenkinsii* growing on cliffs at the Hartbeespoort Dam (139c) and at Fairlands (139d) near Roodepoort in Gauteng. The propagules on the inflorescence (139d) will root if they become detached and will then form new plants (backup cloning).

140. *Crassula setulosa* var. *longiciliata*



FIGURE 140a. Sentinel cliffs of the Drakensberg, habitat of *Crassula setulosa* var. *longiciliata*.



FIGURE 140b. *Crassula setulosa* var. *longiciliata* on a south-facing sandstone cliff at Steenkampsberg.

141. *Crassula setulosa* var. *setulosa*



FIGURE 141a. *Crassula setulosa* var. *setulosa* growing on cliffs along the Blyderivierspoort in Mpumalanga.



FIGURE 141b. *Crassula setulosa* var. *setulosa* growing on cliffs along the Blyderivierspoort in Mpumalanga.



FIGURE 141c. Escarpment cliffs of Steenkampberg, habitat of *Crassula setulosa* var. *setulosa*.

142. *Crassula sladenii*



FIGURE 142a. *Crassula sladenii* growing on dolomite cliffs on Sonberg, Orange River Valley in southern Namibia.



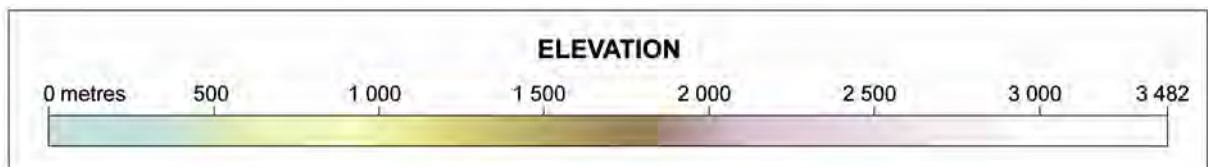
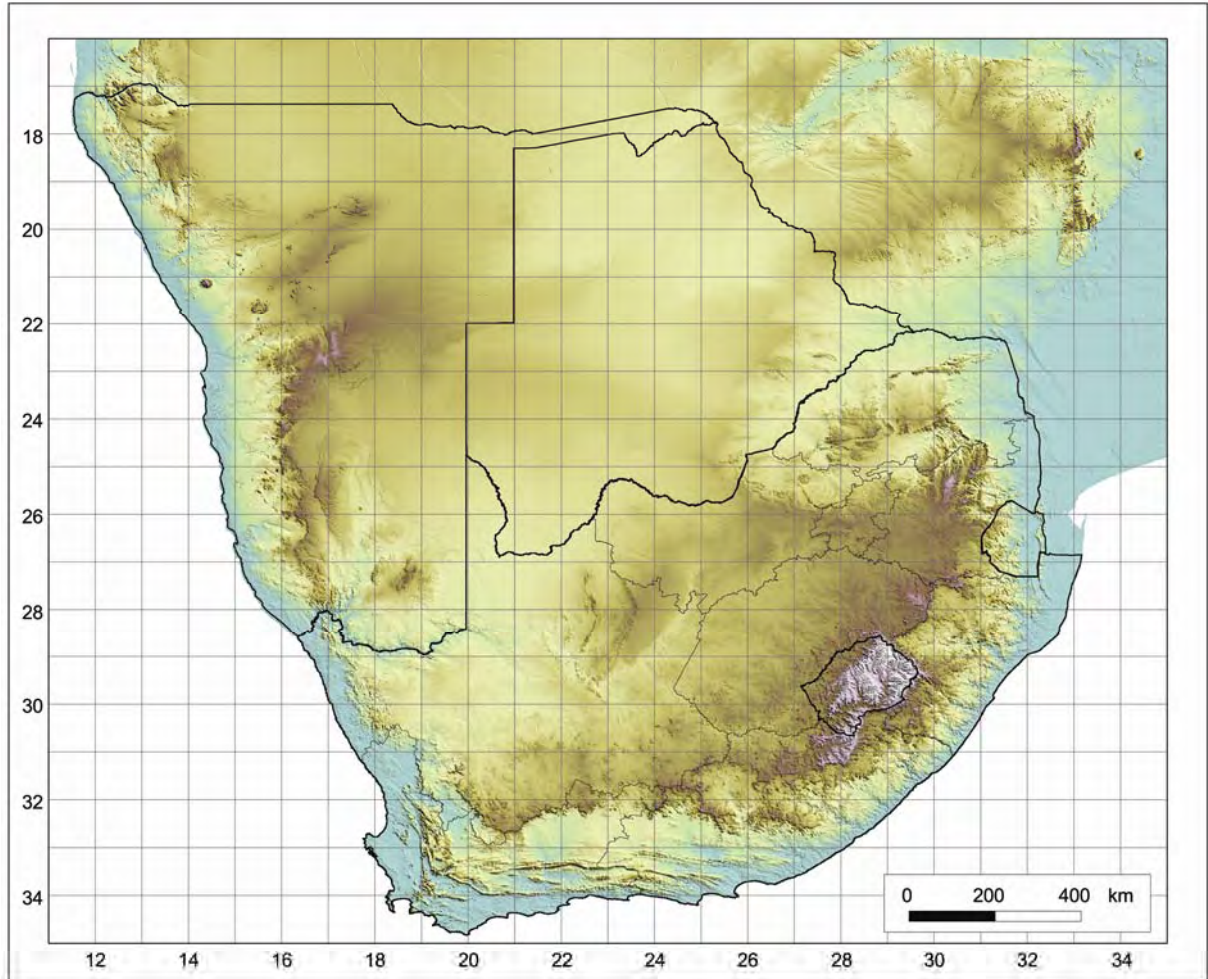
FIGURE 142b. Getting close to a young plant of *Crassula sladenii* growing on the dolomite cliffs of Sonberg, Orange River Valley in southern Namibia.



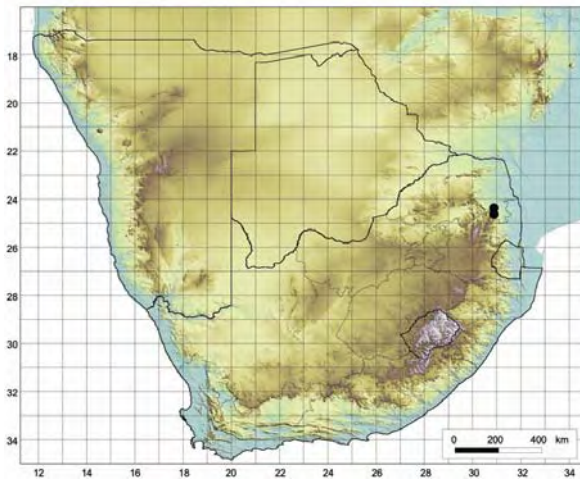
FIGURE 142c. *Crassula sladenii* on dolomite cliffs on Sonberg at the Orange River Valley in southern Namibia.

DISTRIBUTION MAPS

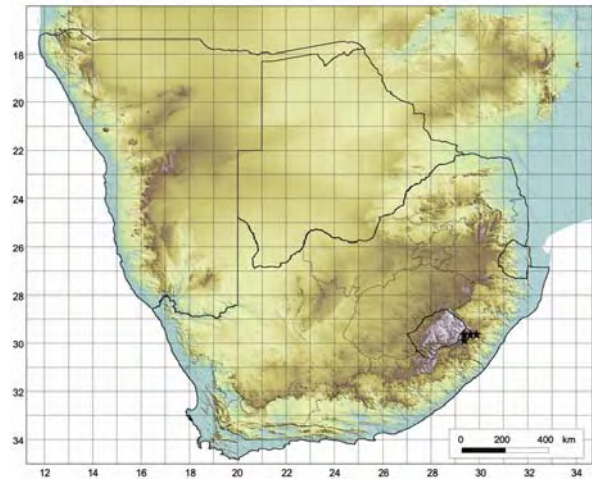
MASTER MAP



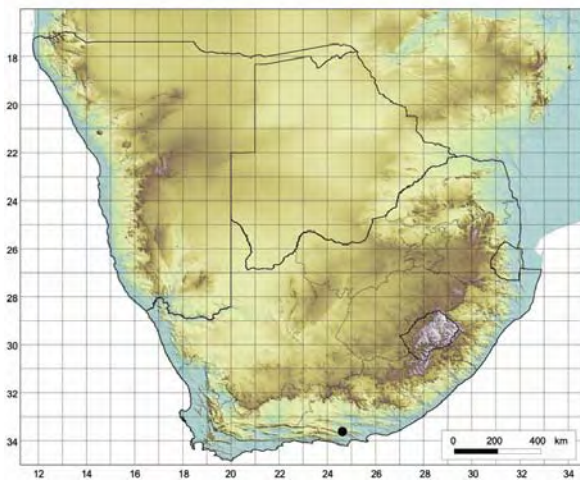
SYMBOLS	
●	sandstone; quartzite (sedimentary)
▲	dolomite (sedimentary)
★	shale; mudstone (sedimentary)
■	granite; dolerite; rhyolite (igneous)
◈	conglomerate (sedimentary)
●	geological-preference varied



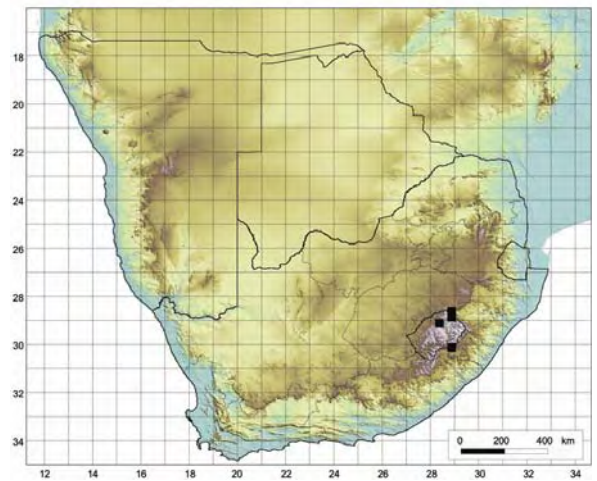
MAP 1. *Pyrrosia schimperiana*.



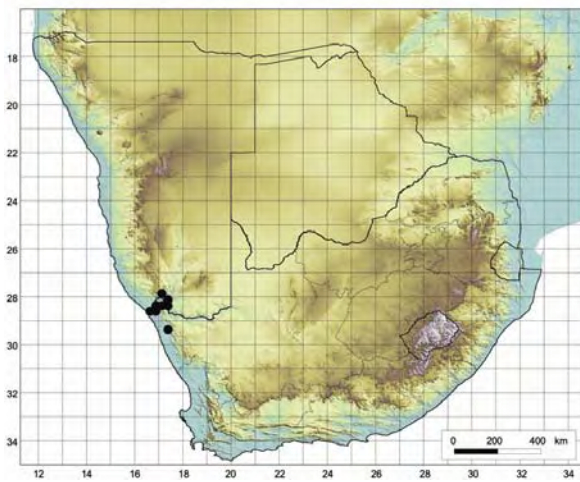
MAP 2. *Cyrtanthus falcatus*.



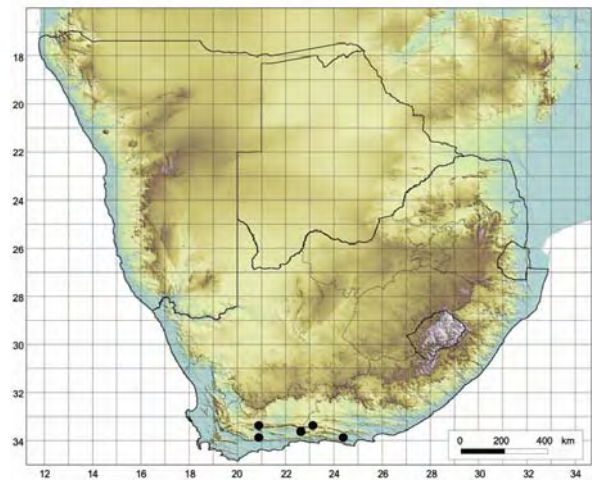
MAP 3. *Cyrtanthus flammosus*.



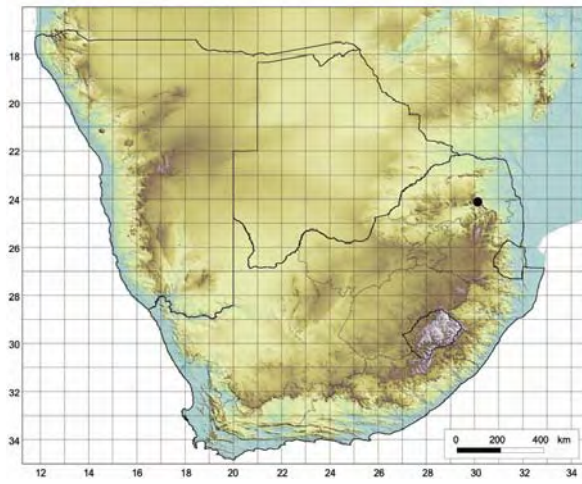
MAP 4. *Cyrtanthus flanagani*.



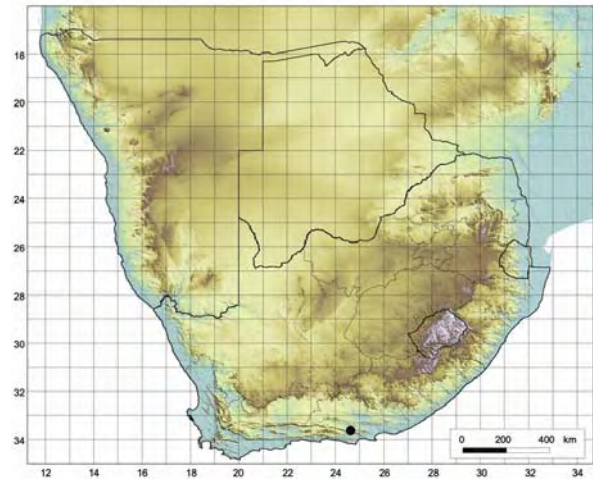
MAP 5. *Cyrtanthus herrei*.



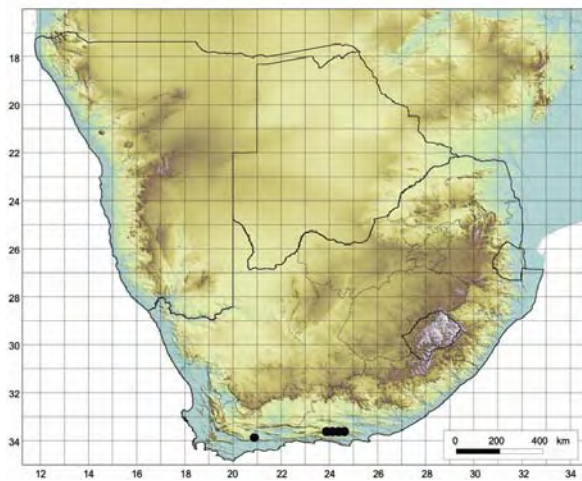
MAP 6. *Cyrtanthus inaequalis*.



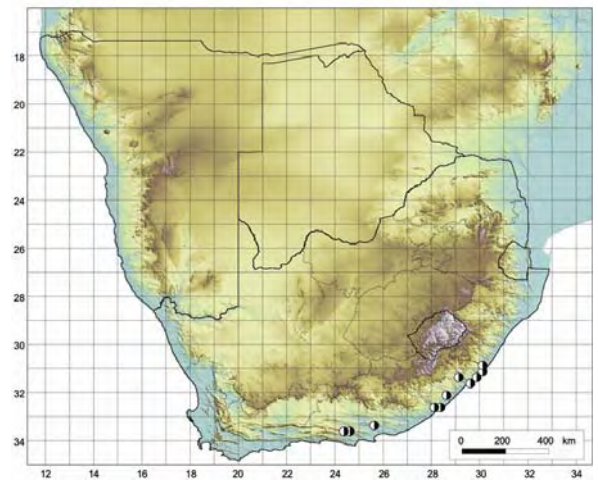
MAP 7. *Cyrtanthus junodii*.



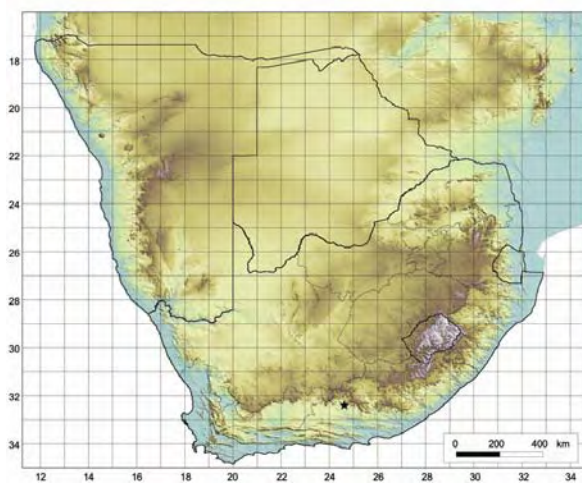
MAP 8. *Cyrtanthus labiatus*.



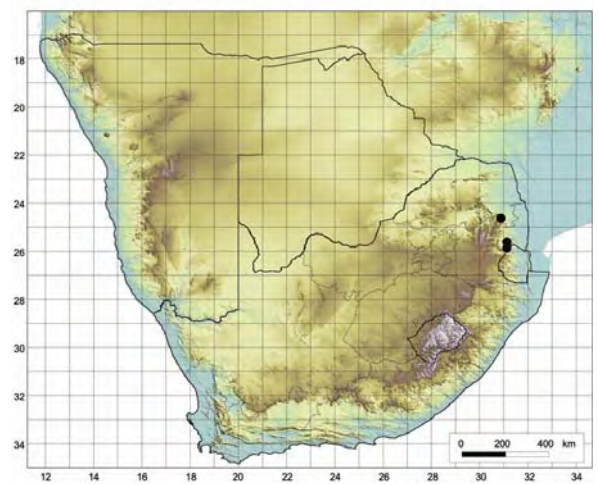
MAP 9. *Cyrtanthus montanus*.



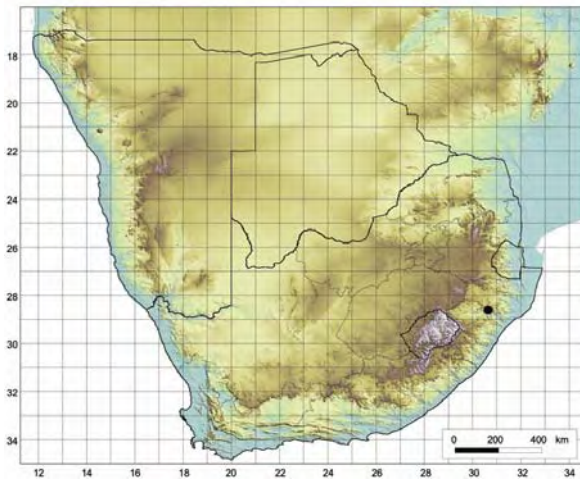
MAP 10. *Haemanthus albiflos*.



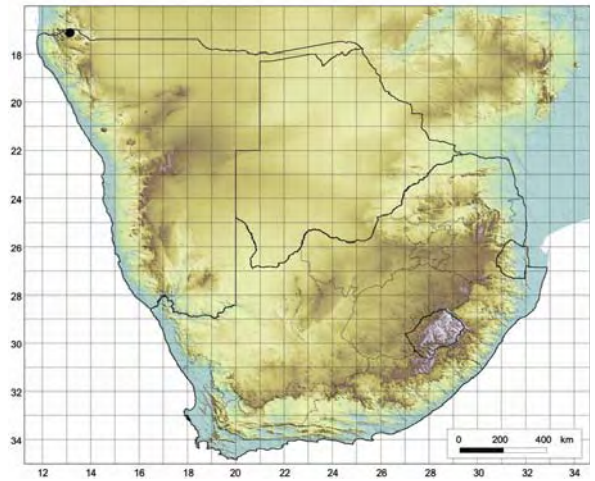
MAP 11. *Haemanthus humilis* subsp. *humilis*.



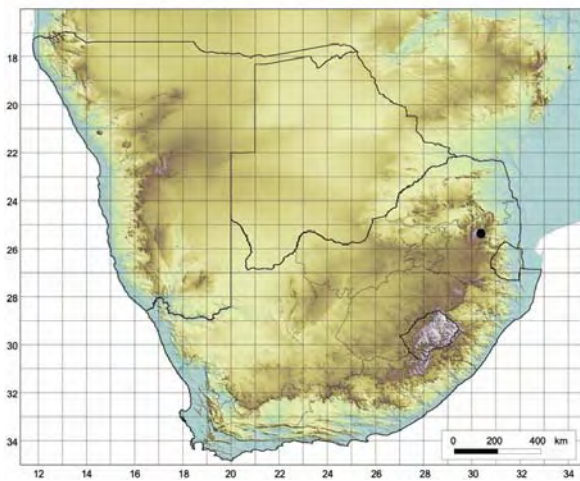
MAP 12. *Haemanthus paucifolius*.



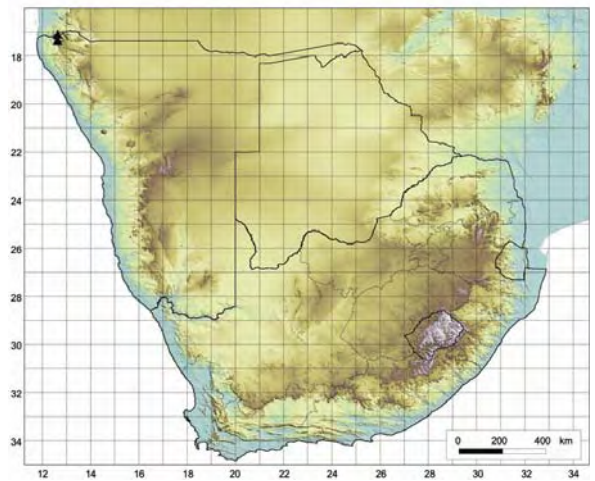
MAP 13. *Aloe arborescens* subsp. *mzimnyati*.



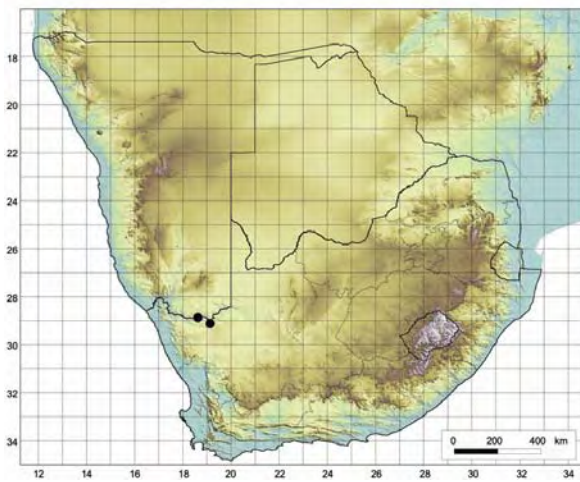
MAP 14. *Aloe catengiana* (Omavanda form).



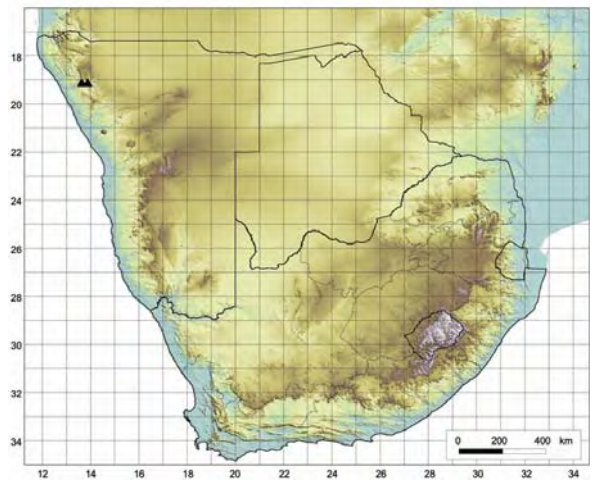
MAP 15. *Aloe challsii*.



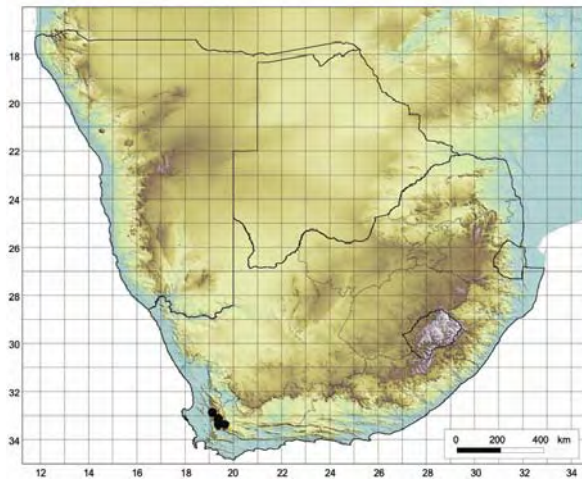
MAP 16. *Aloe corallina*.



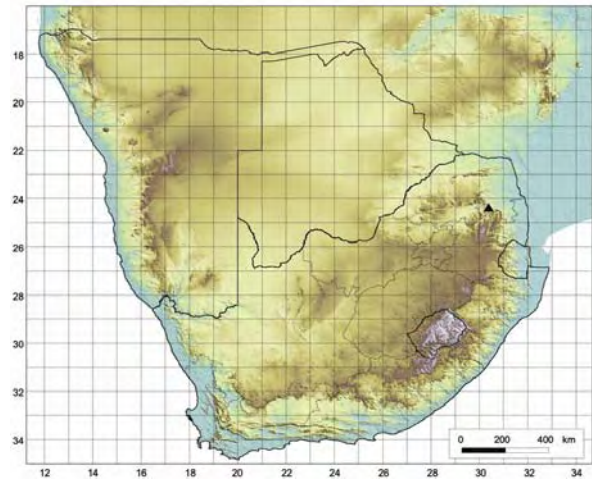
MAP 17. *Aloe dabenorisana*.



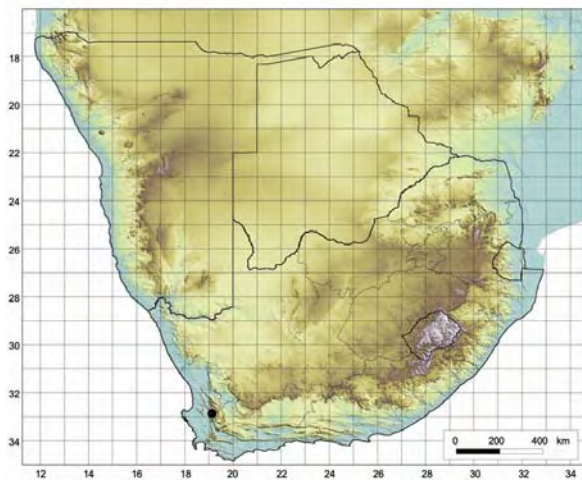
MAP 18. *Aloe dewinteri*.



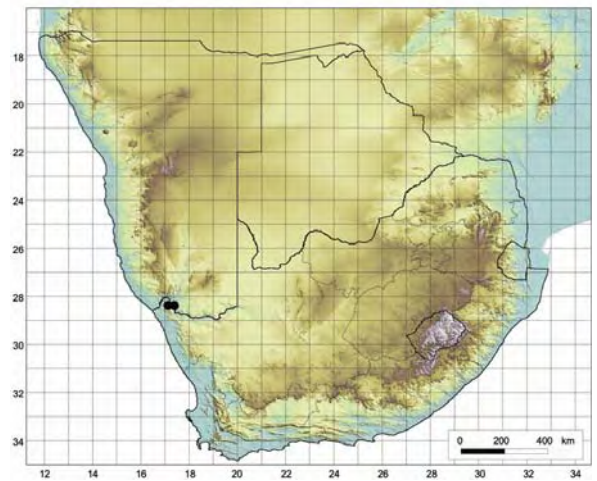
MAP 19. *Aloe haemanthifolia*.



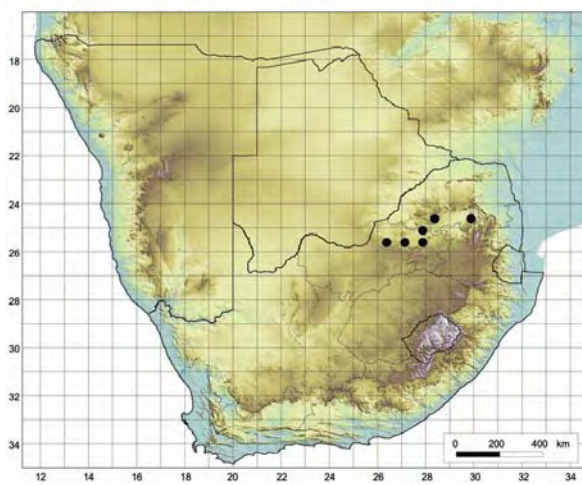
MAP 20. *Aloe hardyi*.



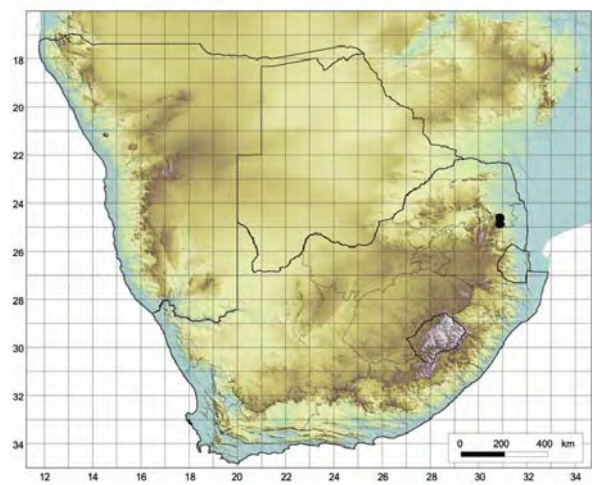
MAP 21. *Aloe kouebokkeveldensis*.



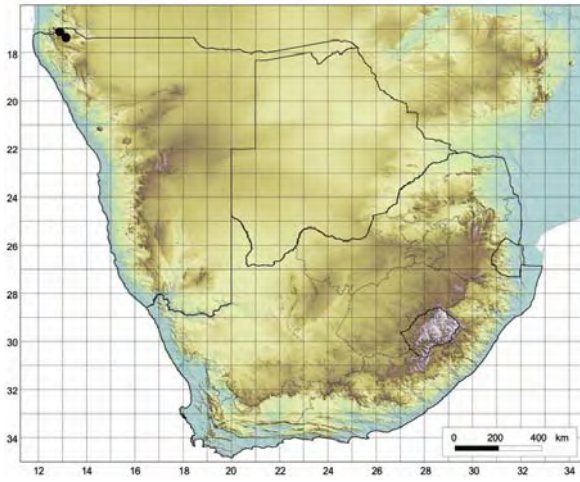
MAP 22. *Aloe meyeri*.



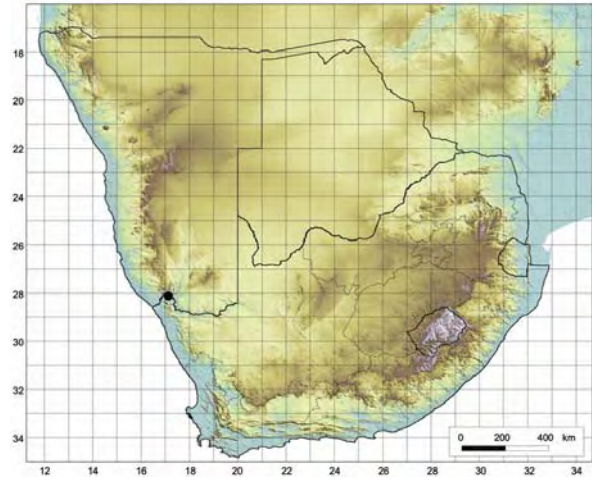
MAP 23. *Aloe mutabilis*.



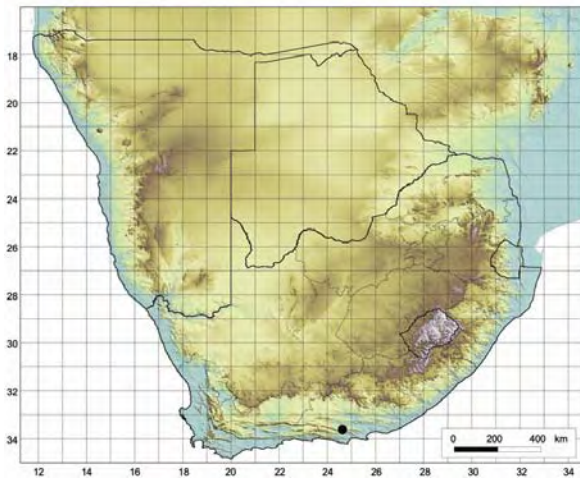
MAP 24. *Aloe nubigena*.



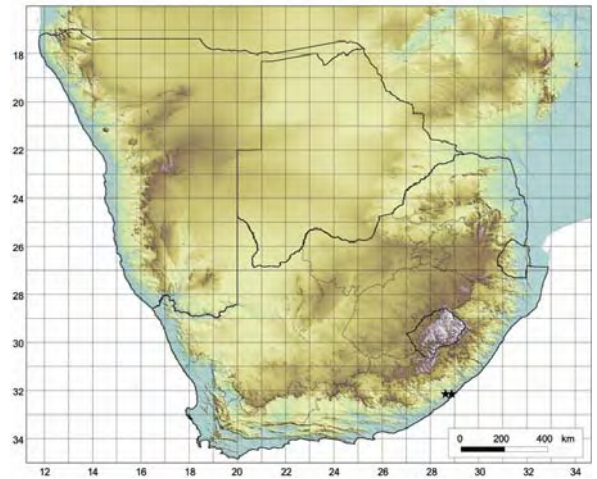
MAP 25. *Aloe omavandae*.



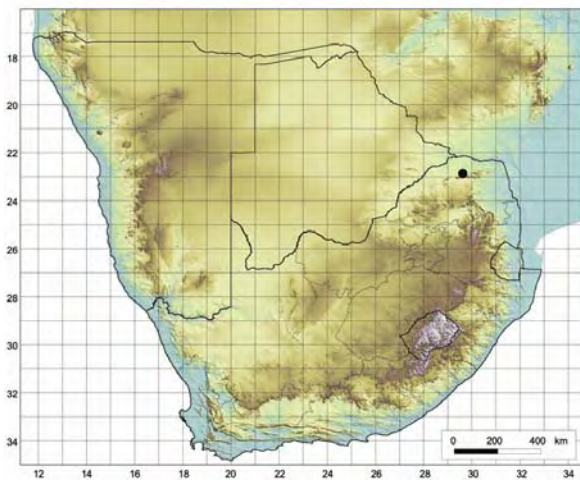
MAP 26. *Aloe pavelkae*.



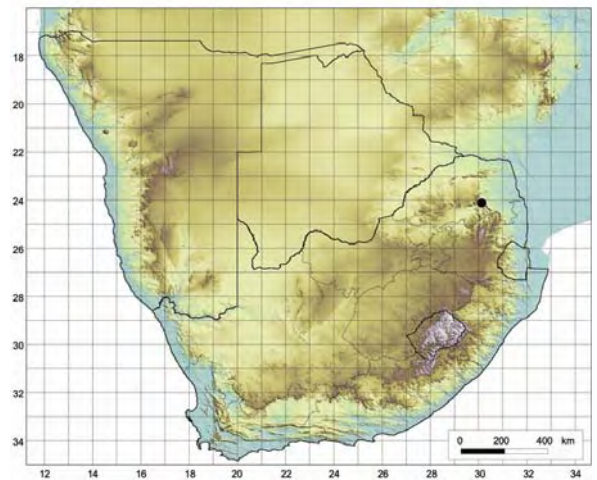
MAP 27. *Aloe pictifolia*.



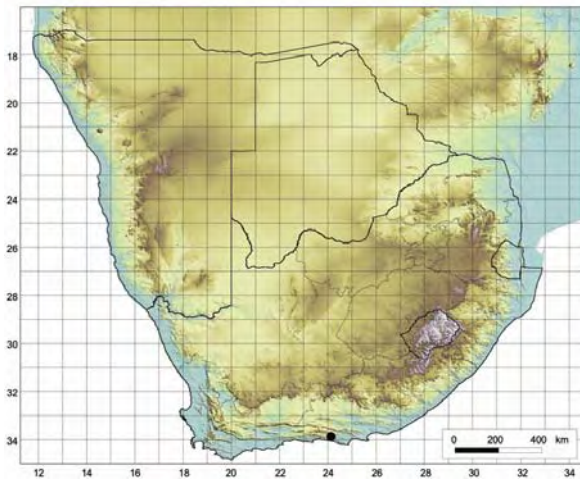
MAP 28. *Aloe reynoldsii*.



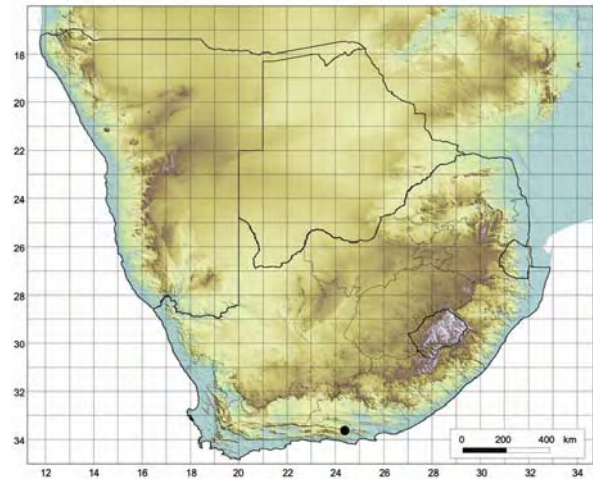
MAP 29. *Aloe soutpansbergensis*.



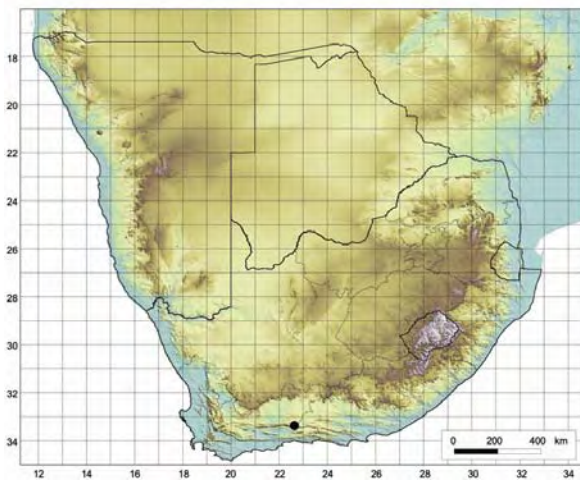
MAP 30. *Aloe thompsoniae*.



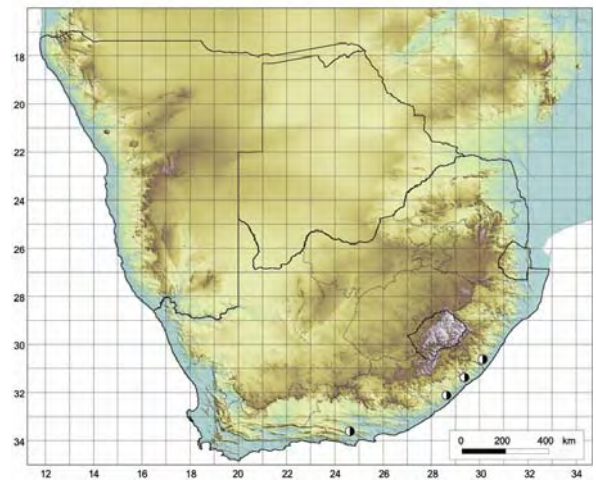
MAP 31. *Bulbine cremnophila*.



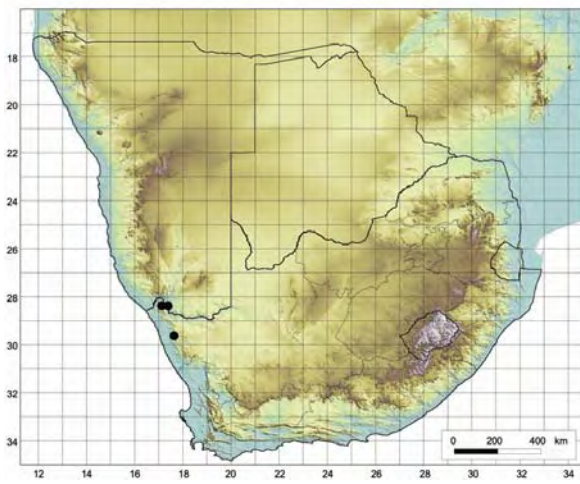
MAP 32. *Bulbine latifolia* var. *curvata*.



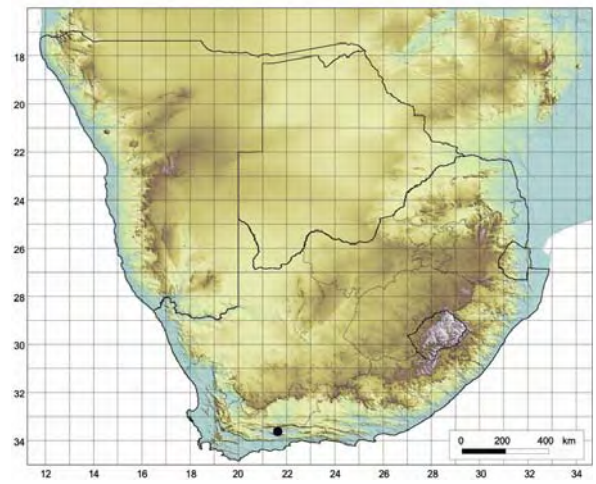
MAP 33. *Bulbine meiringii*.



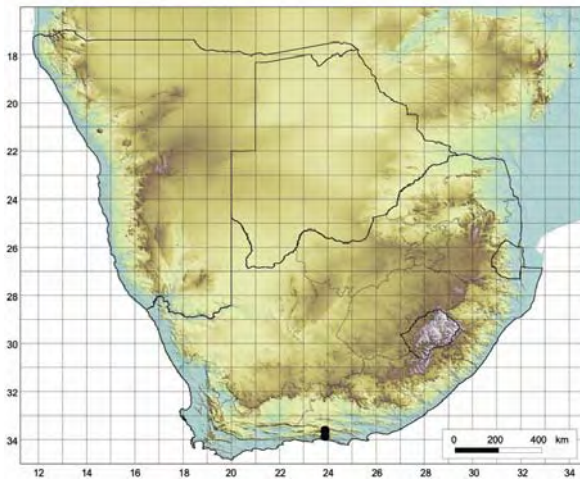
MAP 34. *Bulbine natalensis*.



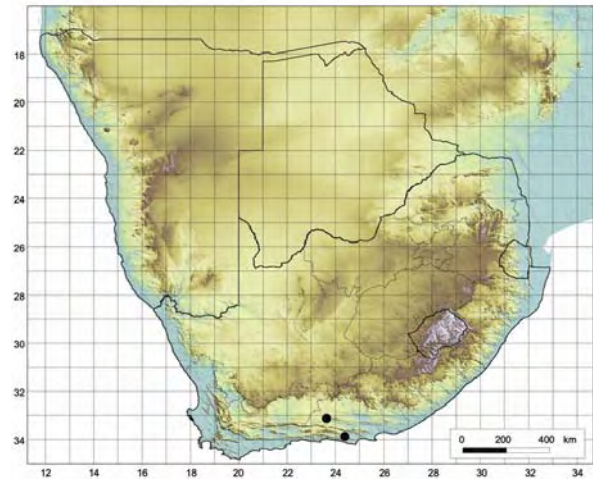
MAP 35. *Bulbine pendens*.



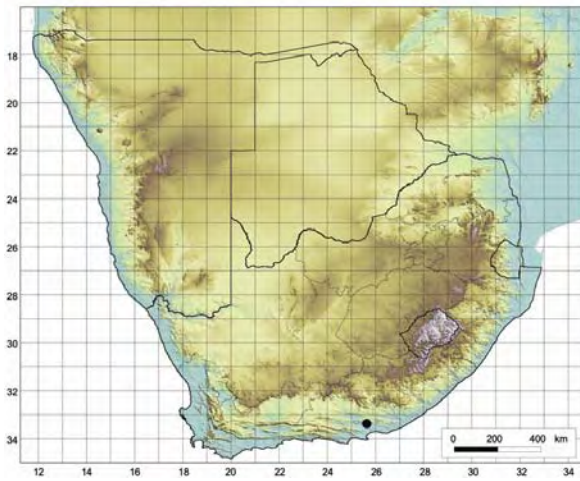
MAP 36. *Bulbine ramosa*.



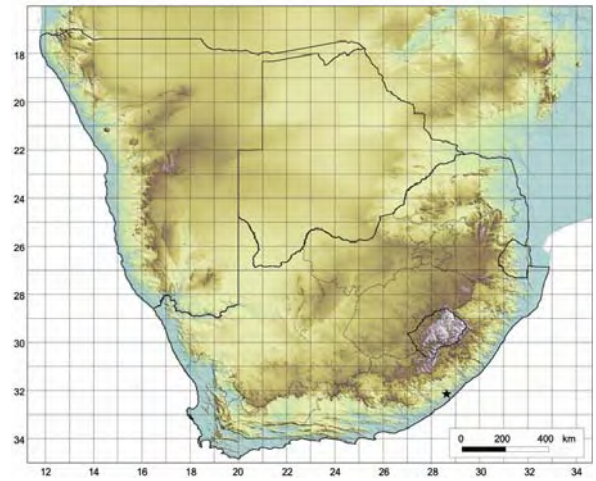
MAP 37. *Bulbine retinens*.



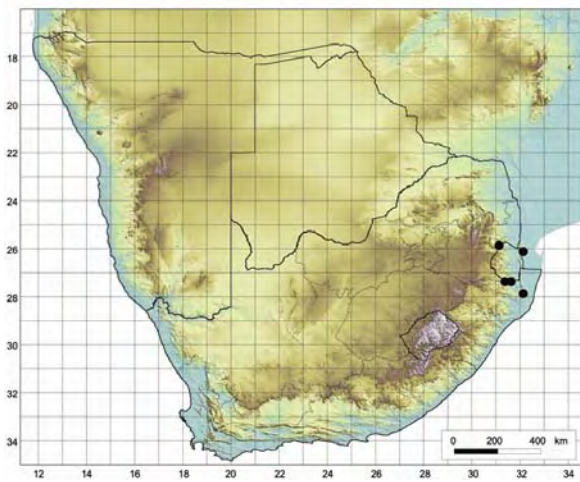
MAP 38. *Bulbine rupicola*.



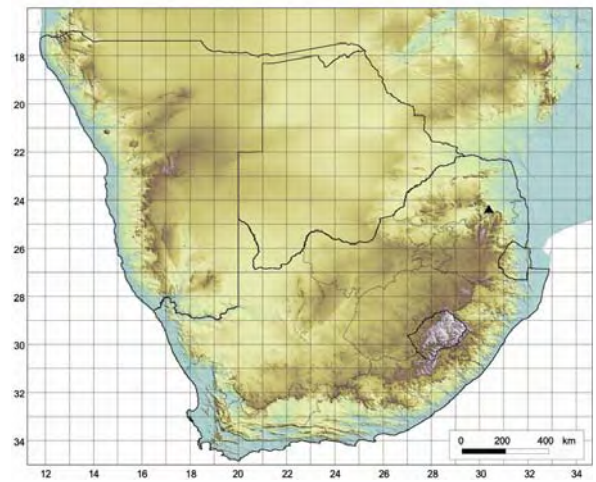
MAP 39. *Bulbine suurbergensis*.



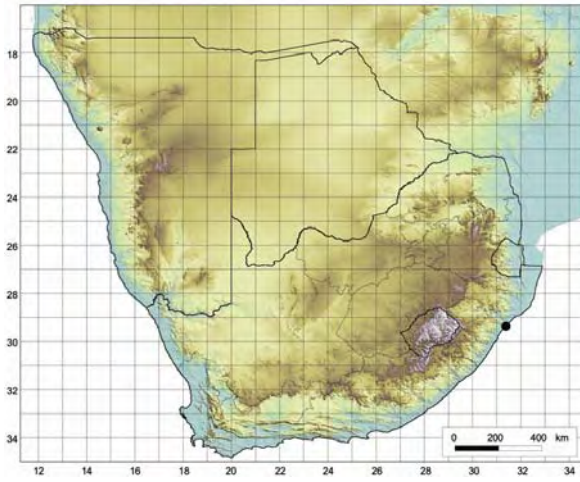
MAP 40. *Bulbine thomasiae*.



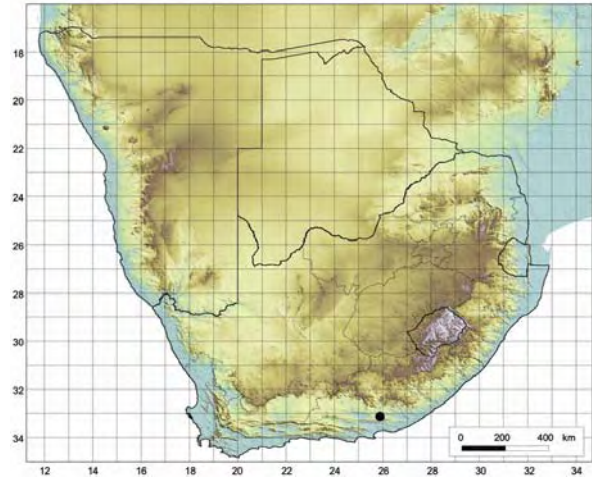
MAP 41. *Gasteria batesiana* var. *batesiana*.



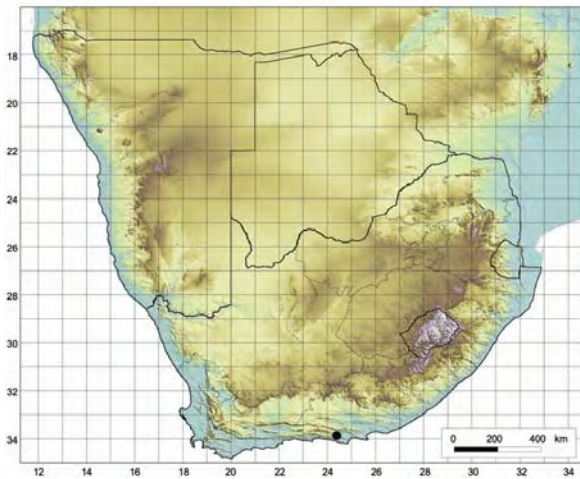
MAP 42. *Gasteria batesiana* var. *dolomitica*.



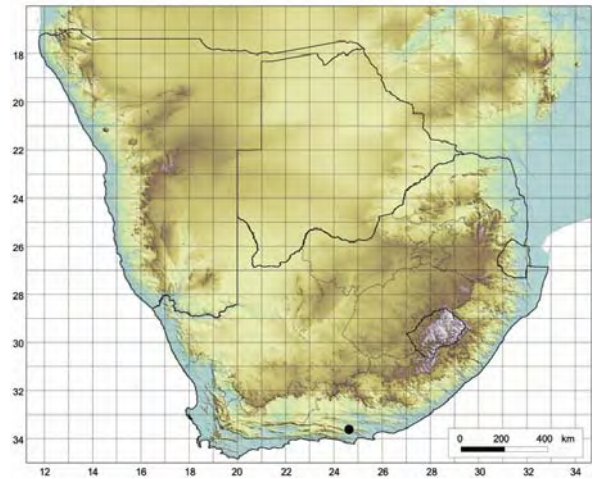
MAP 43. *Gasteria croucheri* subsp. *pendulifolia*.



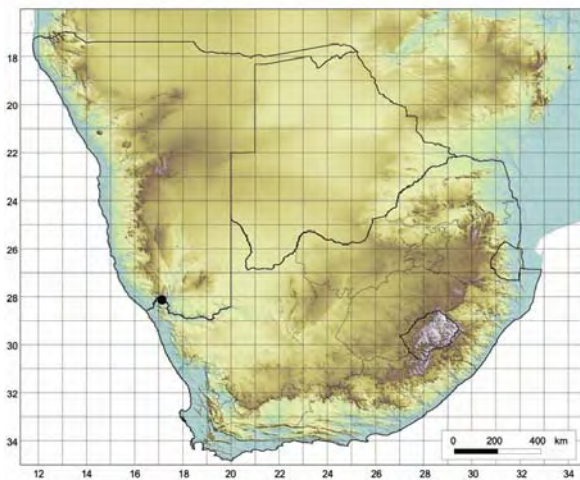
MAP 44. *Gasteria doreeniae*.



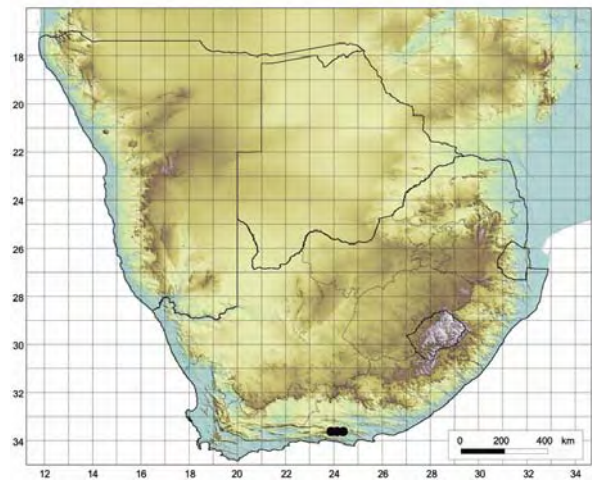
MAP 45. *Gasteria glauca*.



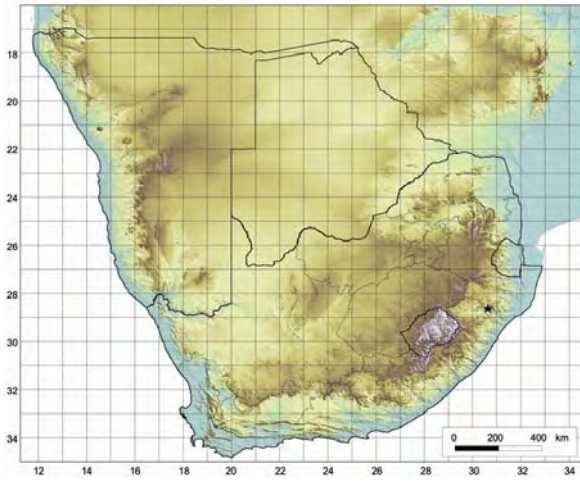
MAP 46. *Gasteria glomerata*.



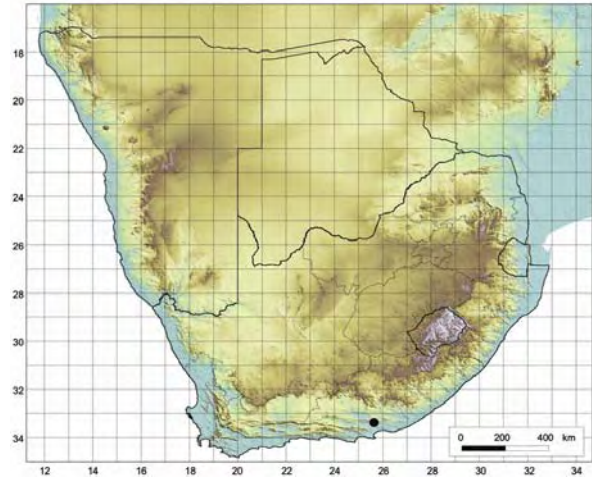
MAP 47. *Gasteria pillansii* var. *ernesti-ruschii*.



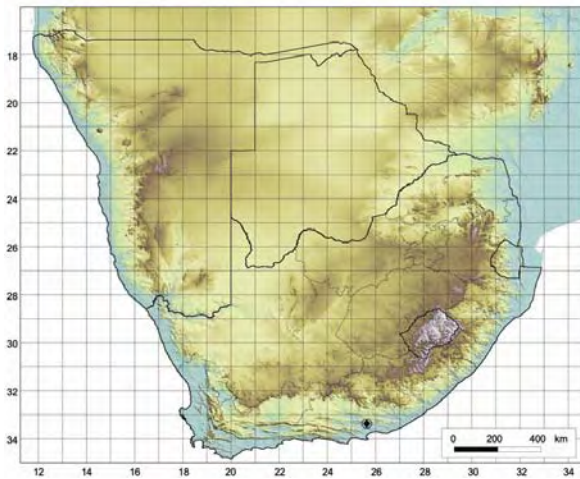
MAP 48. *Gasteria rawlinsonii*.



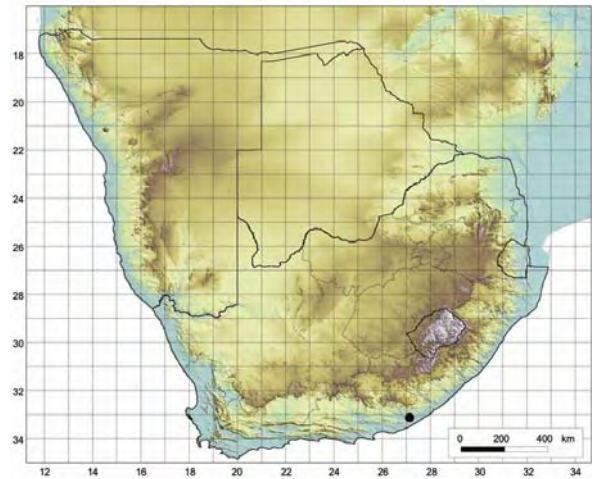
MAP 49. *Gasteria tukhelensis*.



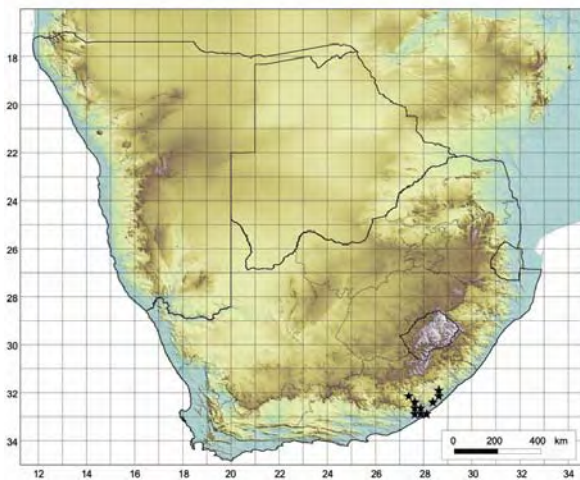
MAP 50. *Haworthia angustifolia* var. *baylissii*.



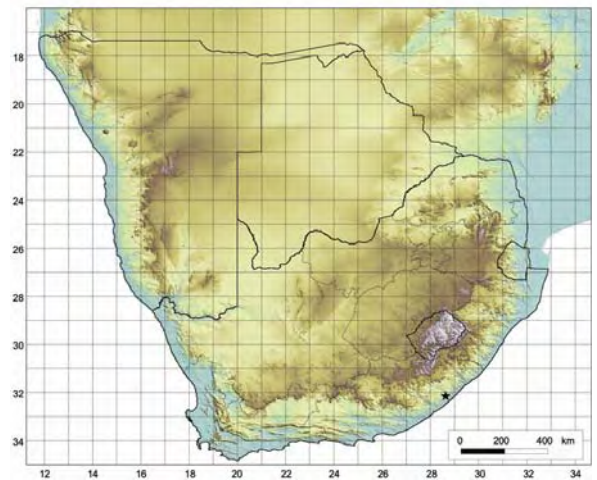
MAP 51. *Haworthia attenuata* var. *attenuata*.



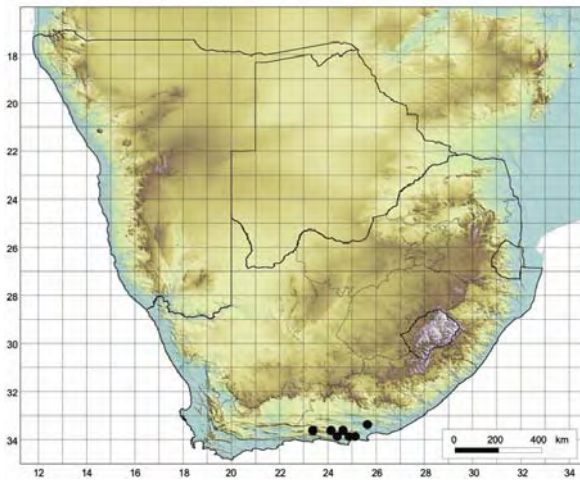
MAP 52. *Haworthia cymbiformis* var. *ramosa*.



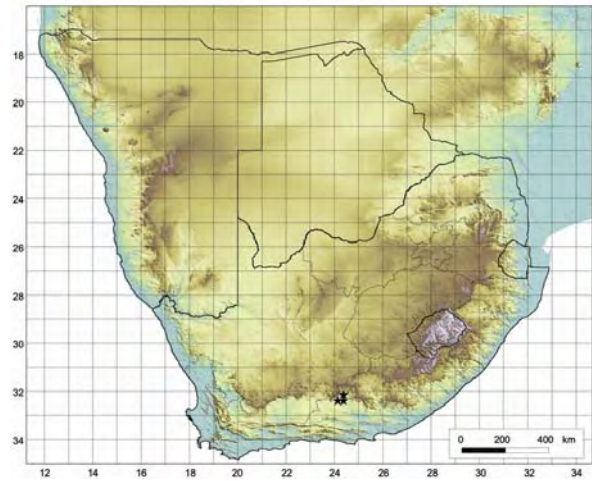
MAP 53. *Haworthia cymbiformis* var. *setulifera*.



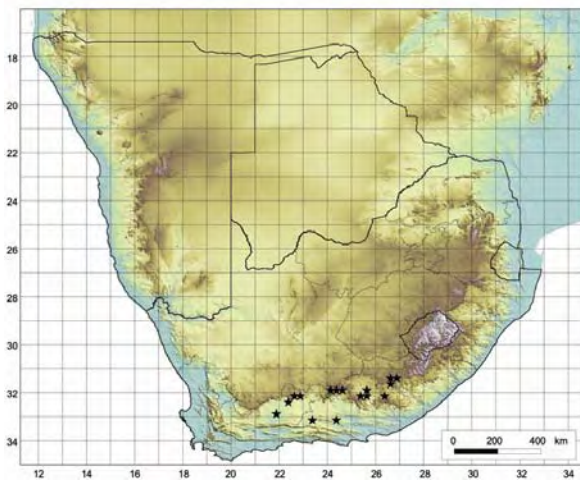
MAP 54. *Haworthia glabrata*.



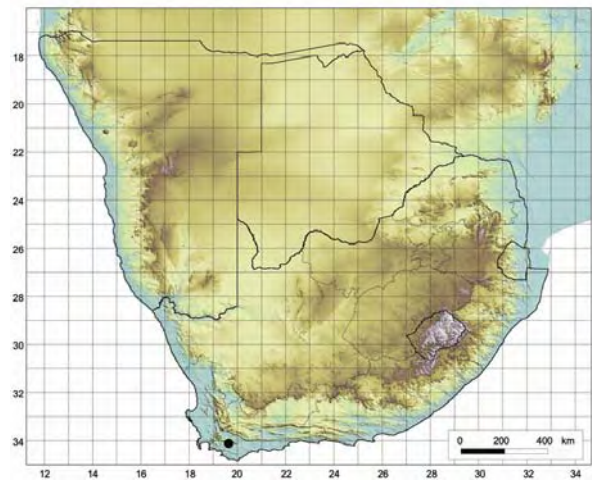
MAP 55. *Haworthia gracilis* var. *picturata*.



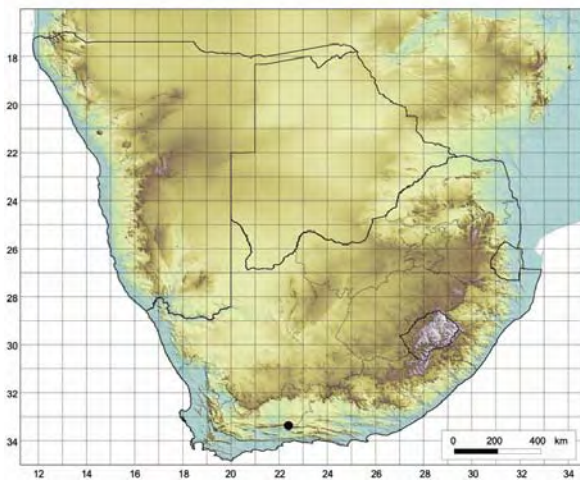
MAP 56. *Haworthia marumiana* var. *batesiana*.



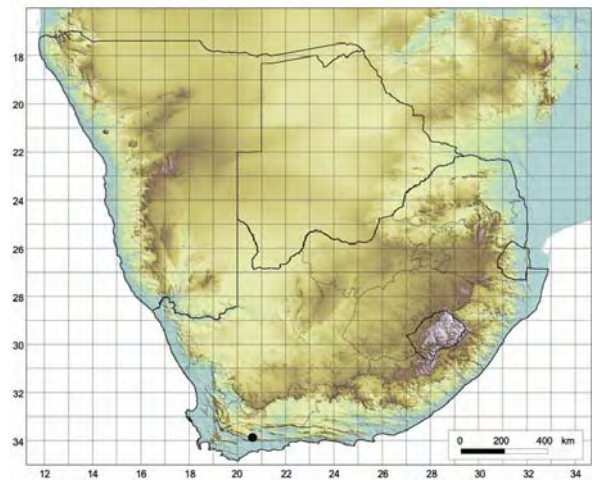
MAP 57. *Haworthia marumiana* var. *marumiana*.



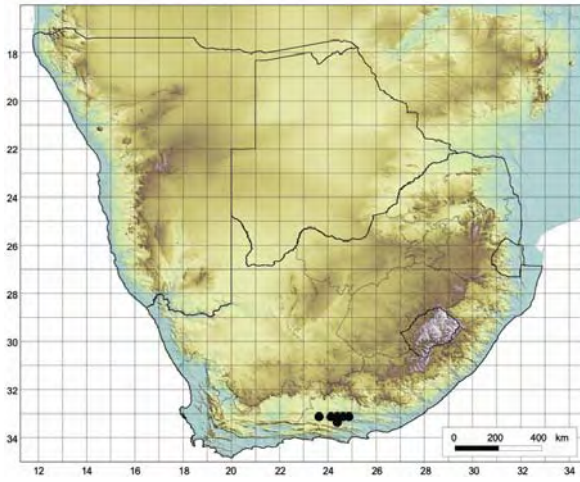
MAP 58. *Haworthia mirabilis* var. *consanguinea*.



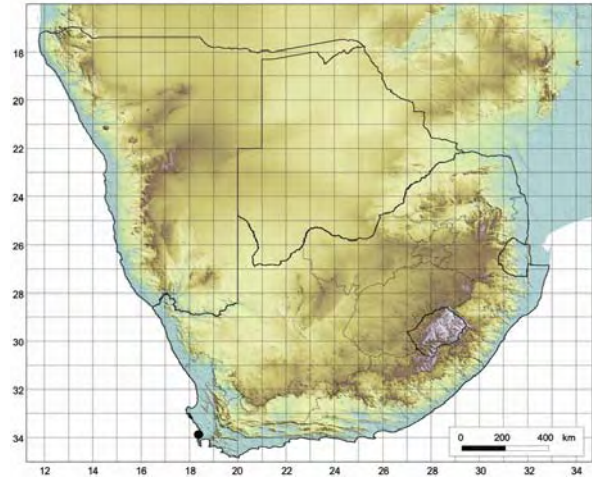
MAP 59. *Haworthia scabra* var. *starkiana*.



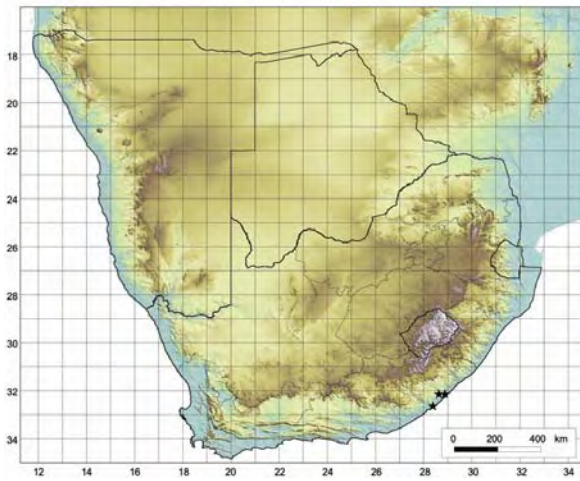
MAP 60. *Haworthia turgida* var. *turgida*.



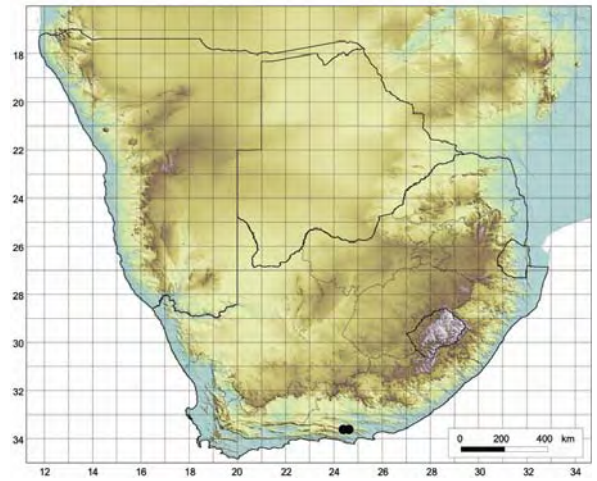
MAP 61. *Haworthia zantneriana*.



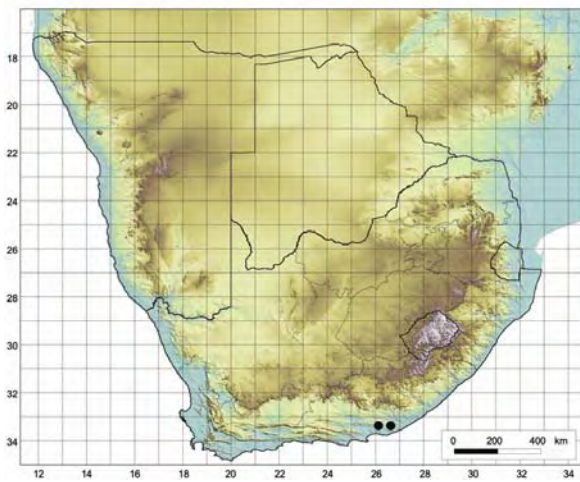
MAP 62. *Trachyandra tabularis*.



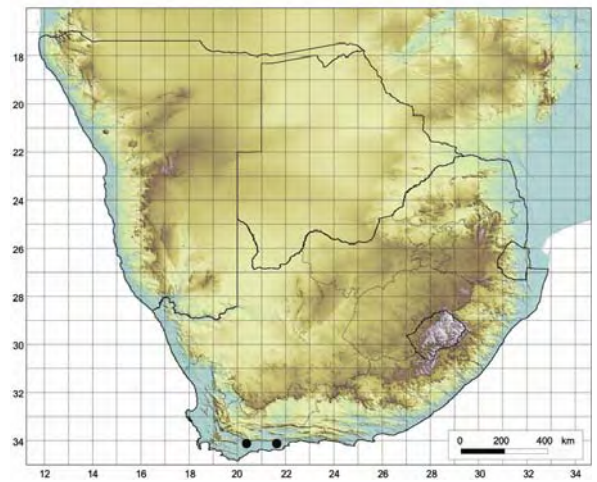
MAP 63. *Albuca batteniana*.



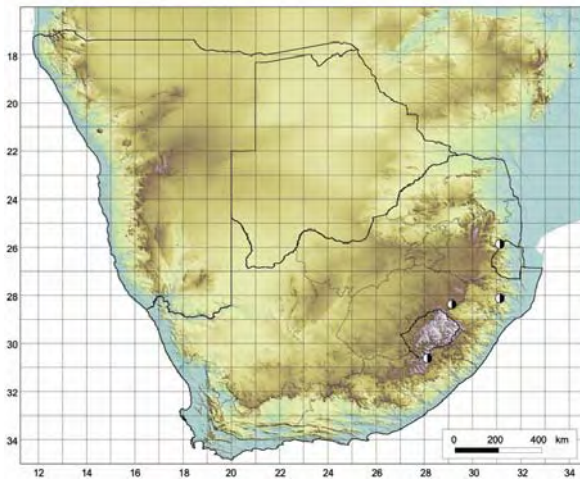
MAP 64. *Albuca cremnophila*.



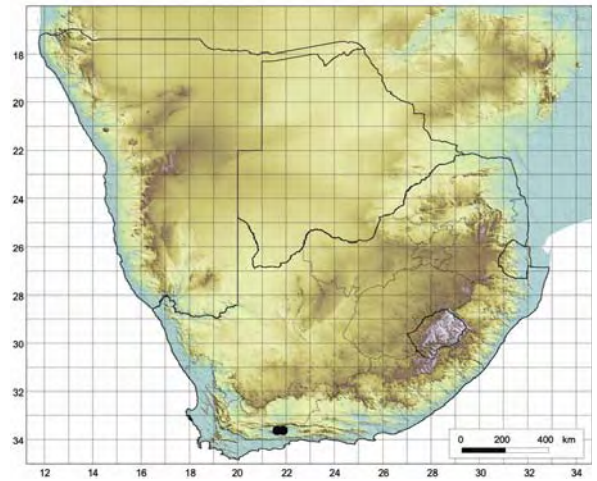
MAP 65. *Albuca crudenii*.



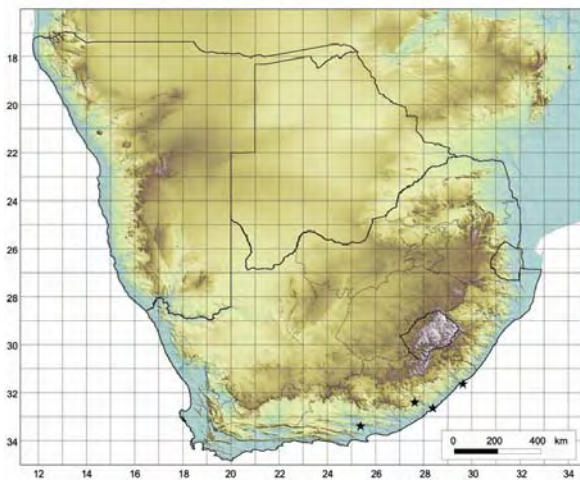
MAP 66. *Albuca kirstenii*.



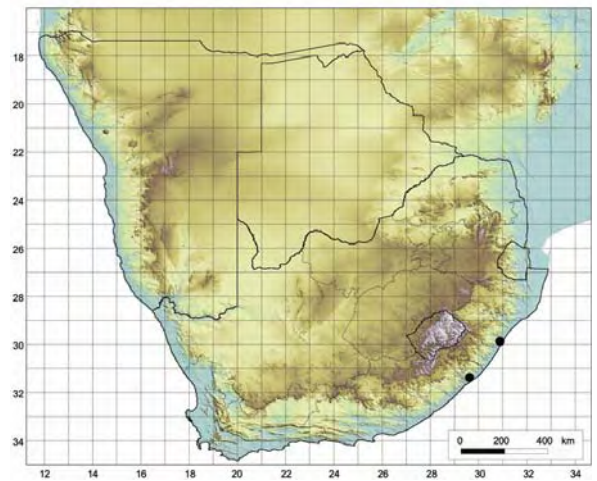
MAP 67. *Albuca shawii*.



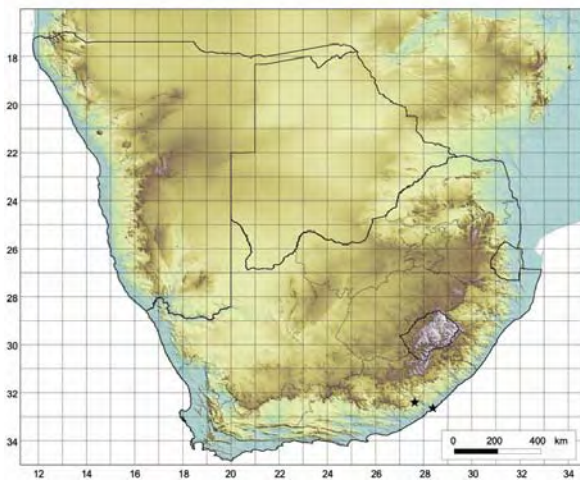
MAP 68. *Albuca thermarum*.



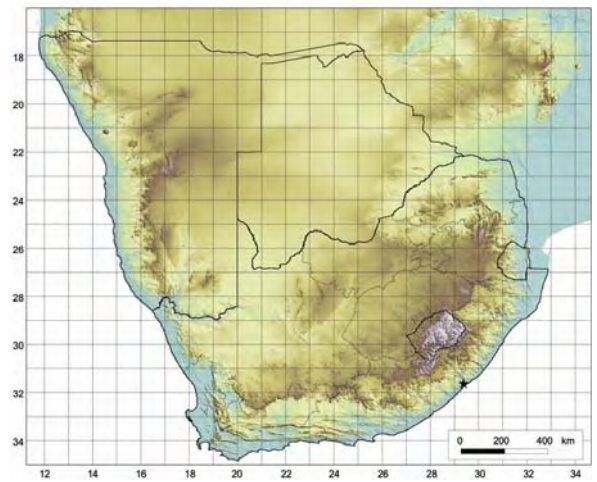
MAP 69. *Drimia cremnophila*.



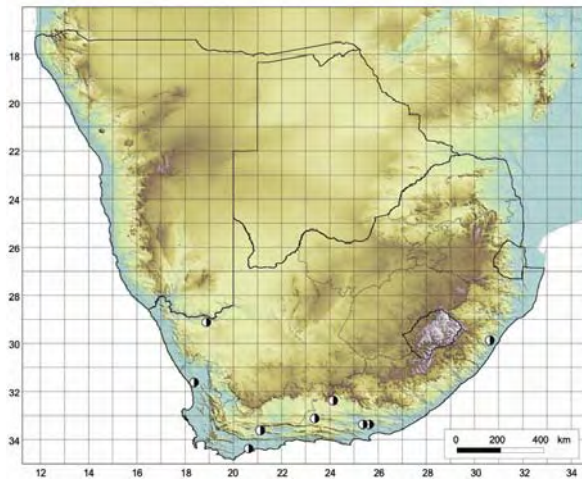
MAP 70. *Drimia flagellaris*.



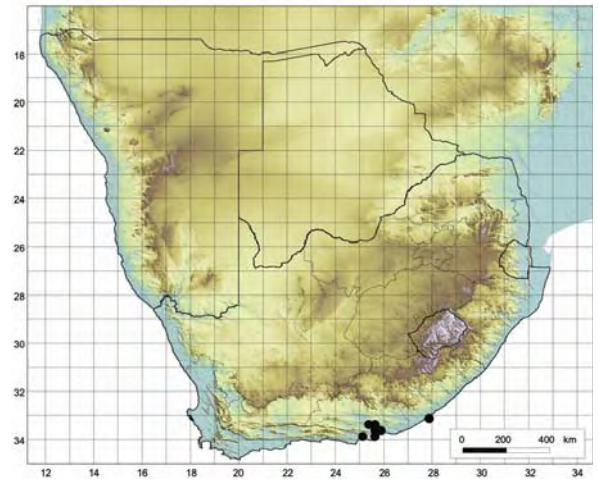
MAP 71. *Drimia loedolfiae*.



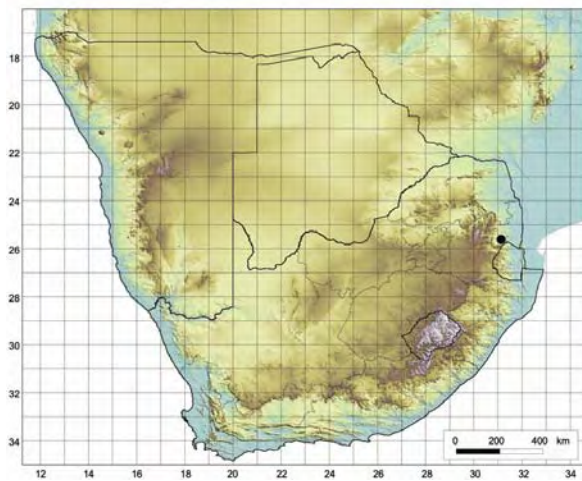
MAP 72. *Drimia mzimvubuensis*.



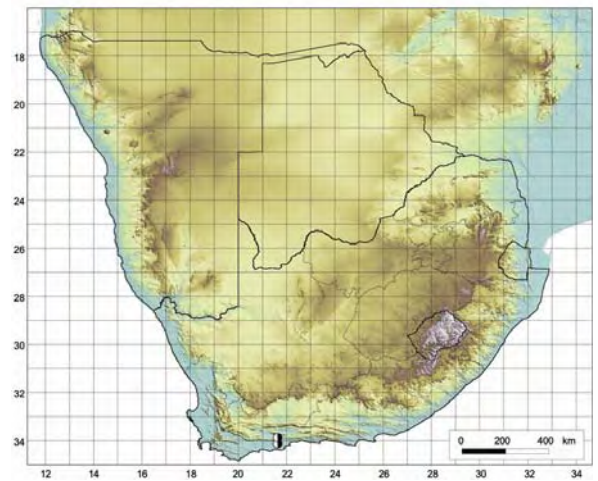
MAP 73. *Drimia uniflora*.



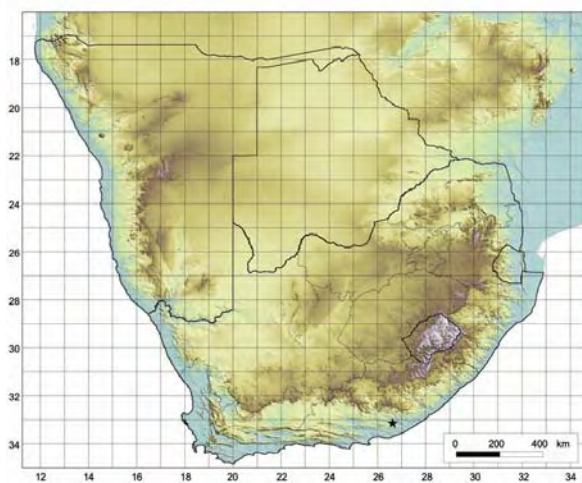
MAP 74. *Ledebouria concolor*.



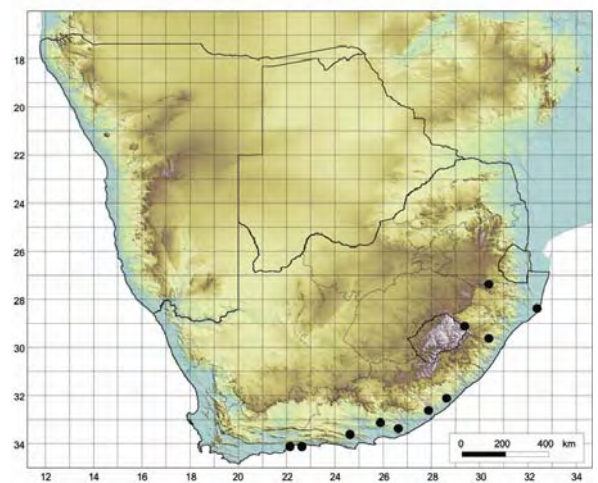
MAP 75. *Ledebouria cremnophila*.



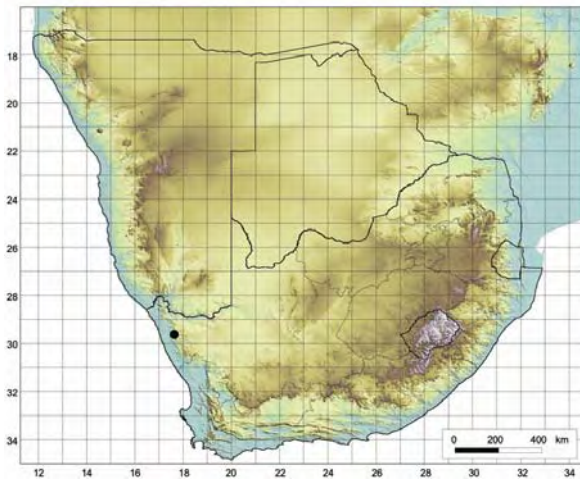
MAP 76. *Ledebouria venterii*.



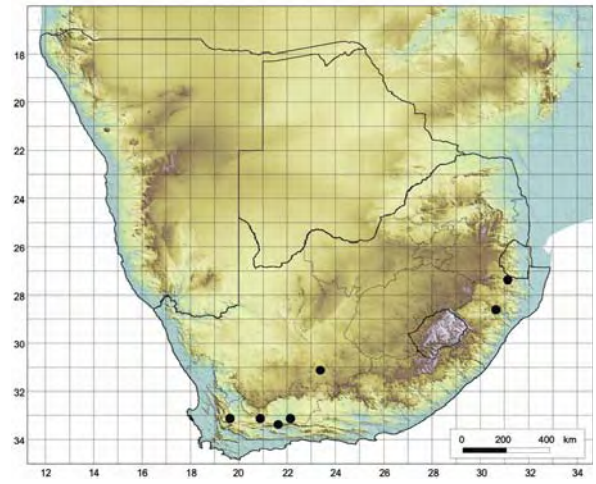
MAP 77. *Ornithogalum juncifolium* var. *emsii*.



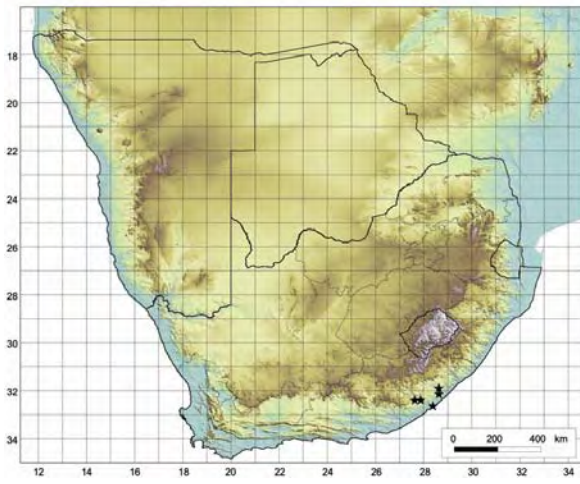
MAP 78. *Ornithogalum longibracteatum*.



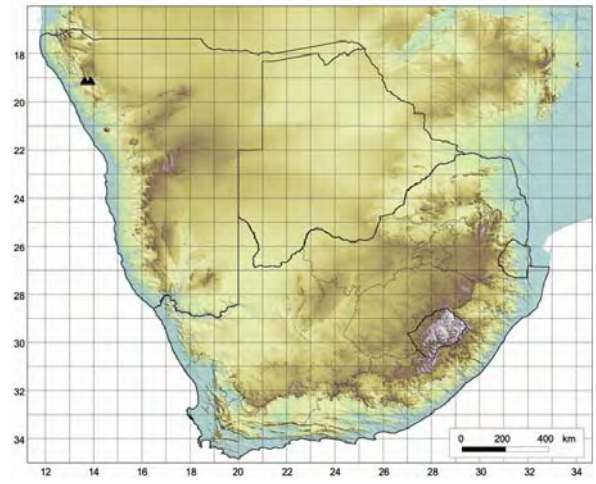
MAP 79. *Ornithogalum pendens*.



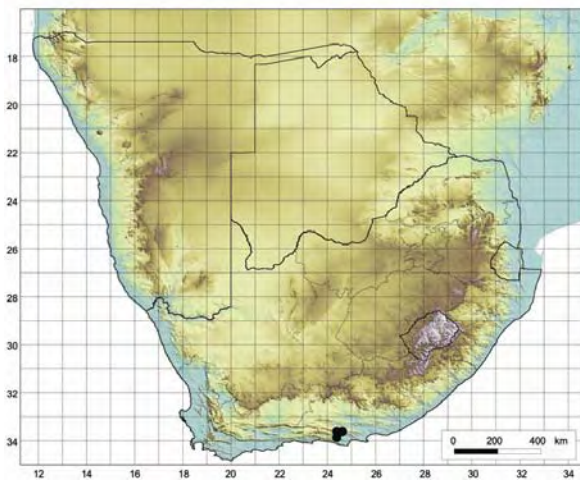
MAP 80. *Schizobasis intricata*.



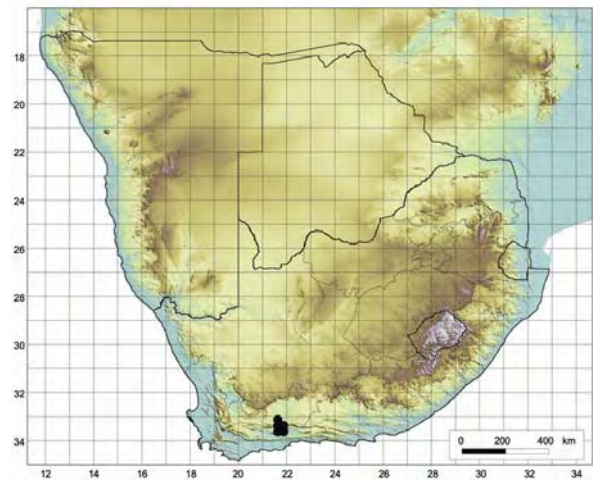
MAP 81. *Huernia pendula*.



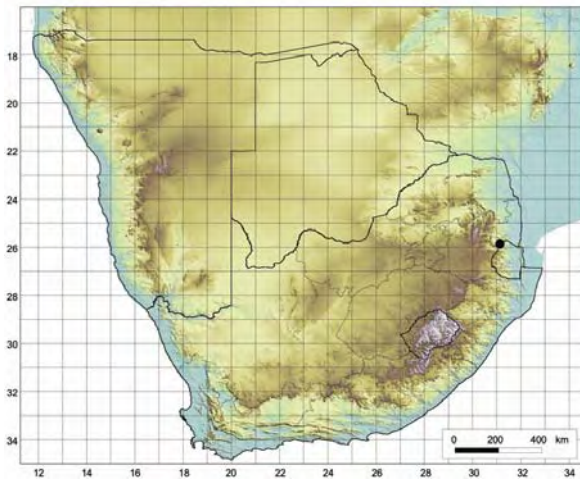
MAP 82. *Lavrania haagnerae*.



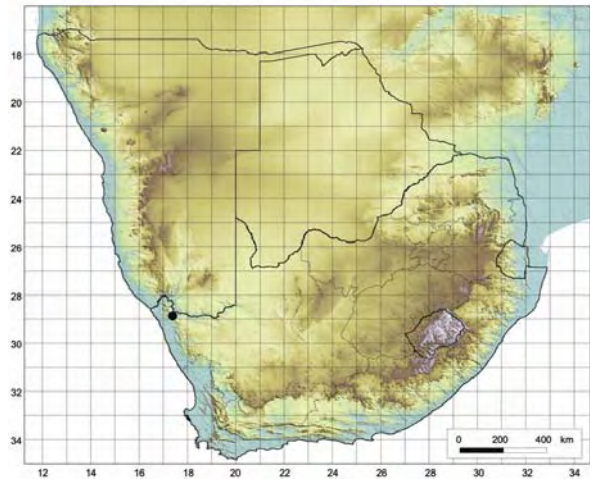
MAP 83. *Tromotriche baylissii*.



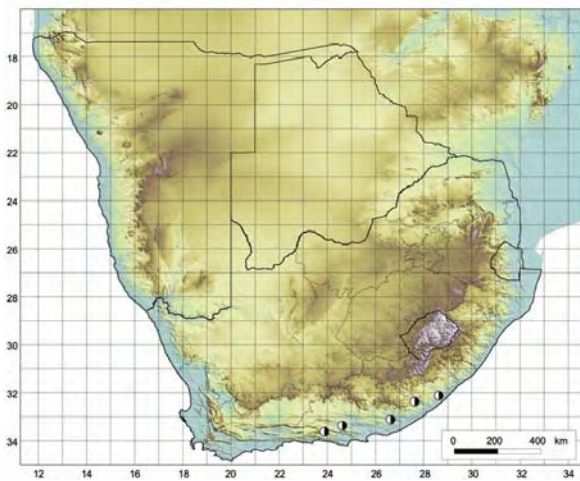
MAP 84. *Tromotriche choanantha*.



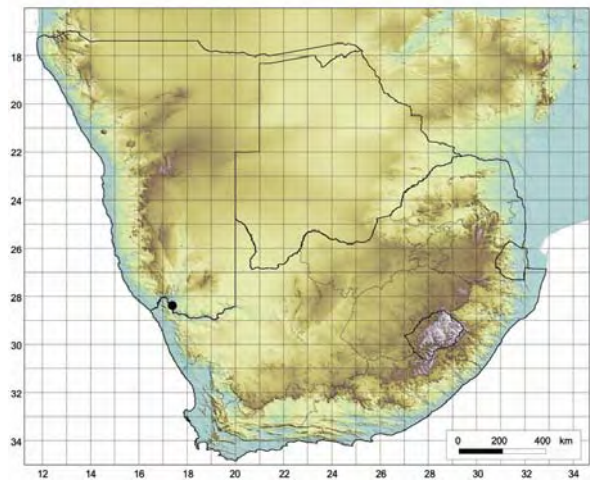
MAP 85. *Kleinia galpinii*.



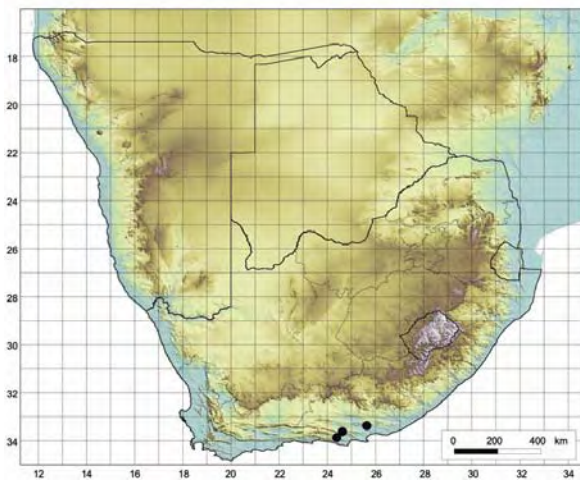
MAP 86. *Othonna armiana*.



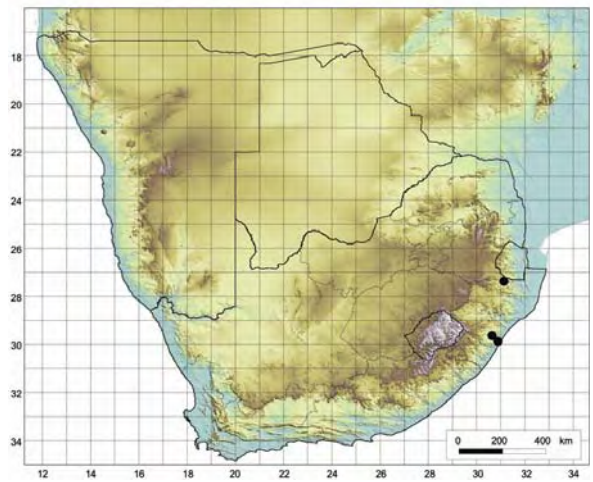
MAP 87. *Othonna capensis*.



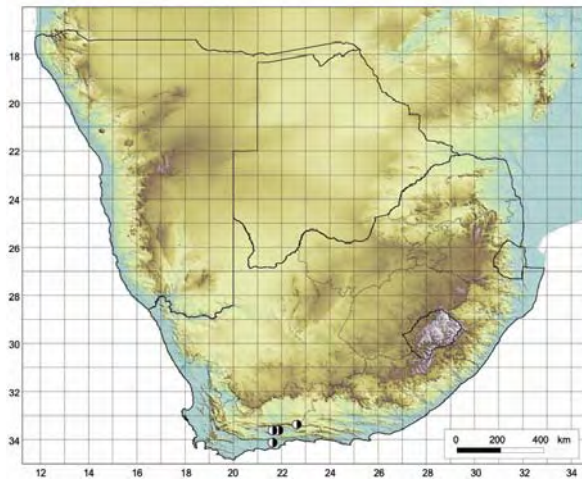
MAP 88. *Othonna cremnophila*.



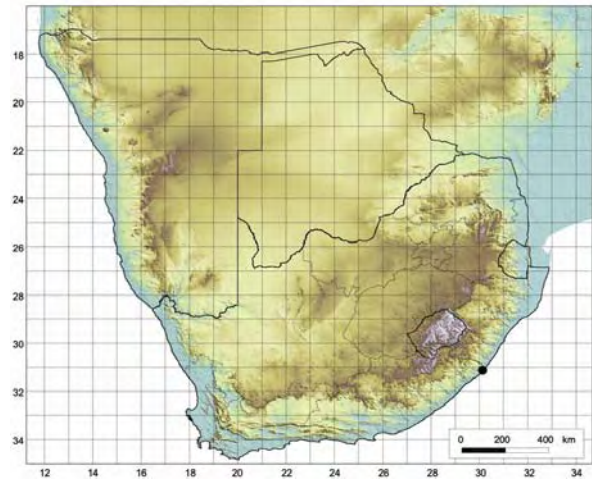
MAP 89. *Othonna triplinervia* (cliff-face forms in tributaries of Gamtoos River).



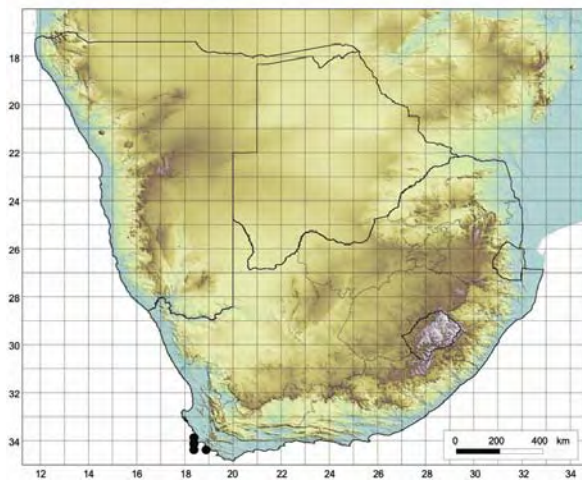
MAP 90. *Senecio medley-woodii*.



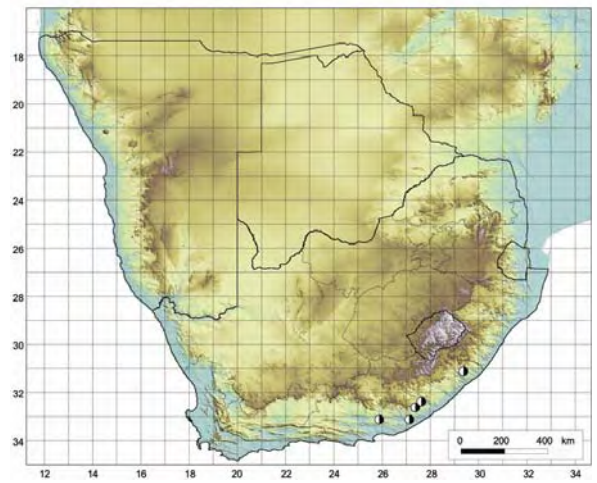
MAP 91. *Senecio muiirii*.



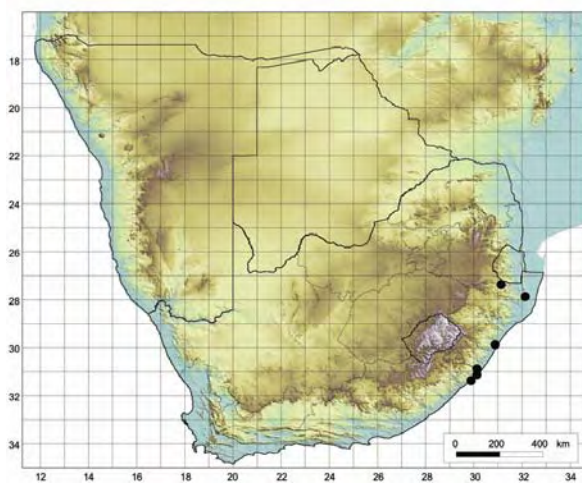
MAP 92. *Senecio pondoensis*.



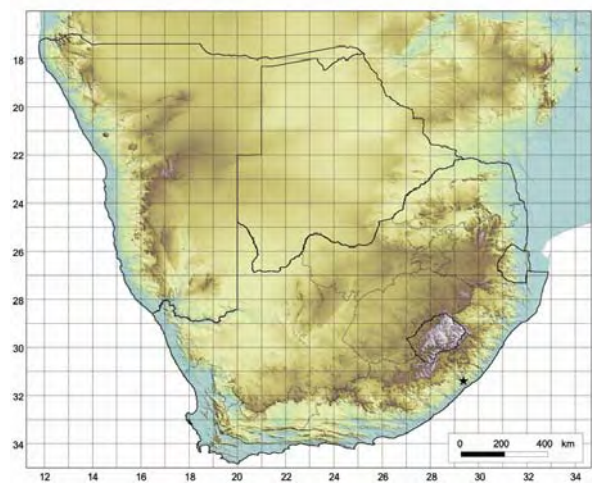
MAP 93. *Senecio serpens*.



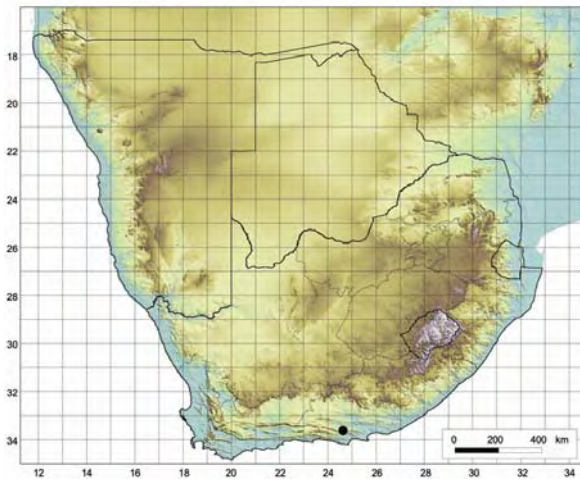
MAP 94. *Senecio talinoides* subsp. *talinoides*.



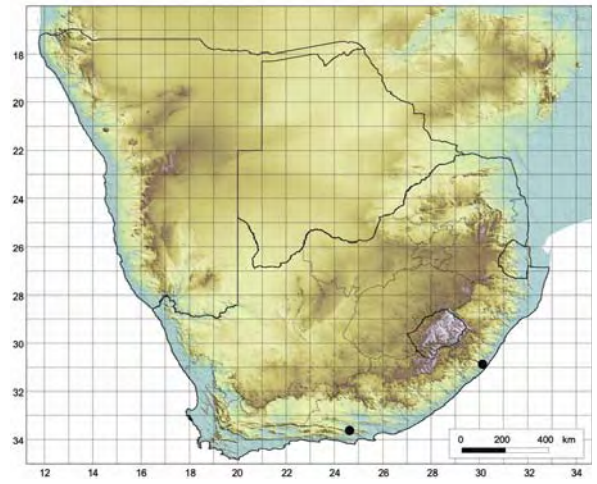
MAP 95. *Rhipsalis baccifera* subsp. *mauritiana*.



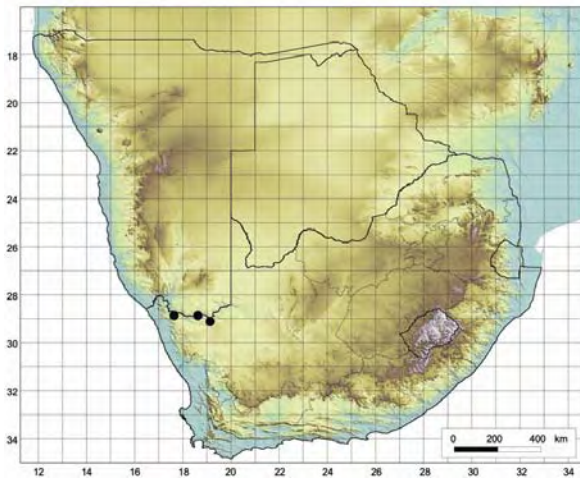
MAP 96. *Adromischus cristatus* var. *mzimvubuensis*.



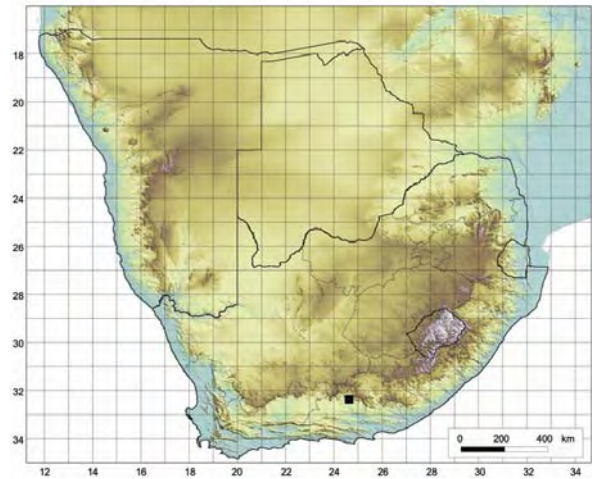
MAP 97. *Adromischus cristatus* var. *schonlandii*.



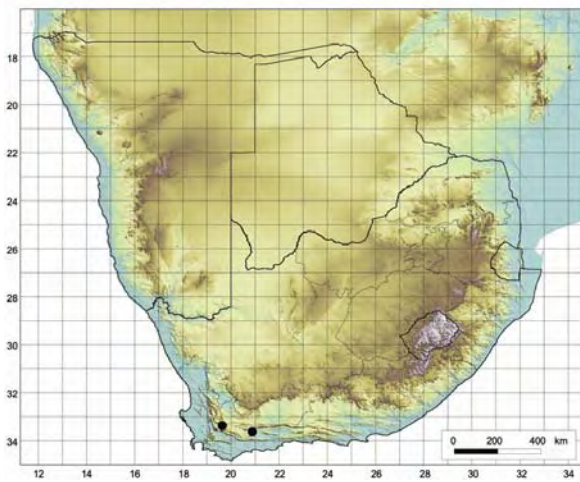
MAP 98. *Adromischus cristatus* var. *zeyheri*.



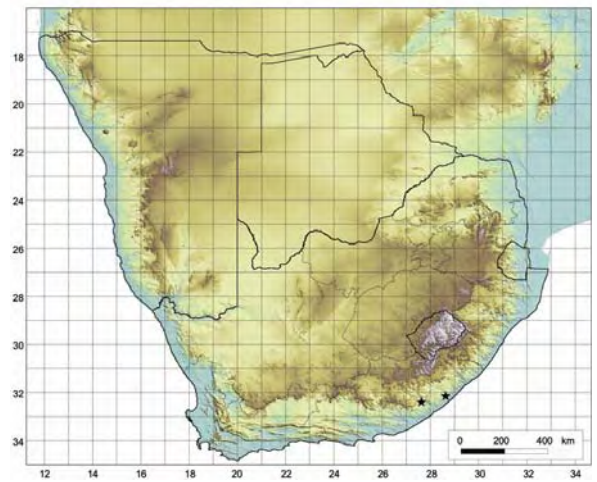
MAP 99. *Adromischus diabolicus*.



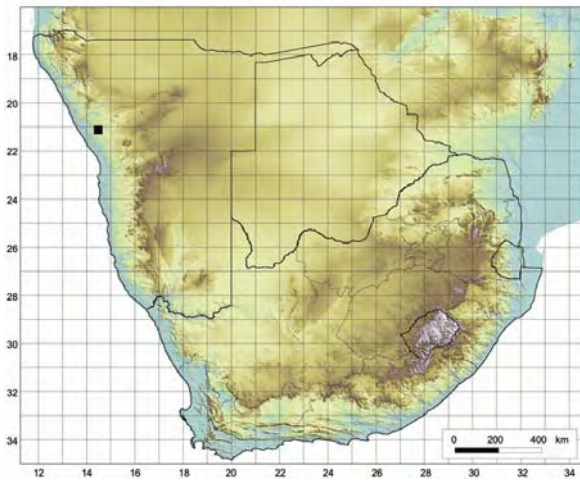
MAP 100. *Adromischus fallax*.



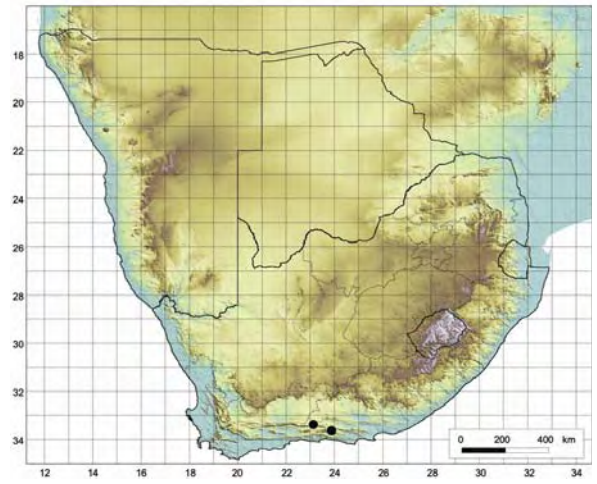
MAP 101. *Adromischus leucophyllus*.



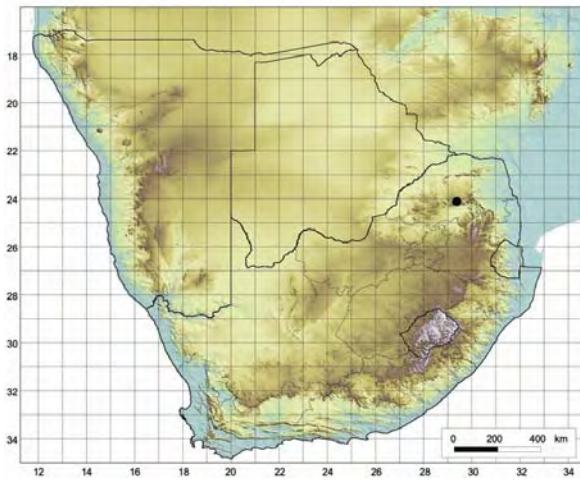
MAP 102. *Adromischus liebenbergii* subsp. *orientalis*.



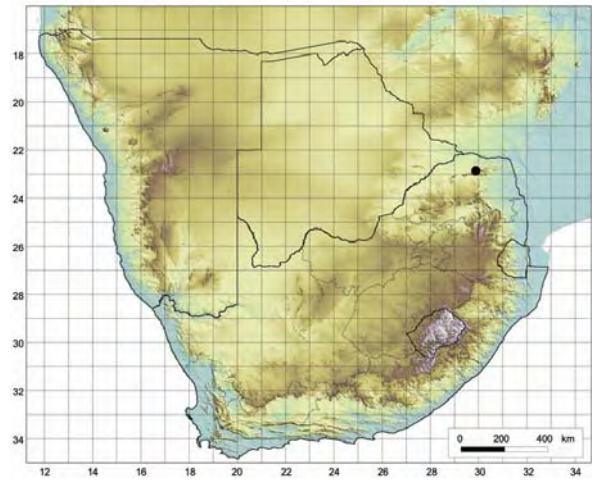
MAP 103. *Adromischus schuldianus* subsp. *brandbergensis*.



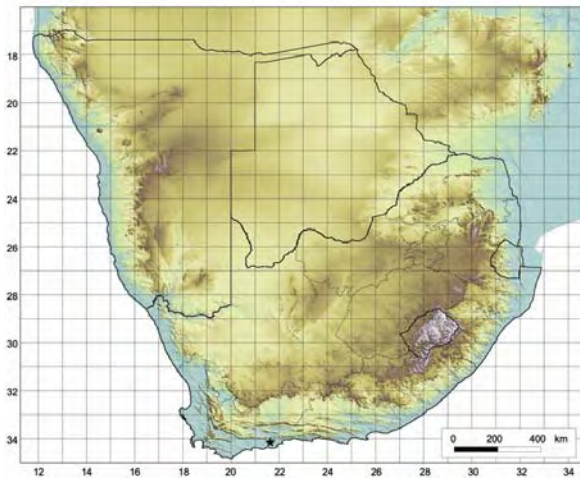
MAP 104. *Adromischus subdistichus*.



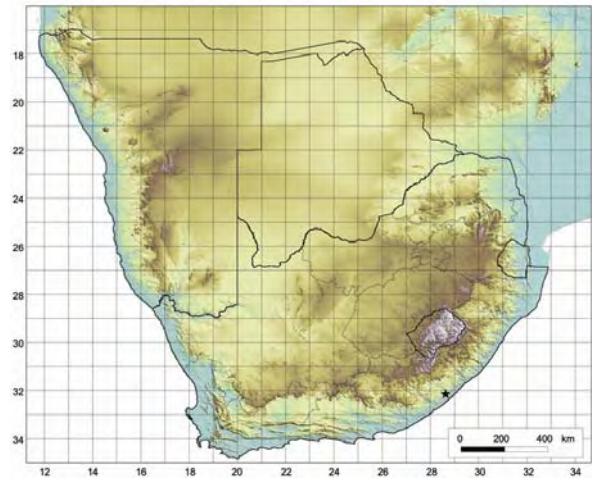
MAP 105. *Adromischus umbraticola* subsp. *ramosus*.



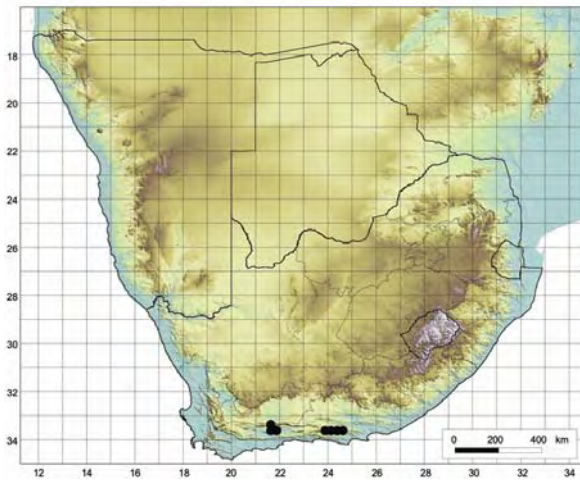
MAP 106. *Cotyledon barbeyi*.



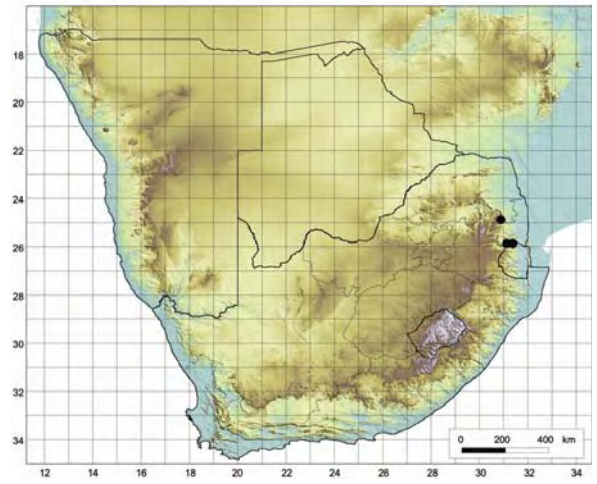
MAP 107. *Cotyledon eliseae*.



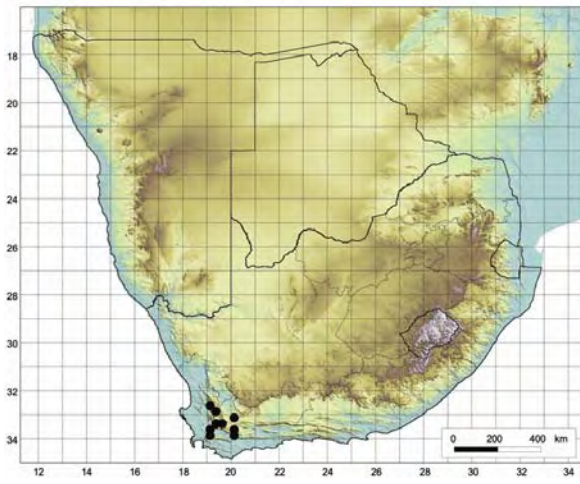
MAP 108. *Cotyledon pendens*.



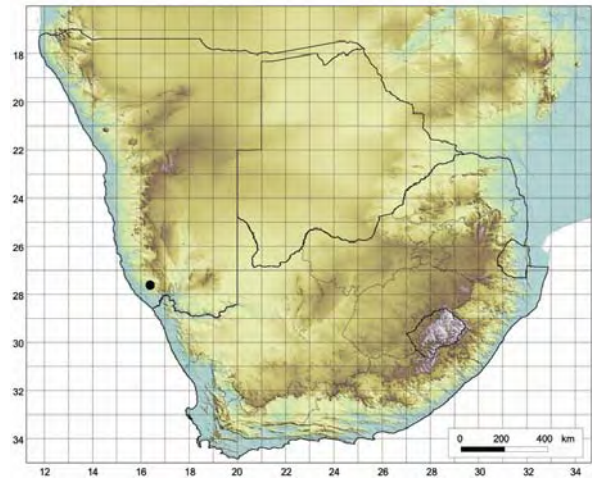
MAP 109. *Cotyledon tomentosa* subsp. *tomentosa*.



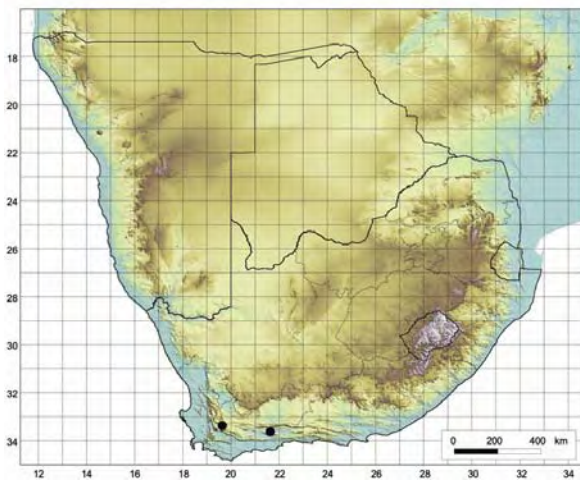
MAP 110. *Crassula alba* var. *pallida*.



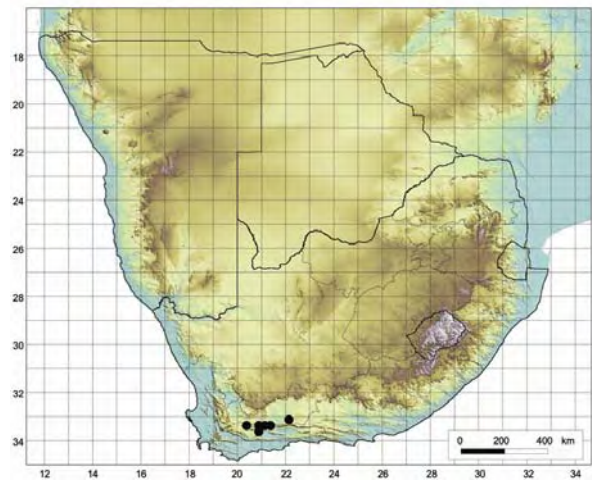
MAP 111. *Crassula atropurpurea* var. *anomala*.



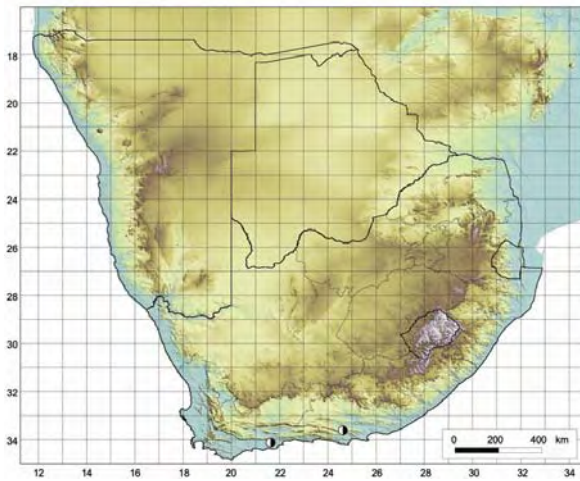
MAP 112. *Crassula aurusbergensis*.



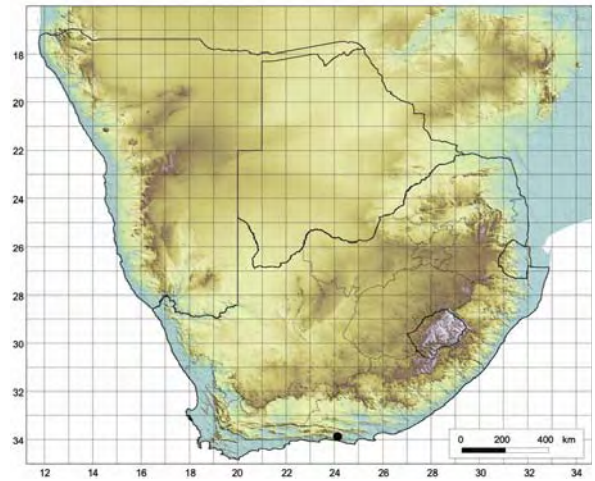
MAP 113. *Crassula badspoortense*.



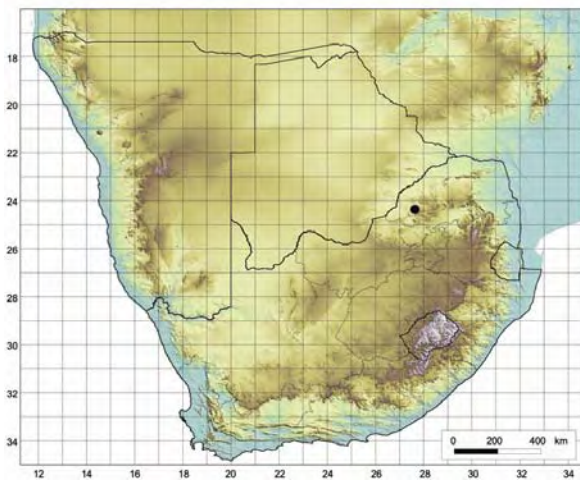
MAP 114. *Crassula brachystachya*.



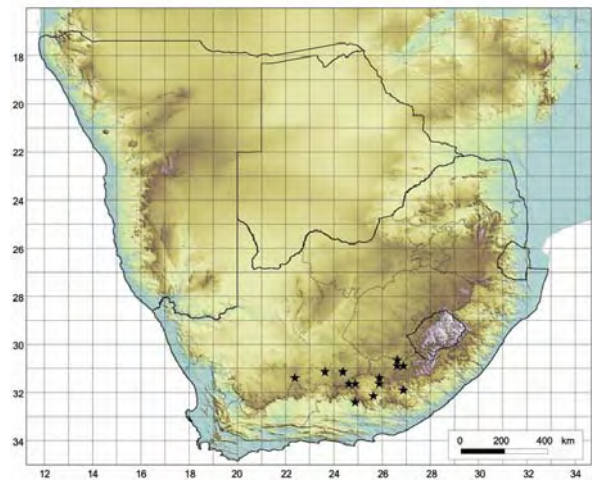
MAP 115. *Crassula capitella* subsp. *thyrsoflora*.



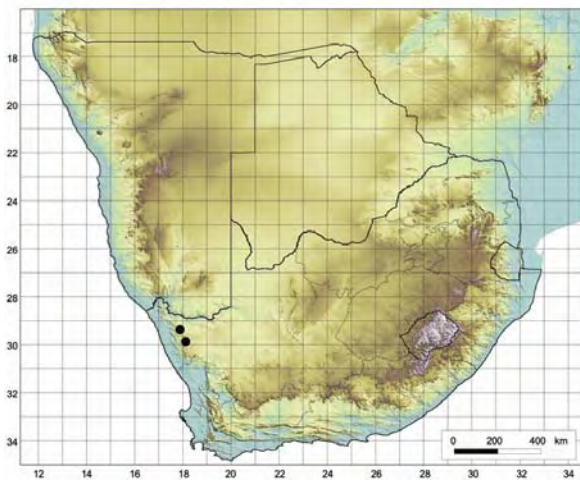
MAP 116. *Crassula cremnophila*.



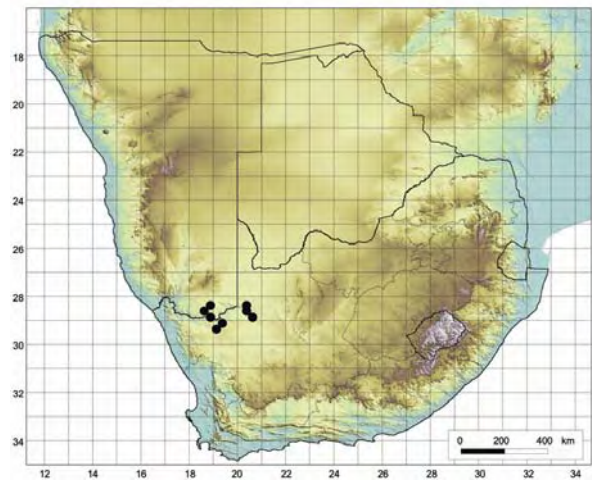
MAP 117. *Crassula cymbiformis*.



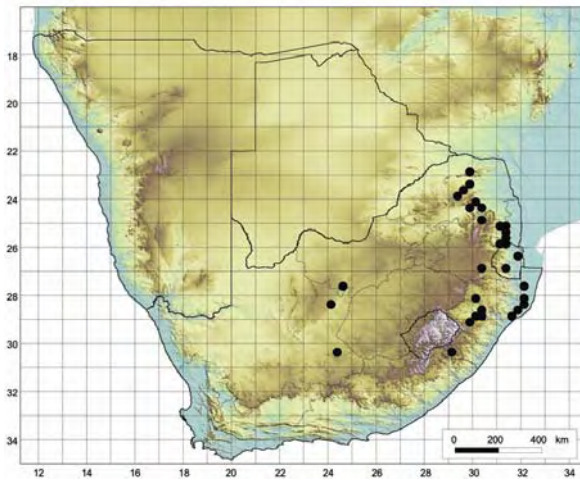
MAP 118. *Crassula exilis* subsp. *cooperi*.



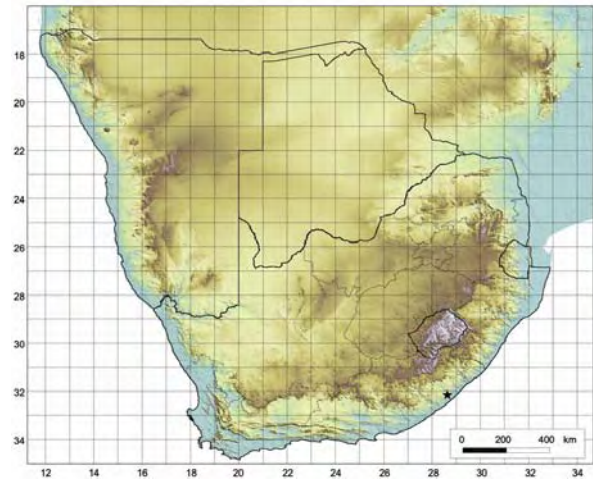
MAP 119. *Crassula exilis* subsp. *exilis*.



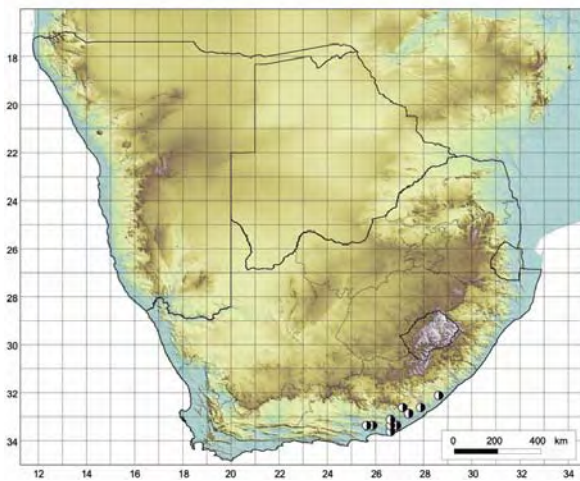
MAP 120. *Crassula exilis* subsp. *sedifolia*.



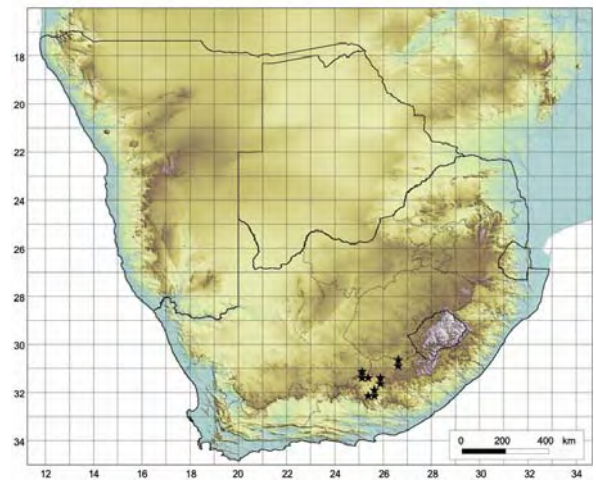
MAP 121. *Crassula expansa* subsp. *fragilis*.



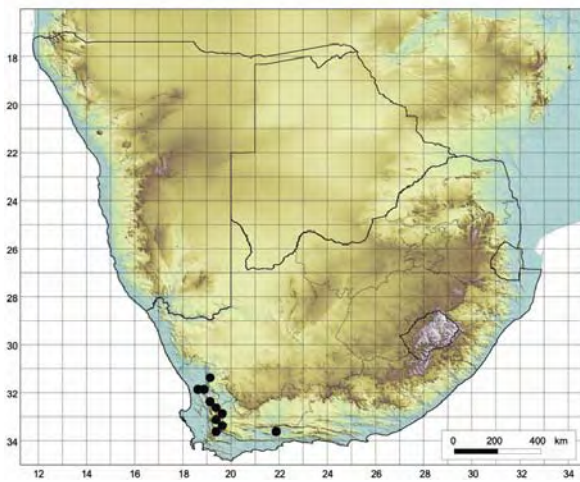
MAP 122. *Crassula foveata*.



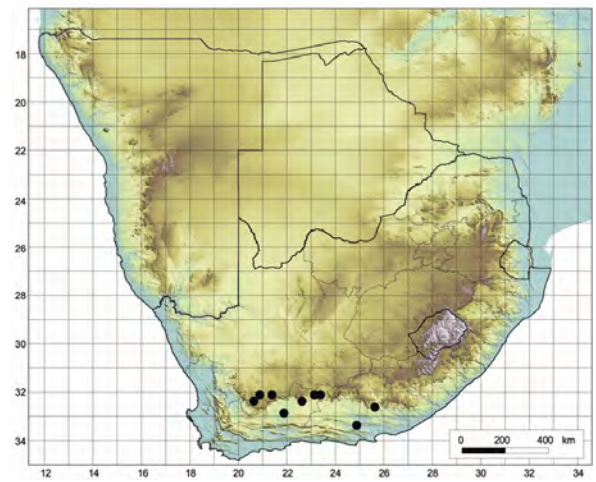
MAP 123. *Crassula intermedia*.



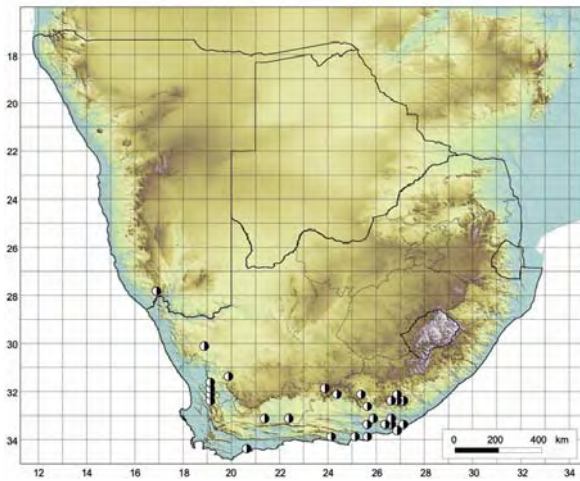
MAP 124. *Crassula lanuginosa* var. *lanuginosa*.



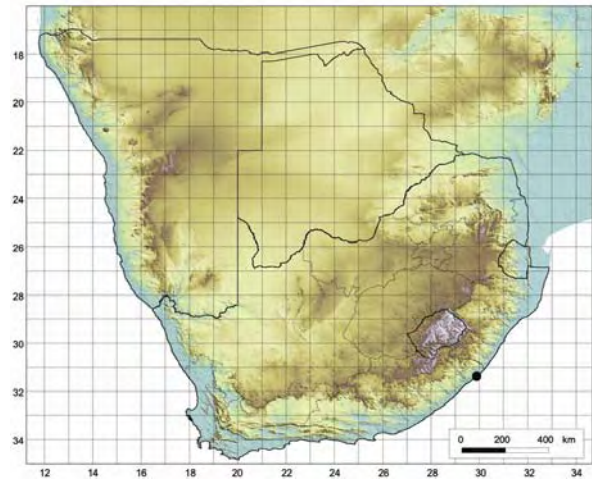
MAP 125. *Crassula montana* subsp. *montana*.



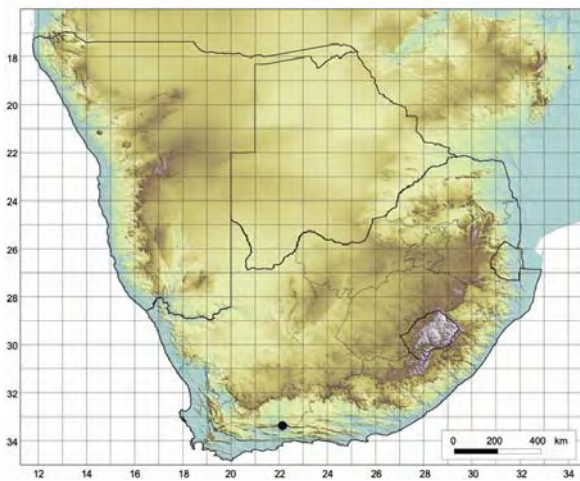
MAP 126. *Crassula montana* subsp. *quadrangularis*.



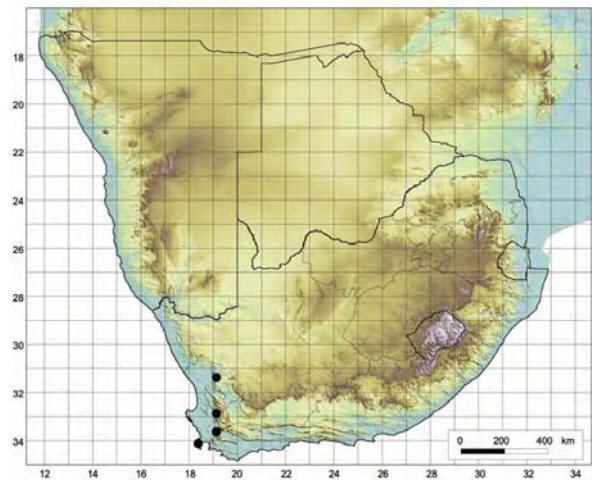
MAP 127. *Crassula nemorosa*.



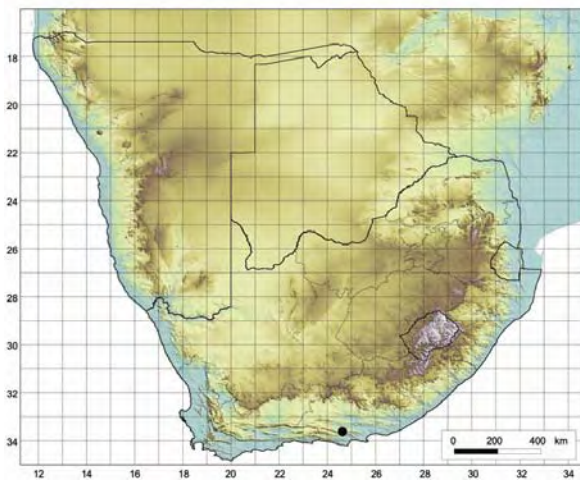
MAP 128. *Crassula orbicularis*.



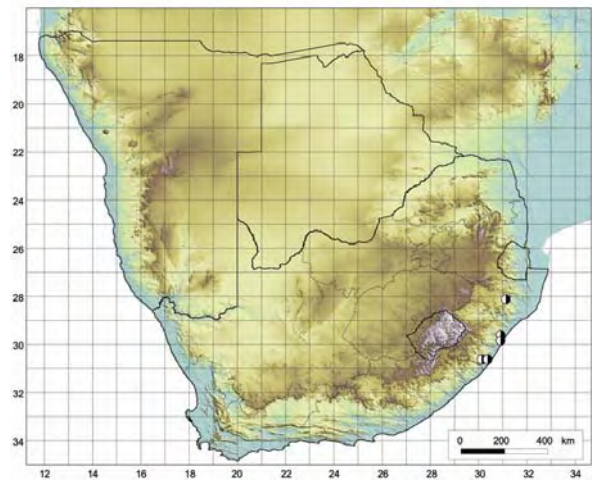
MAP 129. *Crassula peculiaris*.



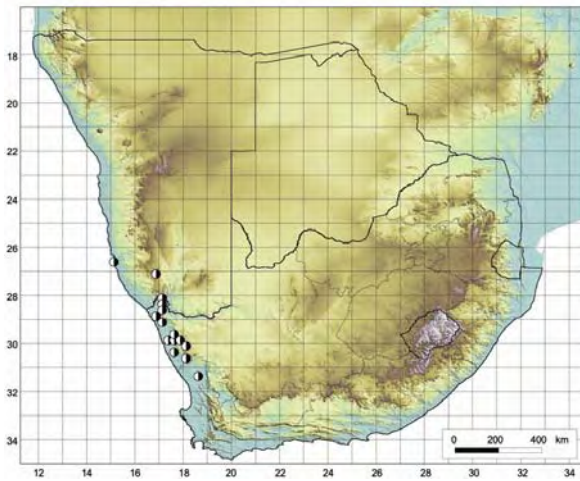
MAP 130. *Crassula pellucida* subsp. *spongiosa*.



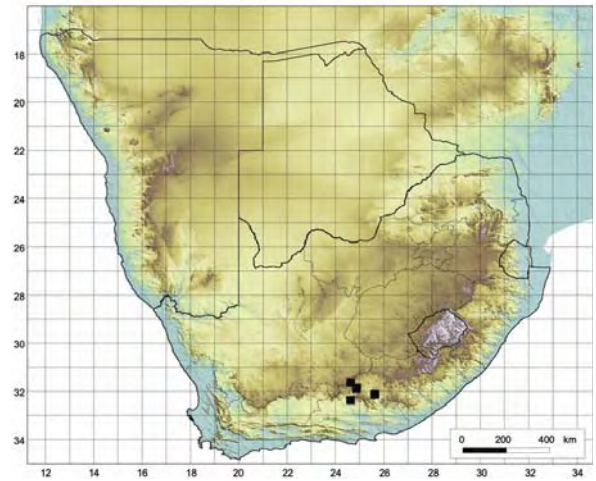
MAP 131. *Crassula perforata* subsp. *kougaensis*.



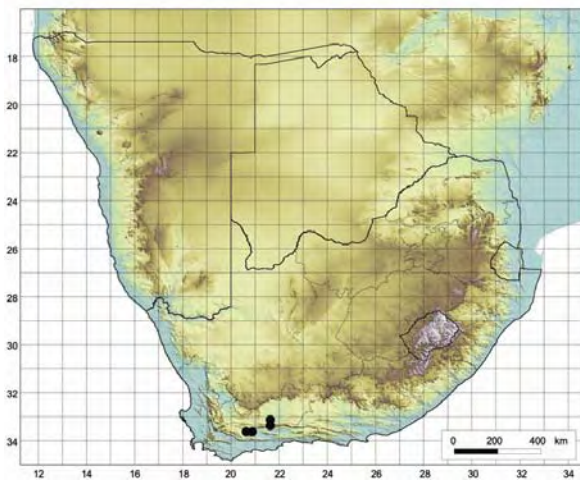
MAP 132. *Crassula perforata* subsp. *perforata*.



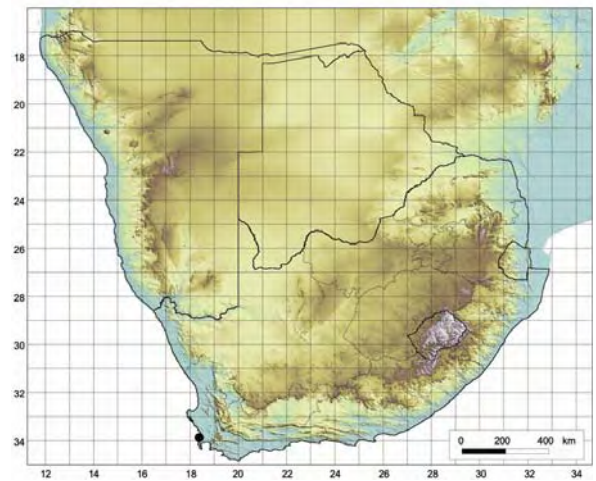
MAP 133. *Crassula pseudohemisphaerica*.



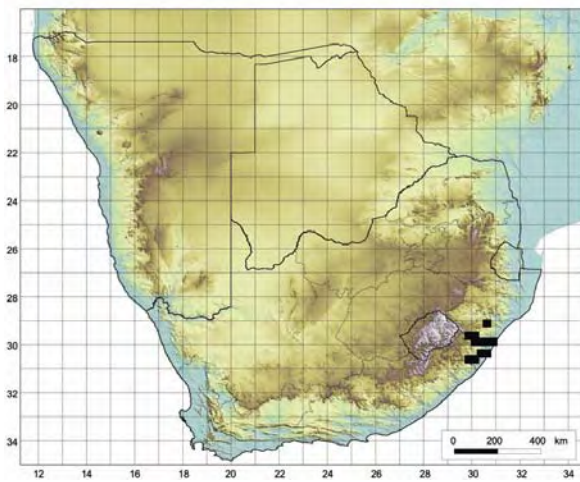
MAP 134. *Crassula pubescens* subsp. *rattrayi*.



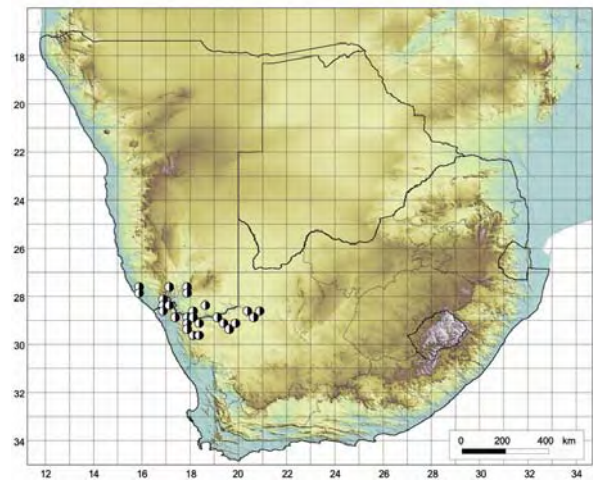
MAP 135. *Crassula rupestris* subsp. *marnieriana*.



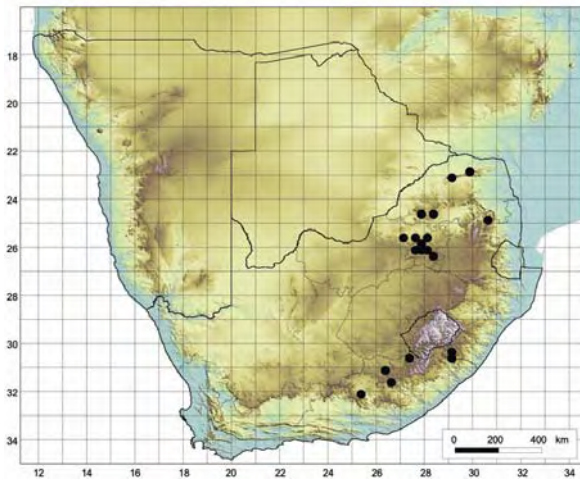
MAP 136. *Crassula rupestris* subsp. *rupestris*.



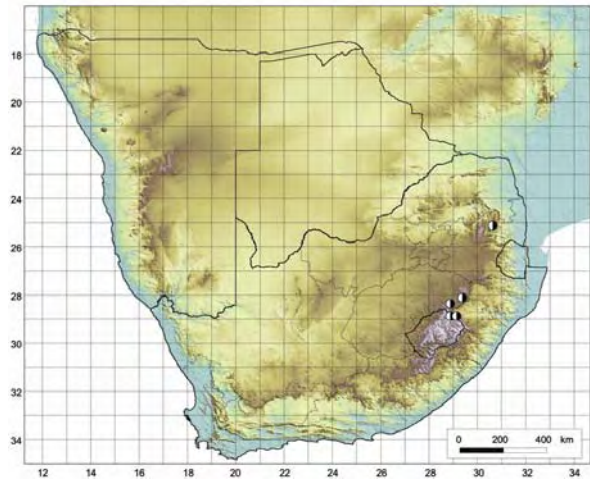
MAP 137. *Crassula sediflora* var. *sediflora*.



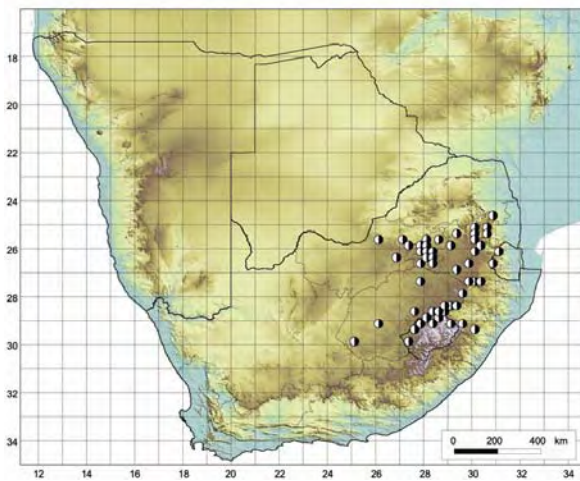
MAP 138. *Crassula sericea* var. *sericea*.



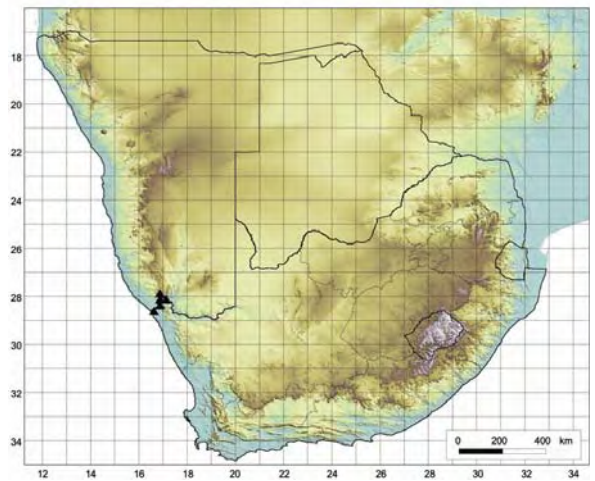
MAP 139. *Crassula setulosa* var. *jenkinsii*.



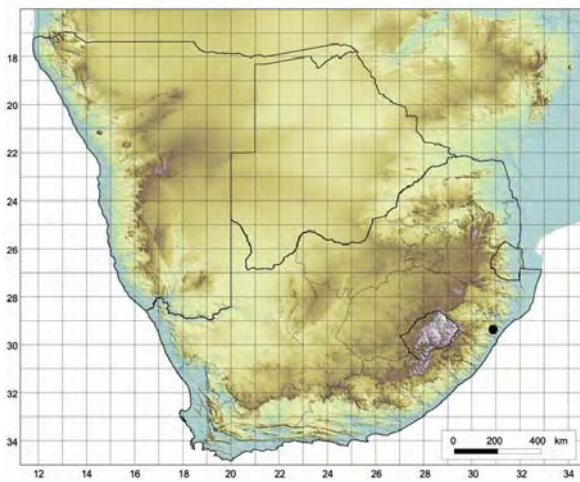
MAP 140. *Crassula setulosa* var. *longiciliata*.



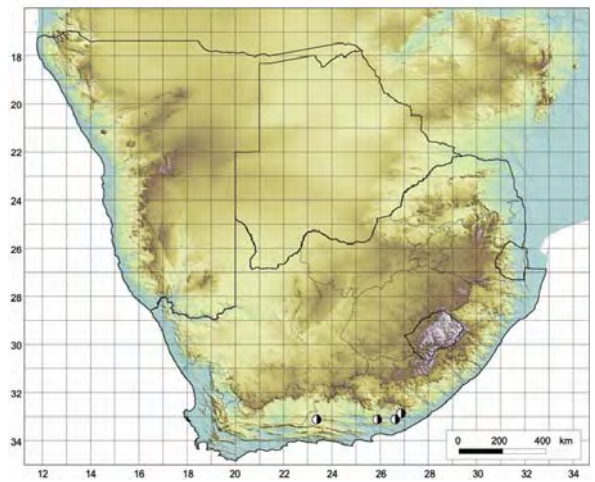
MAP 141. *Crassula setulosa* var. *setulosa*.



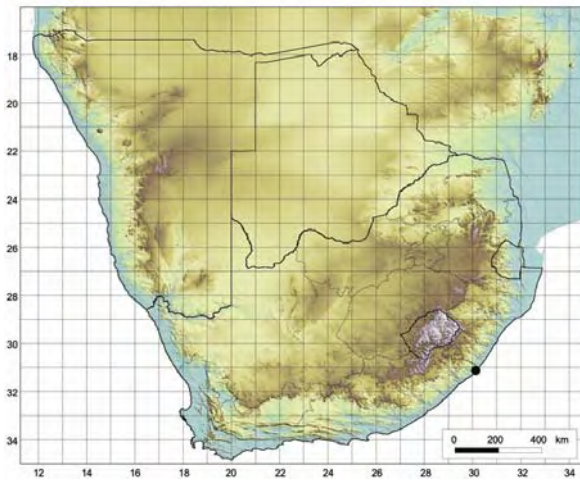
MAP 142. *Crassula sladenii*.



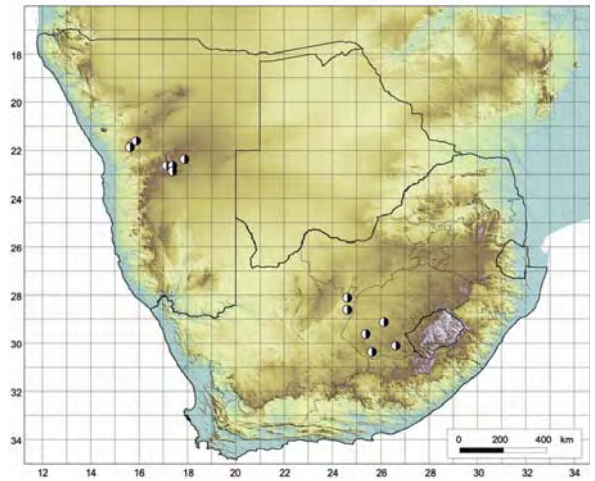
MAP 143. *Crassula smithii*.



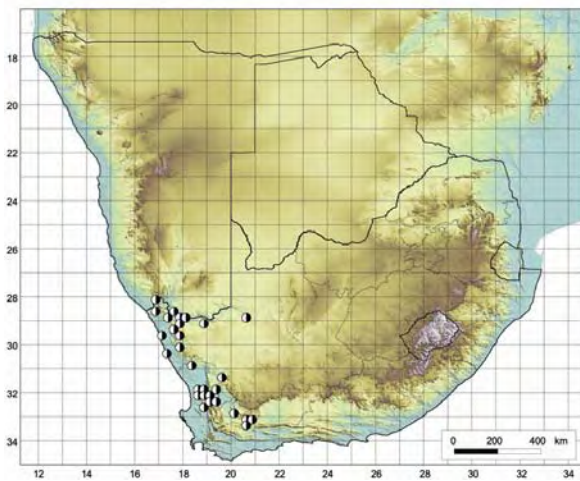
MAP 144. *Crassula socialis*.



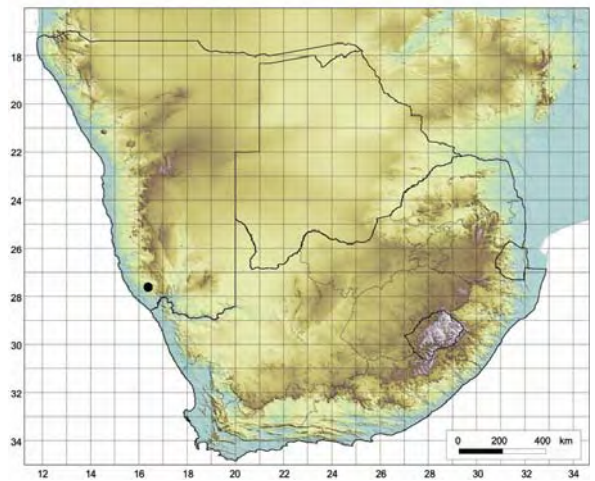
MAP 145. *Crassula streyi*.



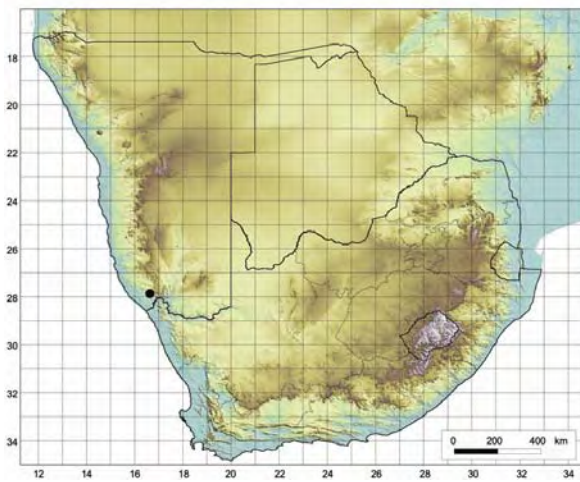
MAP 146. *Crassula tabularis*.



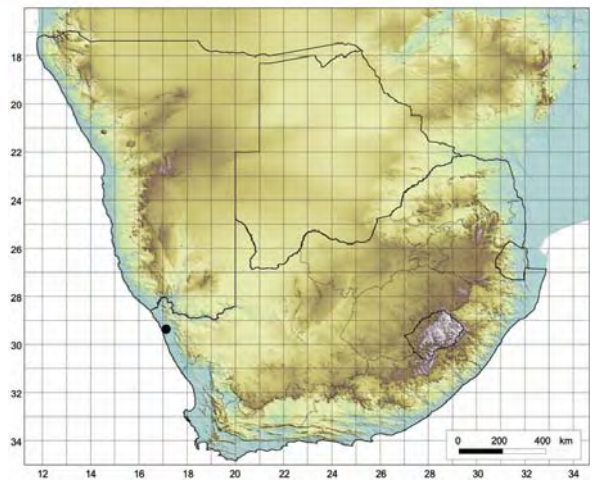
MAP 147. *Crassula tomentosa* var. *glabrifolia*.



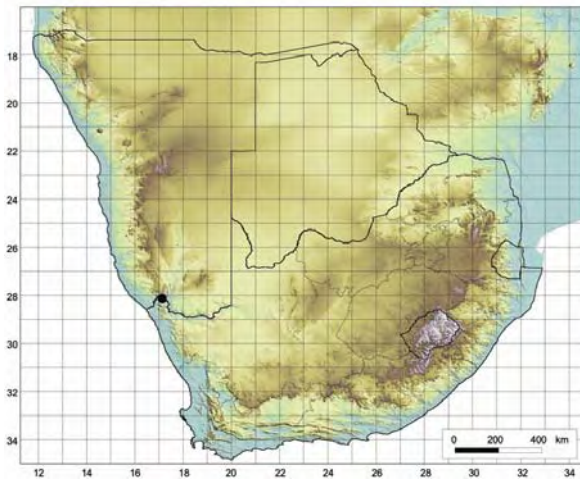
MAP 148. *Tylecodon aurusbergensis*.



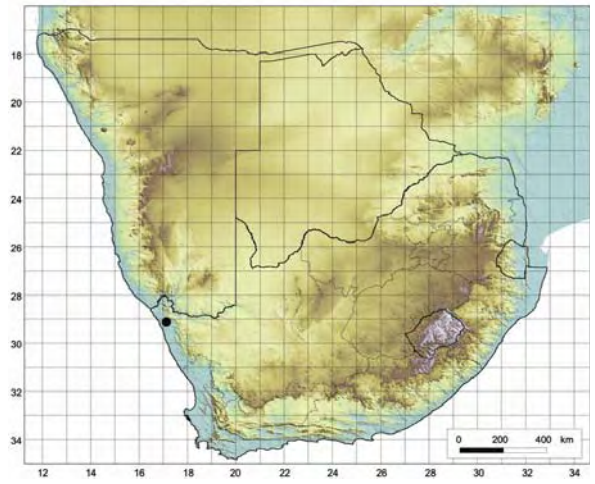
MAP 149. *Tylecodon bleckiae*.



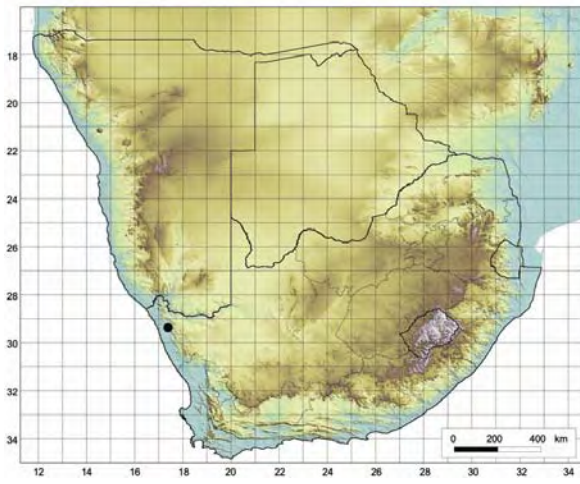
MAP 150. *Tylecodon bodleyae*.



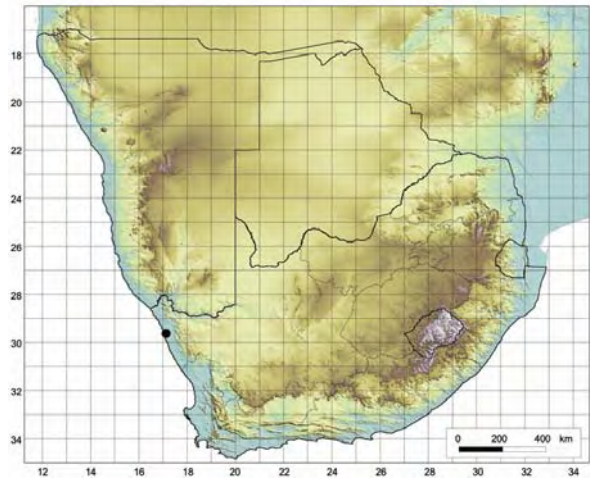
MAP 151. *Tylecodon bruynsii*.



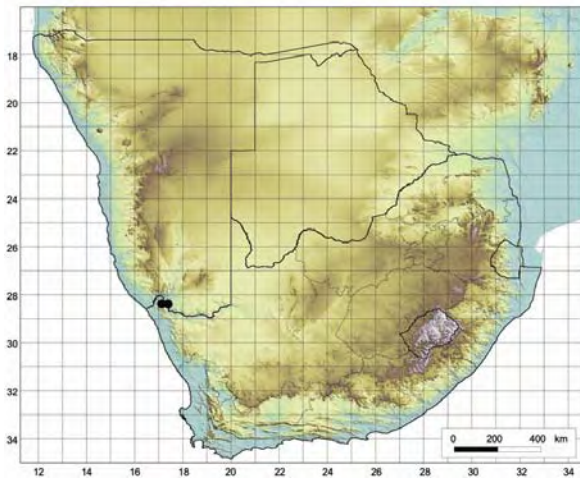
MAP 152. *Tylecodon buchholzianus* var. *fasciculatus*.



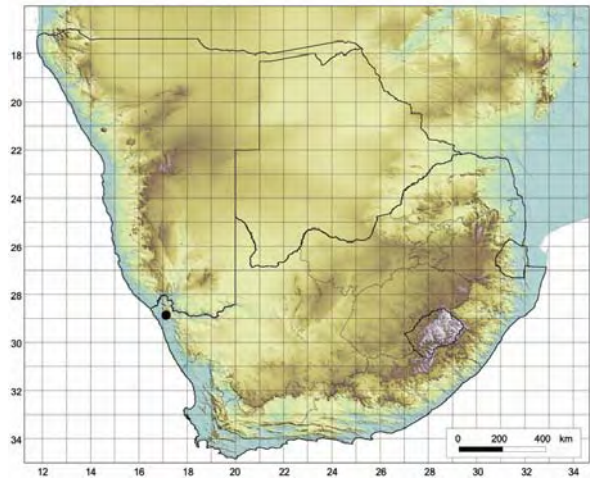
MAP 153. *Tylecodon cordiformis*.



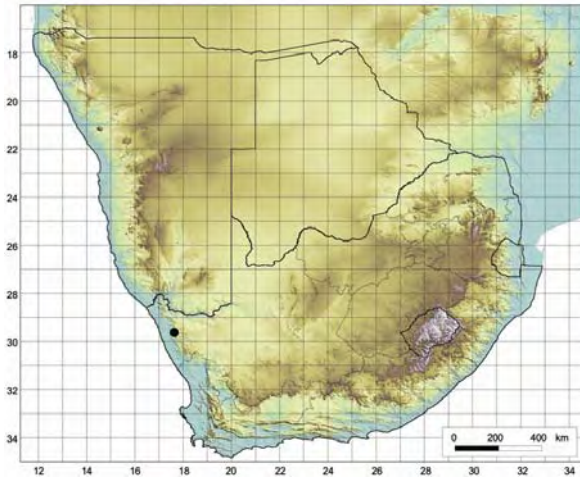
MAP 154. *Tylecodon decipiens*.



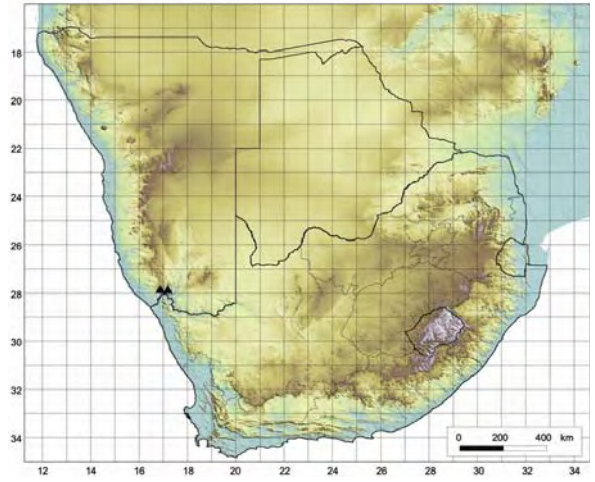
MAP 155. *Tylecodon ellaphieae*.



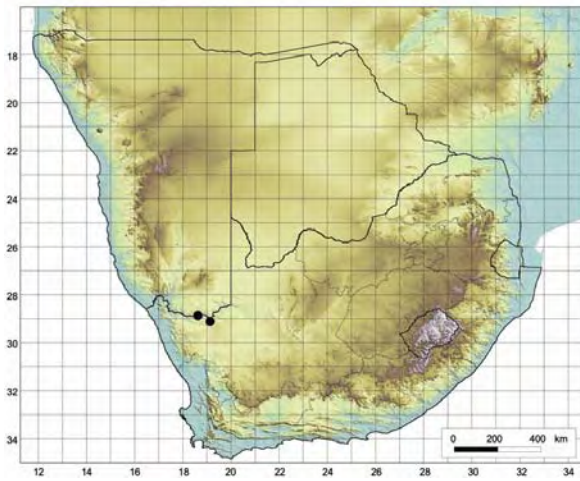
MAP 156. *Tylecodon longipes*.



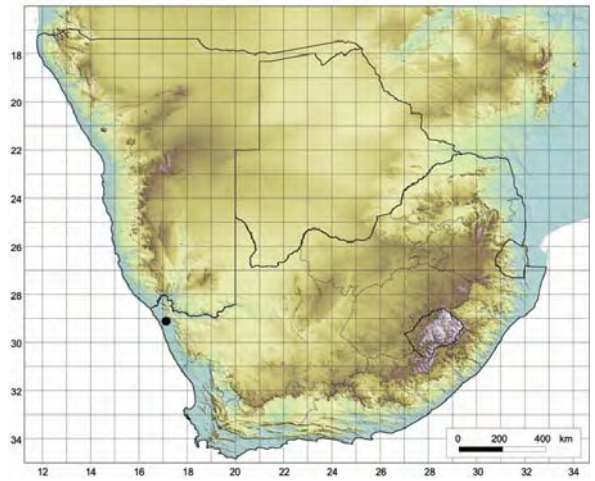
MAP 157. *Tylecodon petrophilus*.



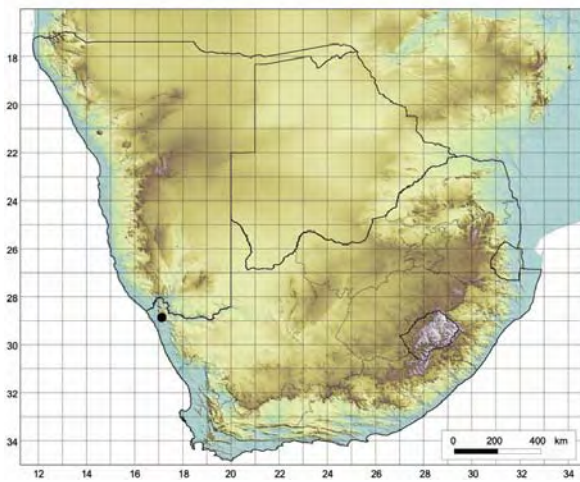
MAP 158. *Tylecodon singularis*.



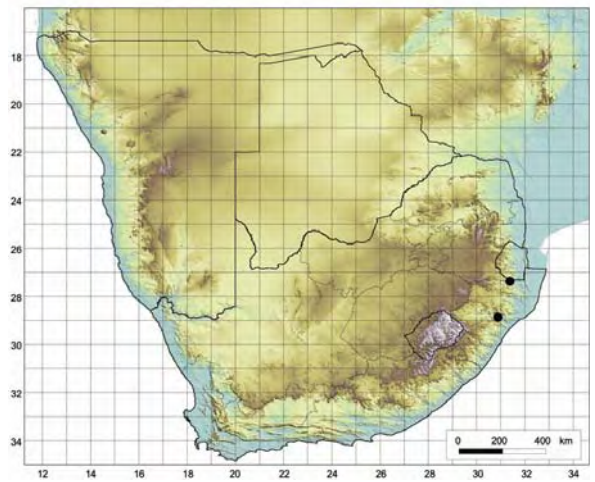
MAP 159. *Tylecodon sulphureus* var.
armianus.



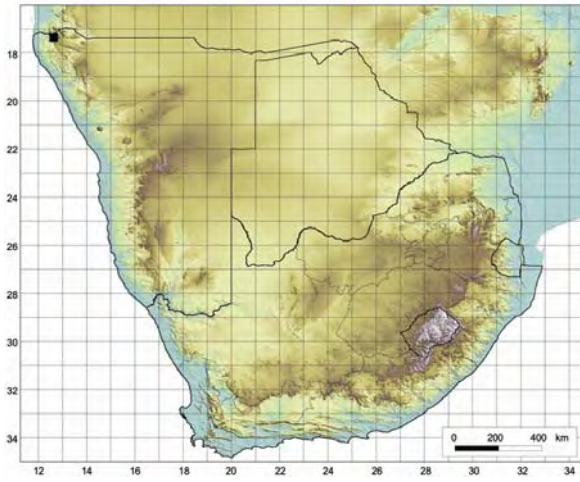
MAP 160. *Tylecodon torulosus*.



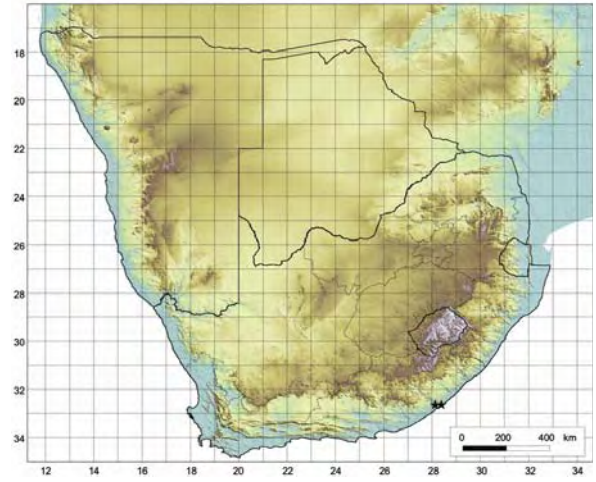
MAP 161. *Tylecodon viridiflorus*.



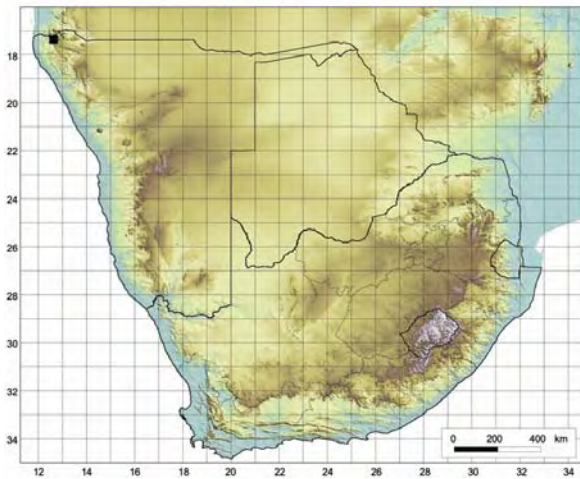
MAP 162. *Pelargonium mutans*.



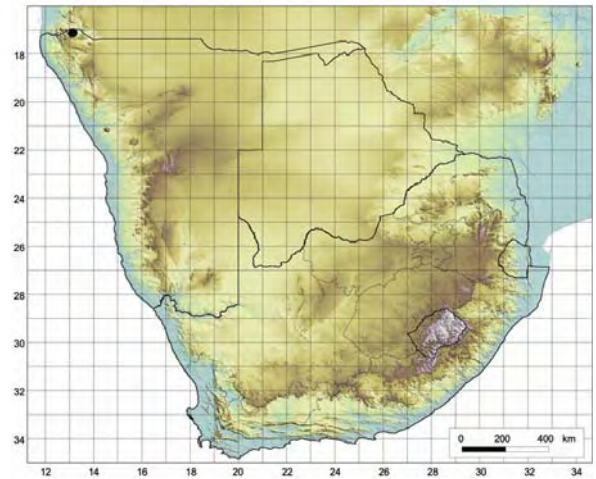
MAP 163. *Pelargonium vanderwaltii*.



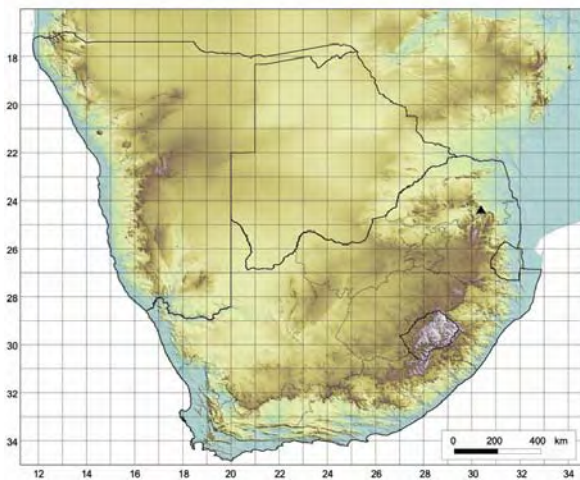
MAP 164. *Streptocarpus kentaniensis*.



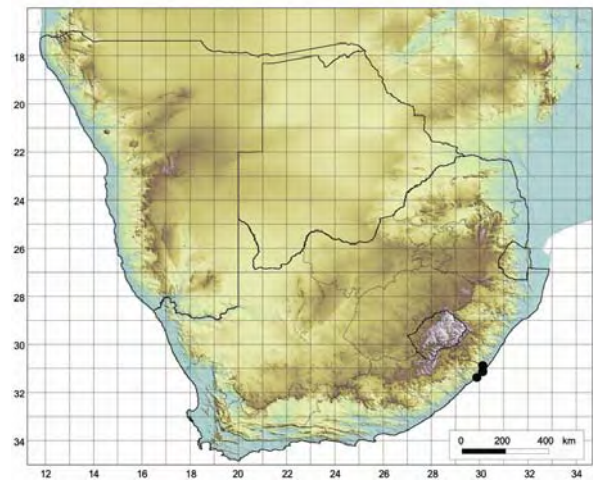
MAP 165. *Aeollanthus haumannii*.



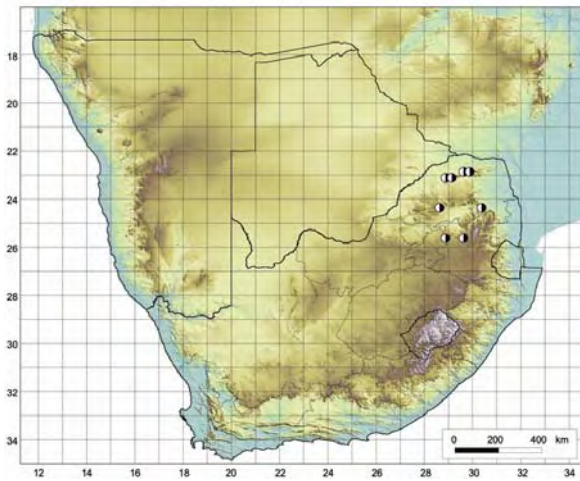
MAP 166. *Aeollanthus rydingianus*.



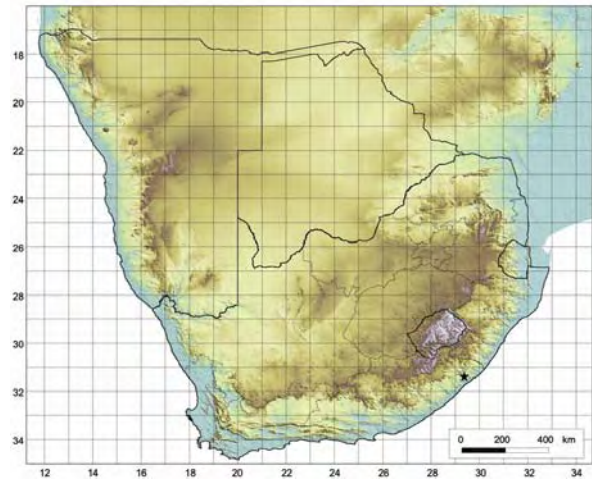
MAP 167. *Plectranthus dolomiticus*.



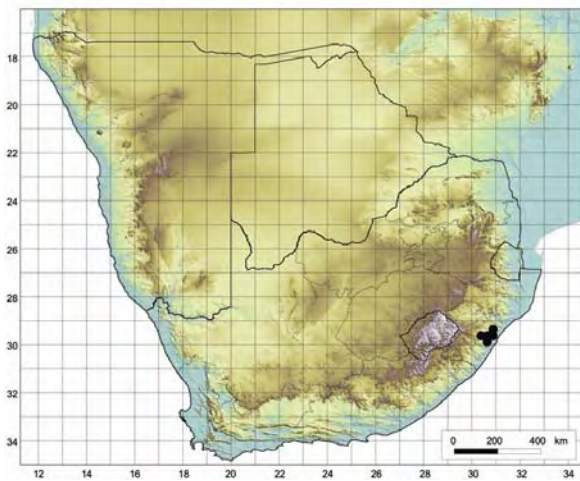
MAP 168. *Plectranthus ernstii*.



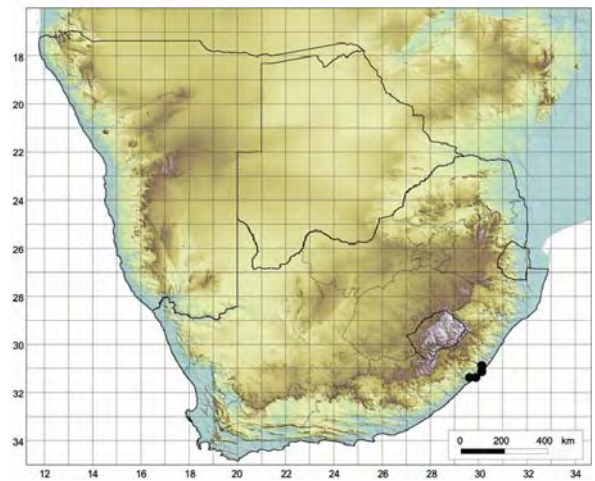
MAP 169. *Plectranthus mutabilis*.



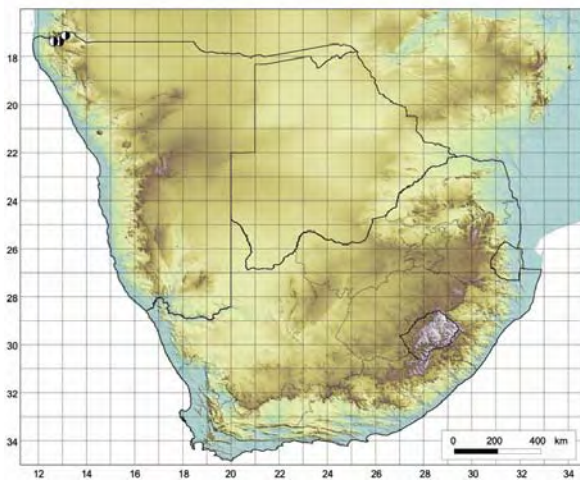
MAP 170. *Plectranthus mzimvubuensis*.



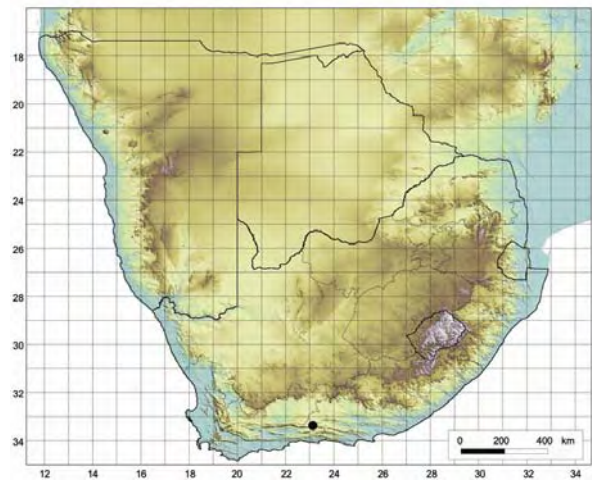
MAP 171. *Plectranthus purpuratus* subsp. *purpuratus*.



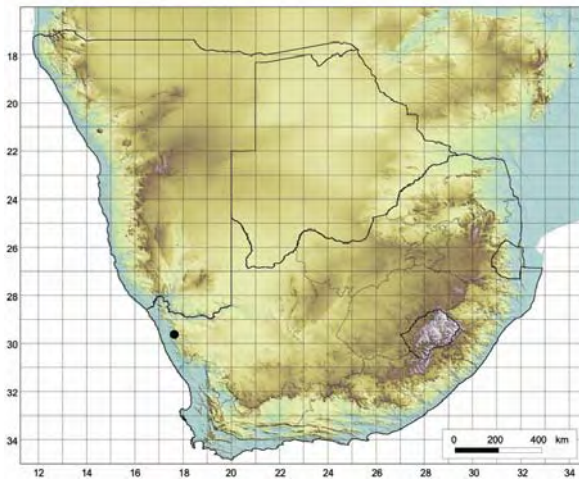
MAP 172. *Plectranthus saccatus* subsp. *pondoensis*.



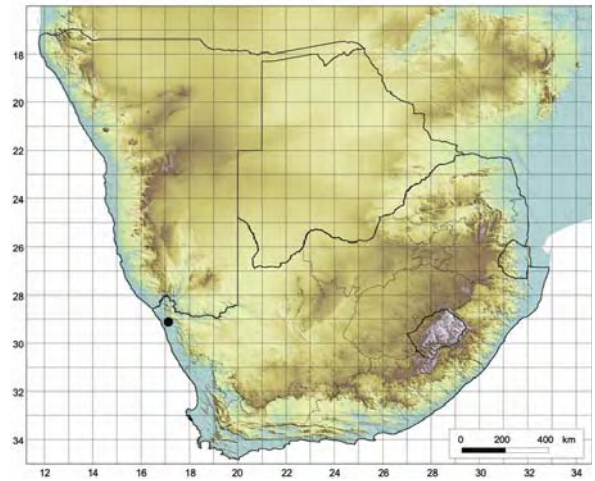
MAP 173. *Tetradenia kaokoensis*.



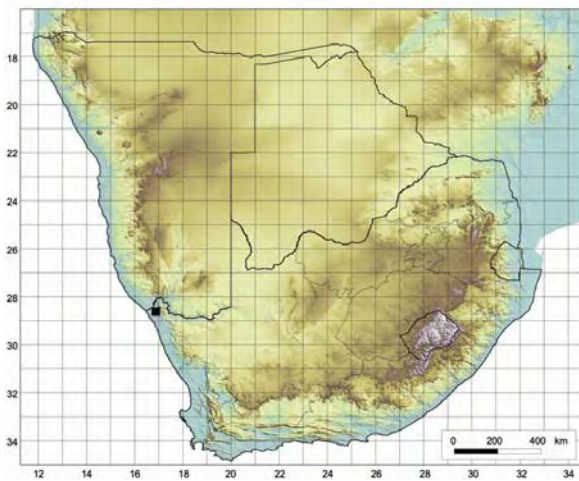
MAP 174. *Carruanthus peersii*.



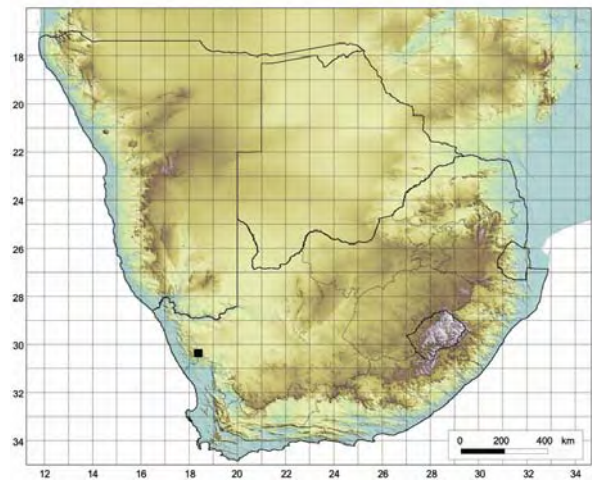
MAP 175. *Conophytum auriflorum* subsp. *turbiniforme*.



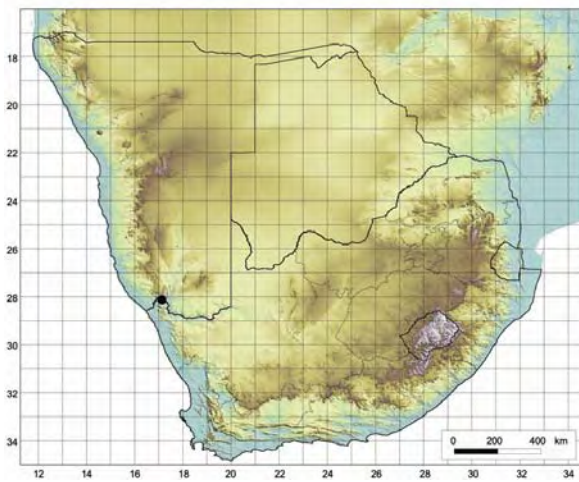
MAP 176. *Conophytum bolusiae* subsp. *bolusiae*.



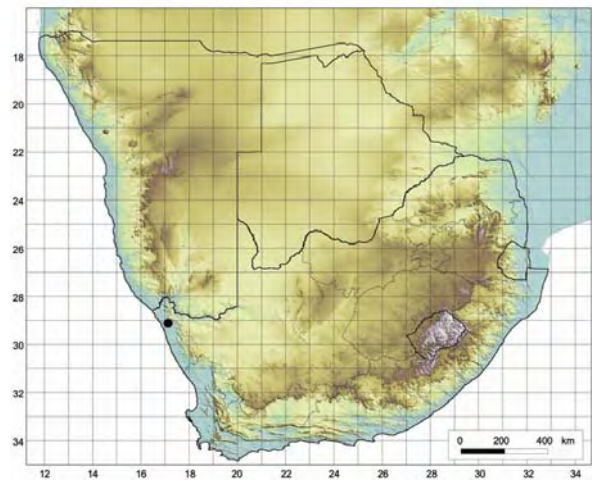
MAP 177. *Conophytum carpianum*.



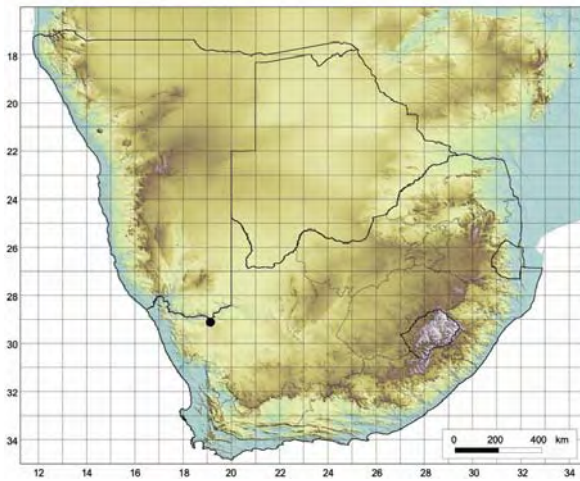
MAP 178. *Conophytum danielii*.



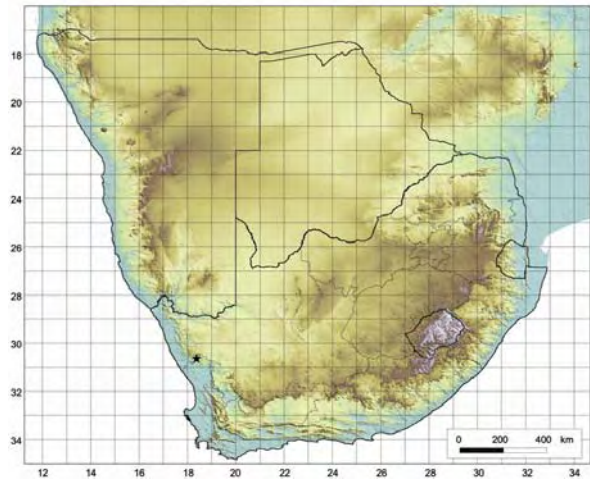
MAP 179. *Conophytum ernstii* subsp. *ernstii*.



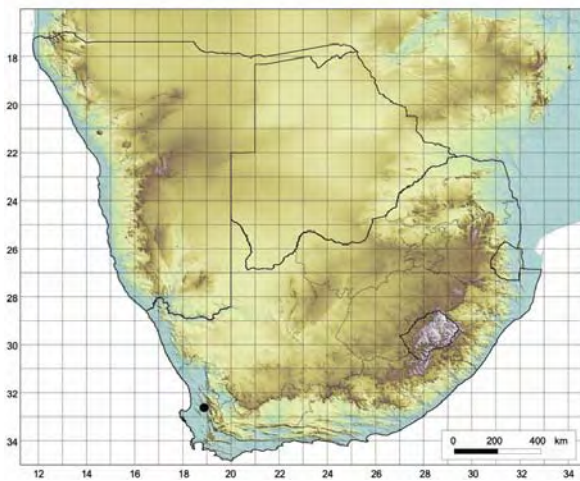
MAP 180. *Conophytum francoiseae*.



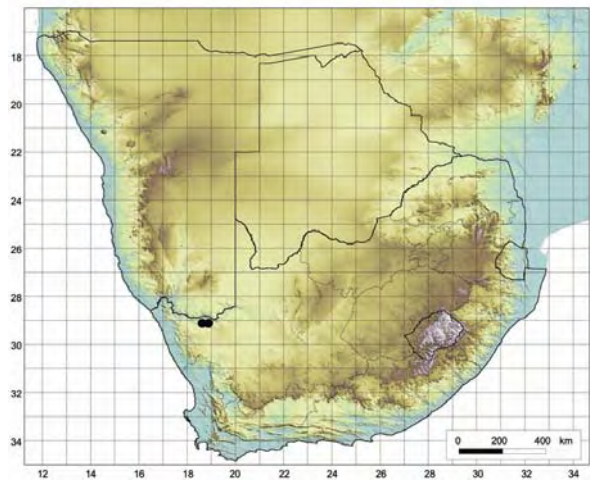
MAP 181. *Conophytum fulleri*.



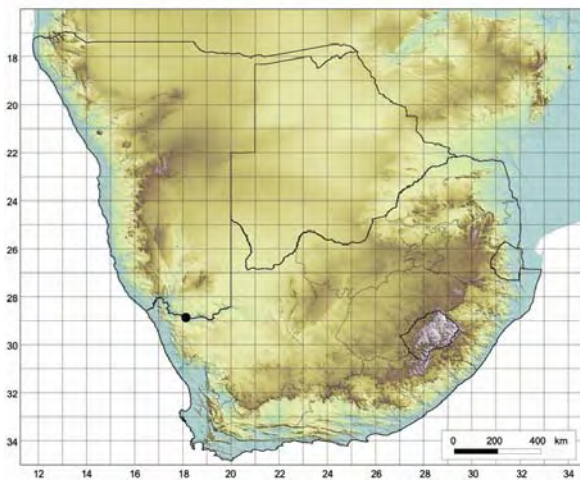
MAP 182. *Conophytum hanae*.



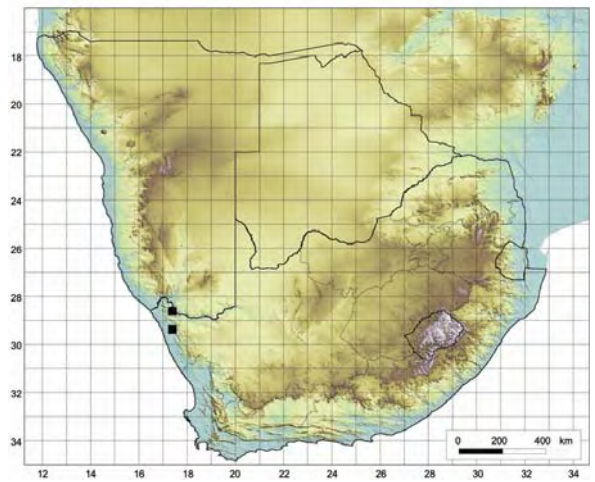
MAP 183. *Conophytum luckhoffii*.



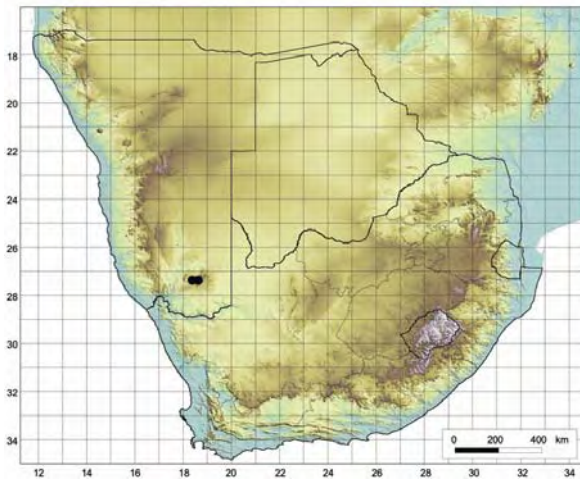
MAP 184. *Conophytum marginatum* subsp. *haramoepense*.



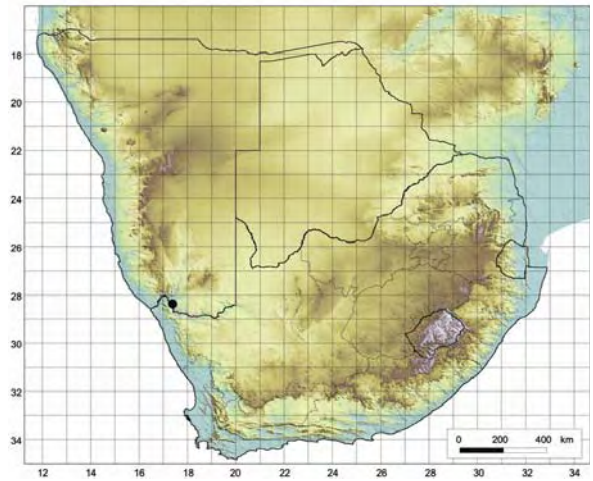
MAP 185. *Conophytum marginatum* subsp. *littlewoodii*.



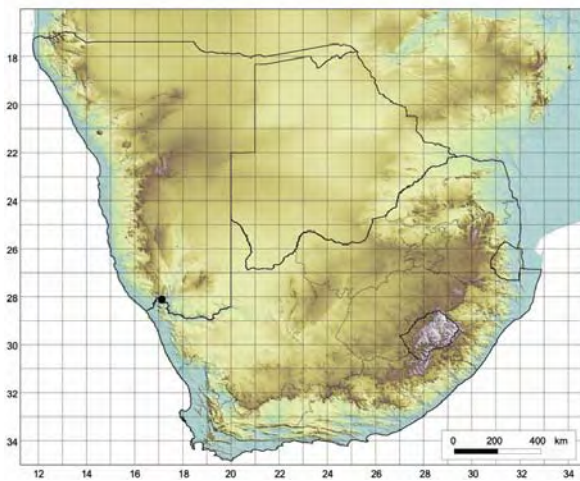
MAP 186. *Conophytum obscurum* subsp. *sponsaliorum*.



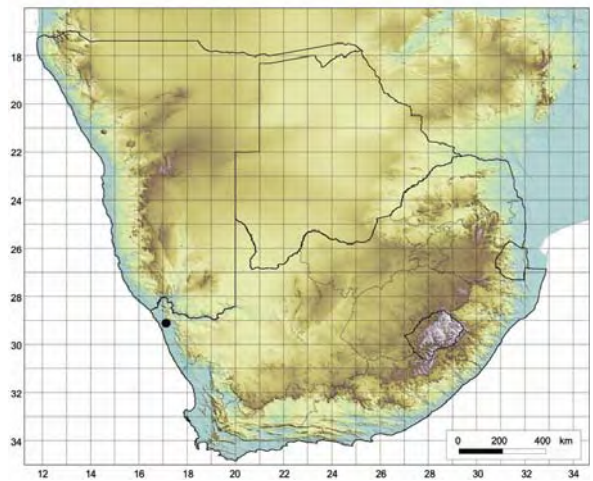
MAP 187. *Conophytum quaesitum* subsp. *densipunctum*.



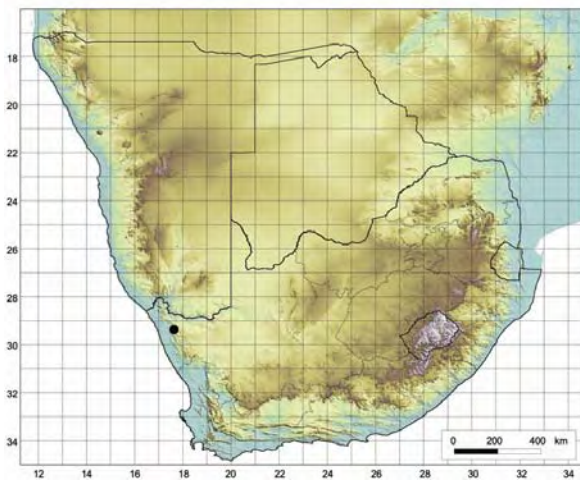
MAP 188. *Conophytum quaesitum* subsp. *quaesitum* var. *rostratum*.



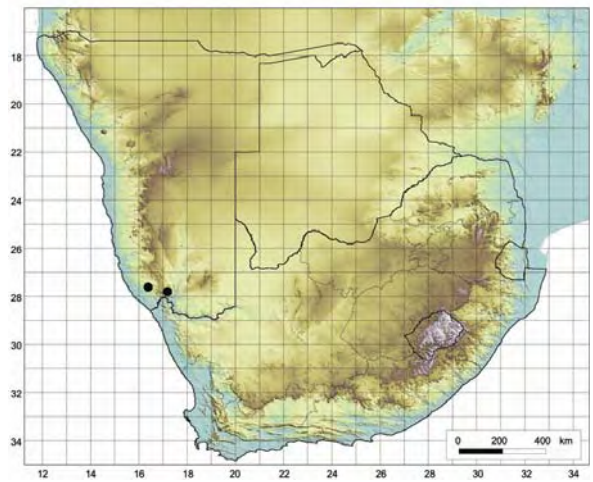
MAP 189. *Conophytum ricardianum* subsp. *ricardianum*.



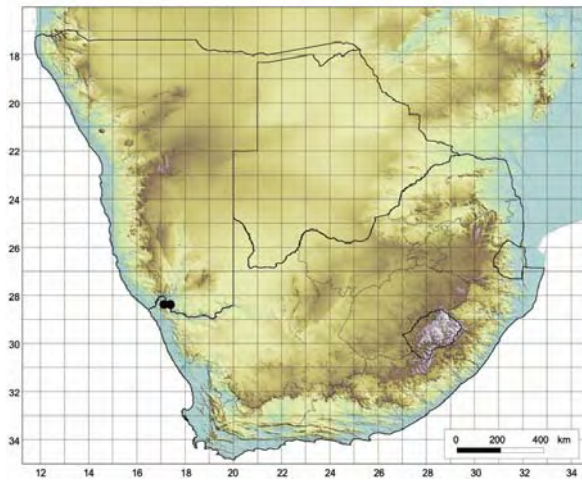
MAP 190. *Conophytum stephanii* subsp. *stephanii*.



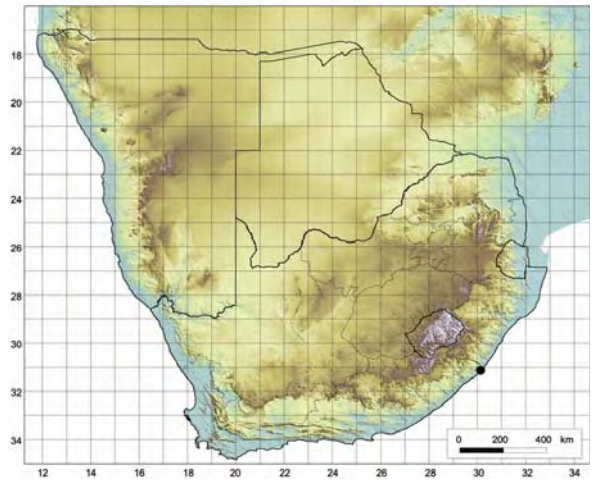
MAP 191. *Conophytum tantillum* subsp. *amicum*.



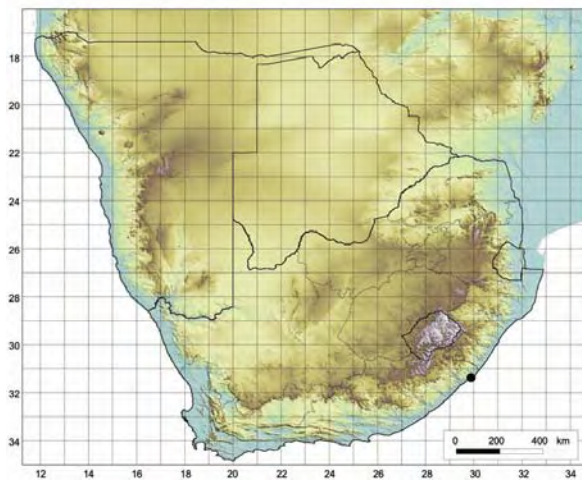
MAP 192. *Conophytum taylorianum* subsp. *ernianum*.



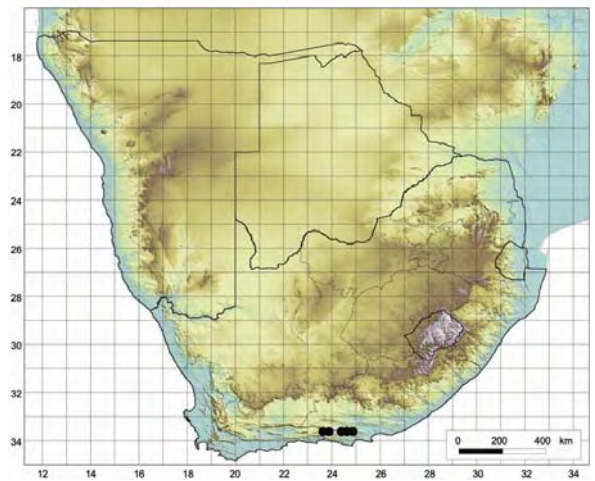
MAP 193. *Conophytum taylorianum* subsp. *rosynense*.



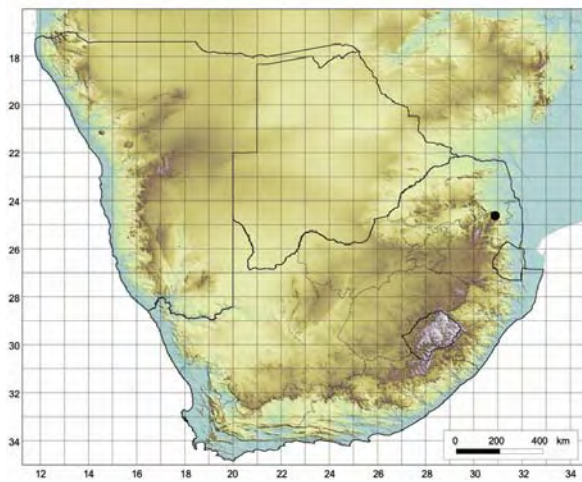
MAP 194. *Delosperma* sp. A.



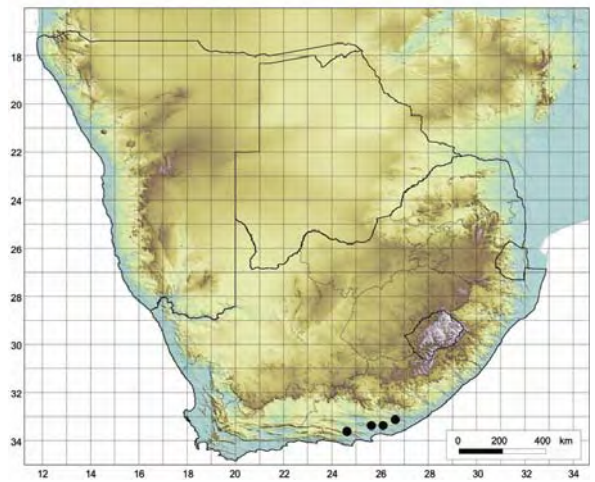
MAP 195. *Delosperma* sp. B.



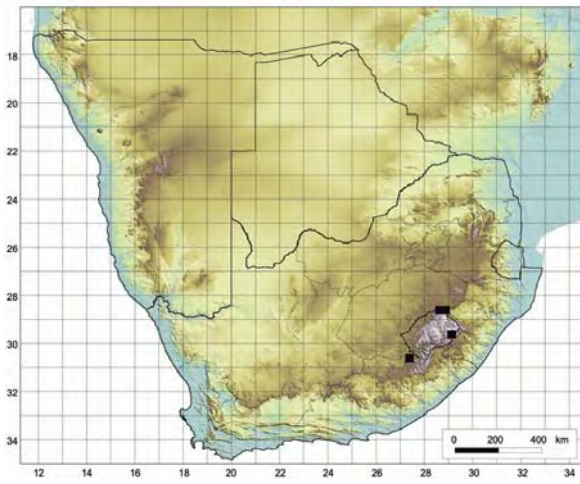
MAP 196. *Delosperma esterhuyensiae*.



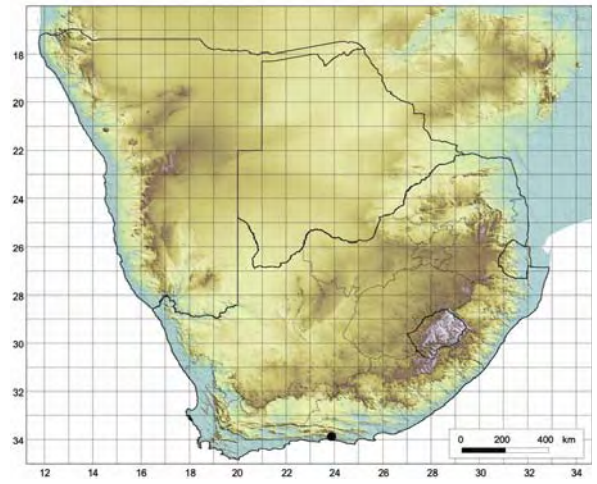
MAP 197. *Delosperma knox-daviesii*.



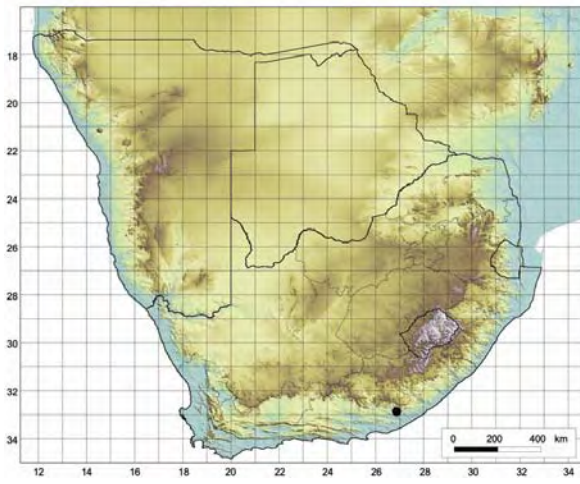
MAP 198. *Delosperma laxipetalum*.



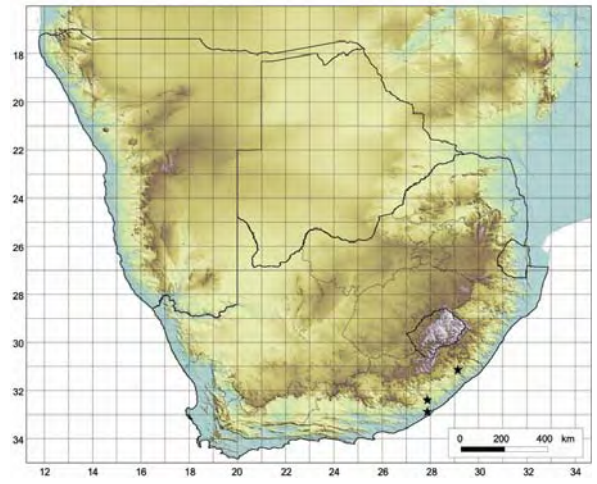
MAP 199. *Delosperma nubigenum*.



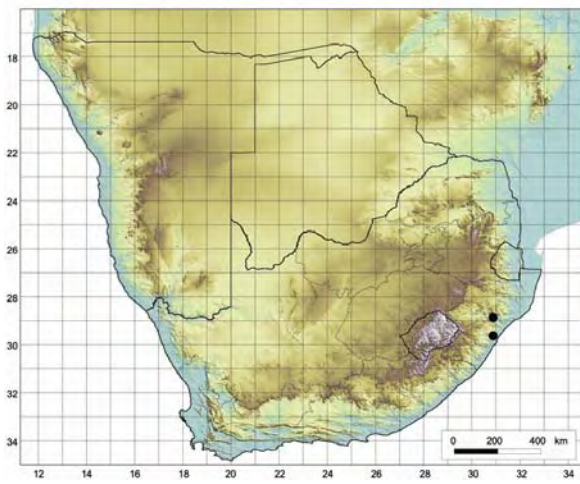
MAP 200. *Delosperma saxicola*.



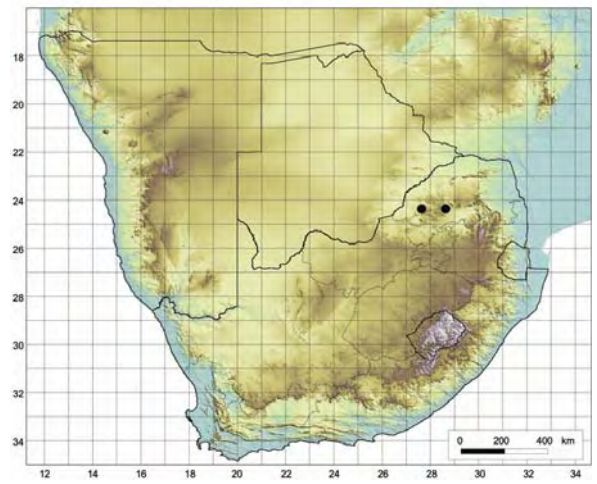
MAP 201. *Delosperma subpetiolatum*.



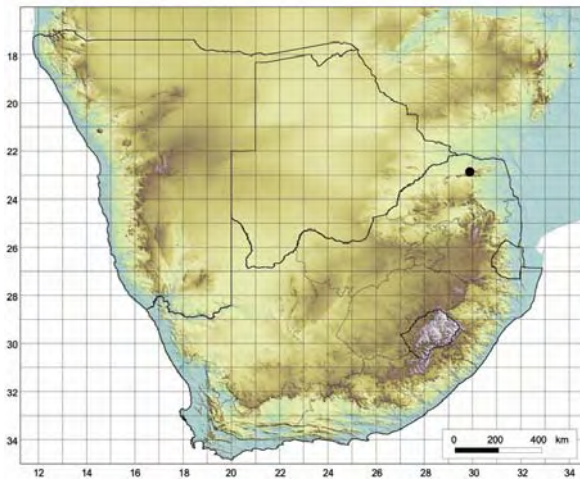
MAP 202. *Delosperma tradescantioides*.



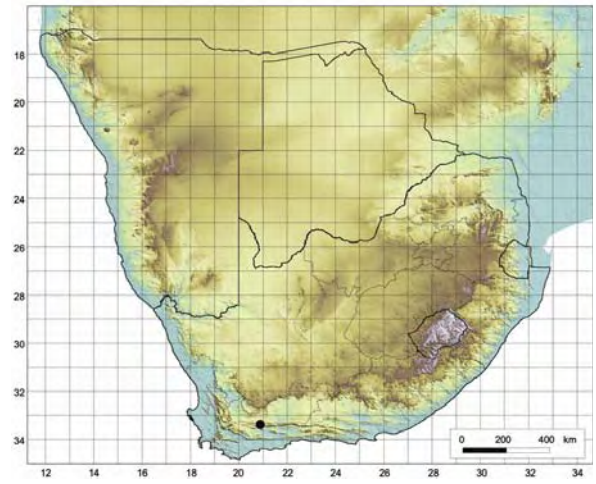
MAP 203. *Delosperma velutinum*.



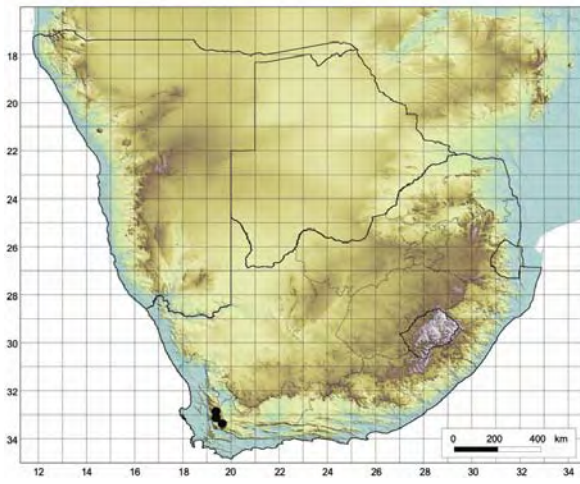
MAP 204. *Delosperma waterbergense*.



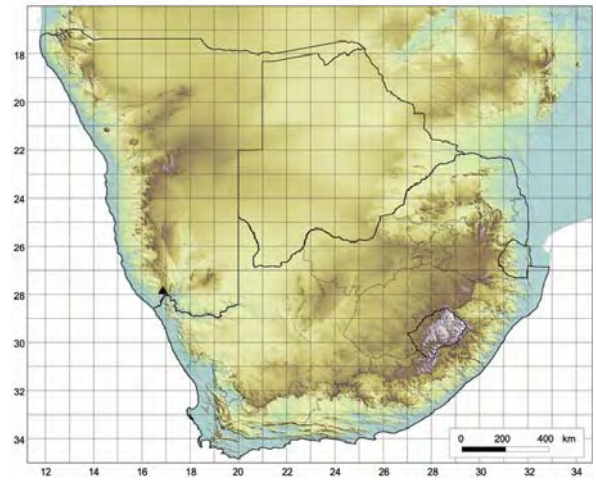
MAP 205. *Delosperma zoutpansbergense*.



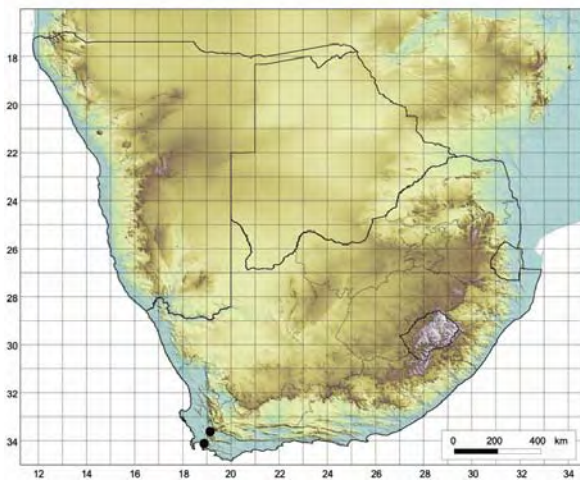
MAP 206. *Drosanthemum anemophilum*.



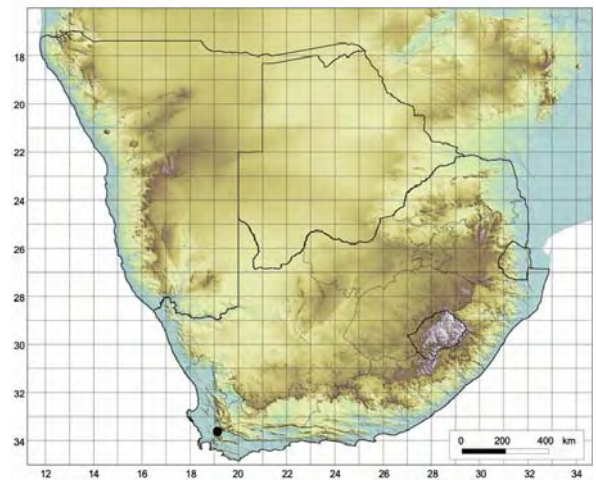
MAP 207. *Drosanthemum expersum*.



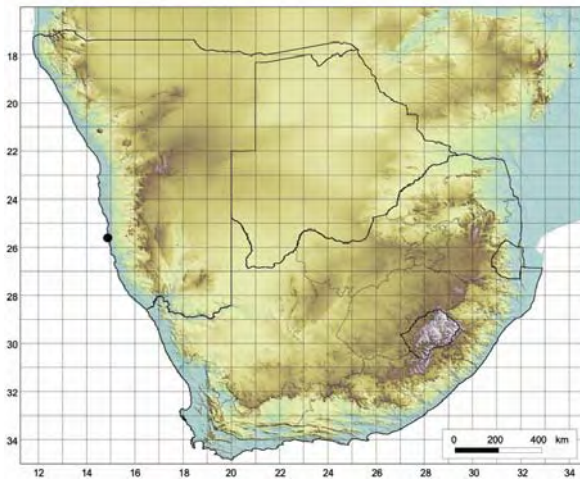
MAP 208. *Drosanthemum inornatum*.



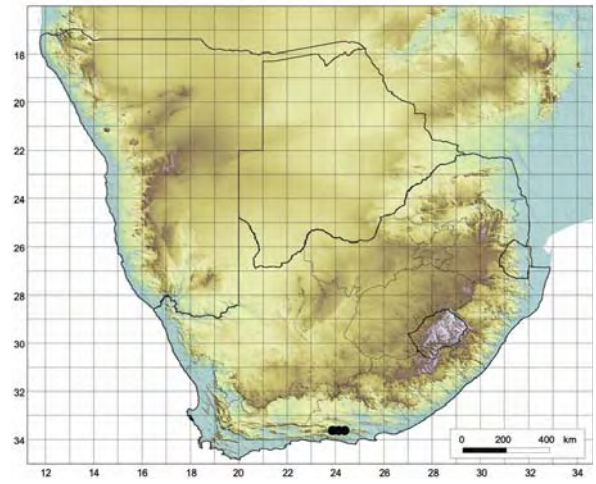
MAP 209. *Erepisia heteropetala*.



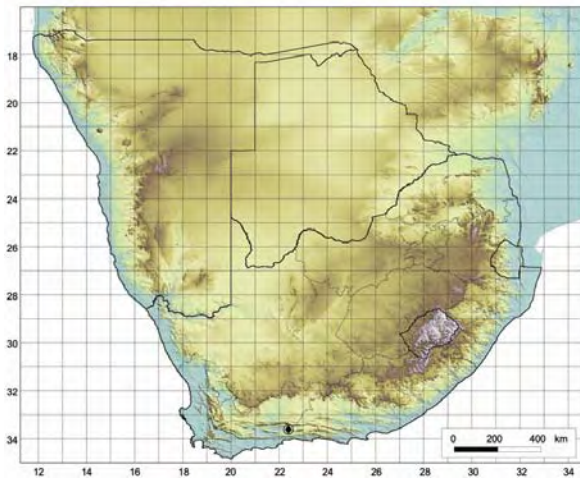
MAP 210. *Esterhuysenia stokoei*.



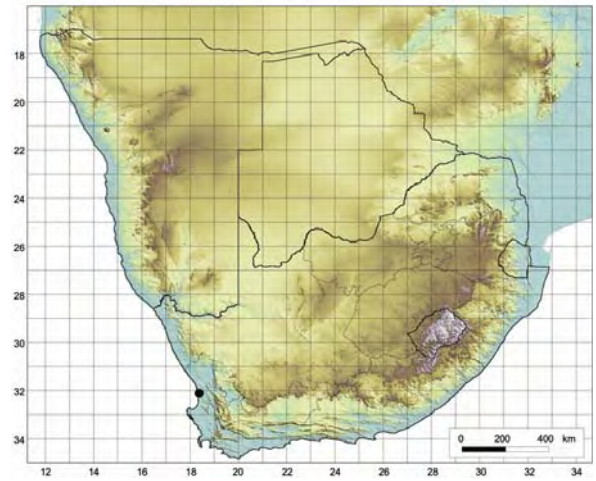
MAP 211. *Jensenobotrya lossowiana*.



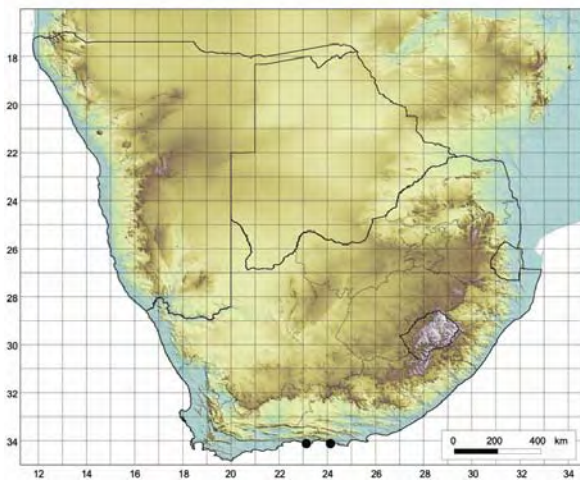
MAP 212. *Lampranthus affinis*.



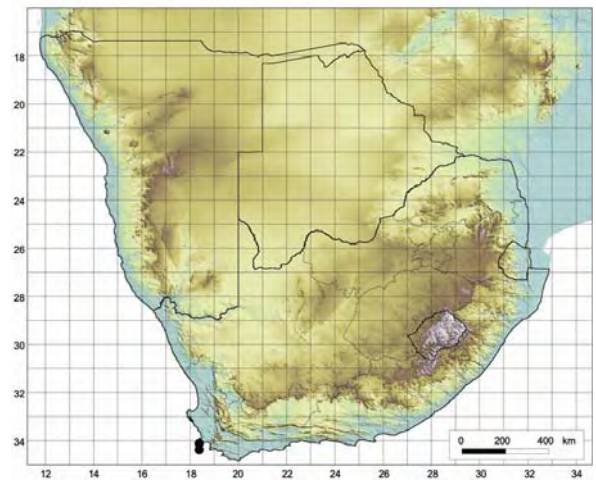
MAP 213. *Machairophyllum brevifolium*.



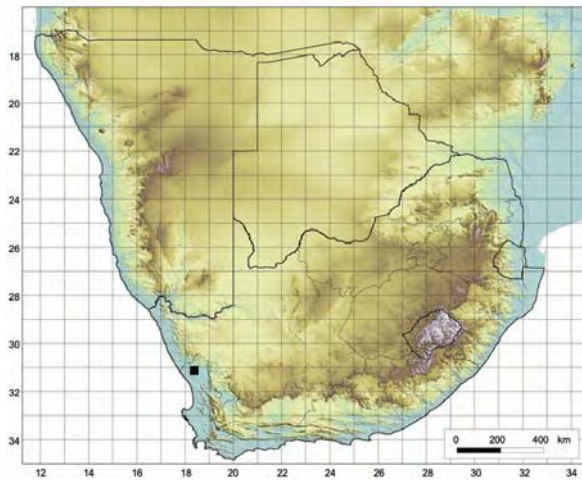
MAP 214. *Oscularia cremnophila*.



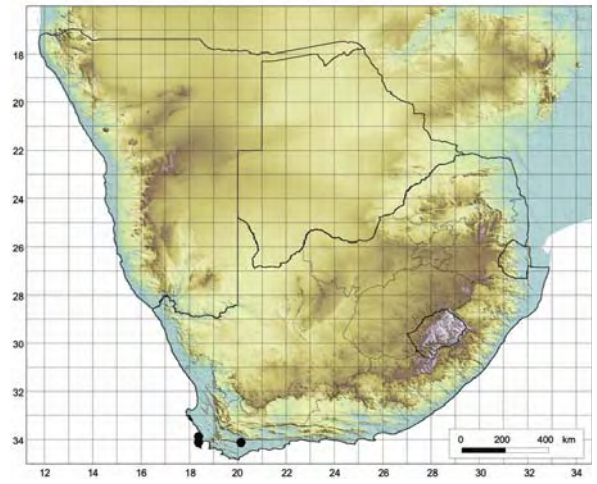
MAP 215. *Ruschia knysnana*.



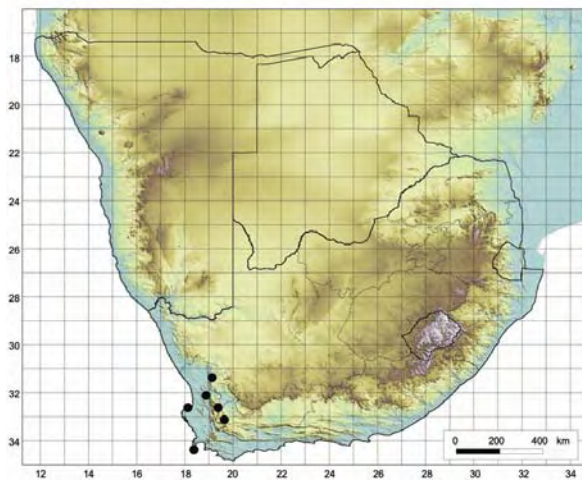
MAP 216. *Ruschia promontorii*.



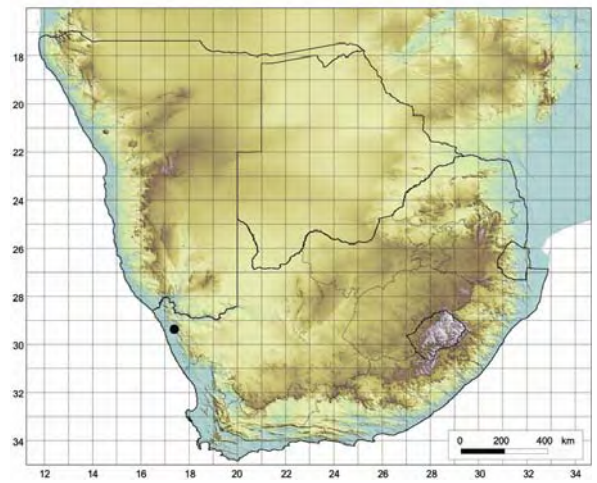
MAP 217. *Scopelogenia bruynsii*.



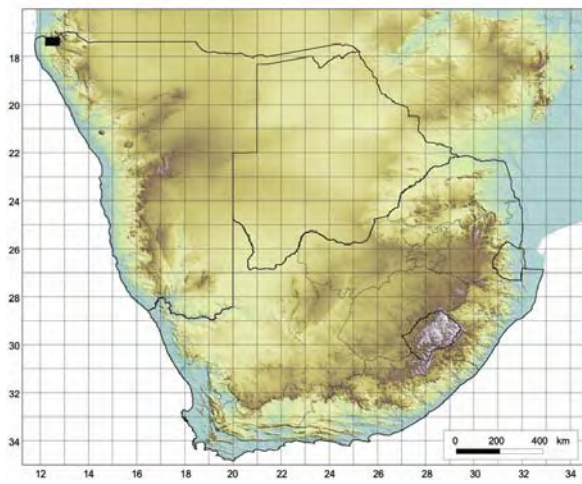
MAP 218. *Scopelogenia verruculata*.



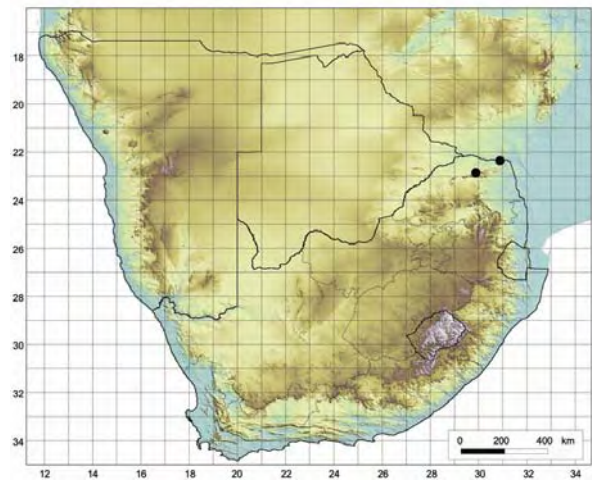
MAP 219. *Oxalis pocockiae*.



MAP 220. *Anacampteros scopata*.



MAP 221. *Dewinteria petrophila*.



MAP 222. *Stemodiopsis rivae*.

SUMMARY

The vertical cliff-face habitat is renowned for many specifically adapted plant species and exhibits a high degree of local endemism. Over the past nine years, only the succulent and bulbous succulent plants on cliff faces in South Africa and Namibia were systematically surveyed and documented. Distinction was made between succulent plants growing on cliffs as part of a wider habitat and those that are found only on cliffs (obligate cremnophytes). Most major cliff-face habitats were visited and all plants on cliffs throughout the study area were documented. A check list of the 220 obligate cremnophytes is provided as well as a description (including adaptive traits) of every succulent cremnophilous taxon encountered.

During the course of this study about 45 new cremnophilous succulent taxa were named, representing almost 20% of the total and proving that cliff habitats are one of the least studied regions, not only in southern Africa but globally. Among the newly described cremnophilous taxa (also see Appendix 1) is the genus *Dewinteria*. New taxa were also named in the following genera: *Adromischus* (2 taxa), *Aeollanthus* (1 taxon), *Albuca* (2 taxa), *Aloe* (4 taxa), *Bulbine* (7 taxa), *Cotyledon* (3 taxa), *Crassula* (4 taxa), *Drimia* (2 taxa), *Drosanthemum* (1 taxon), *Esterhuysenia* (1 taxon), *Gasteria* (3 taxa), *Ornithogalum* (1 taxon), *Plectranthus* (1 taxon), *Senecio* (1 taxon), *Tetradenia* (1 taxon) and *Tylecodon* (4 taxa). A surprising rediscovery was that of *Crassula cymbiformis* [117] in the Limpopo Province. After this species was first collected by Dave Hardy from Ränkins Pass in the Waterberg, it could not be found again in spite of several expeditions to the region. It was, however, recently rediscovered in the nearby Kransberg (Marakele National Park) where large numbers of the plants occur on south-facing cliffs.

Observations made during the present project fully support earlier statements that cliffs are among the most poorly explored and least known habitats on earth. Exploration of the cliffs of the Baynes and Otjihipa Mountains in Namibia revealed *Aloe catengiana* [14] and *Schizostephanus gossweileri*, first records of these plants for Namibia. South Africa and Namibia have a rich and unique cliff-face flora and distribution records of many cremnophilous plants have been extended by the study.

The various cliff-adapted growth forms are also described, discussed and compared to closely related facultative cremnophytes. Using stem length, three basic cliff-face growth forms have been identified: compact or cluster-forming plants ('cliff huggers'), cliff shrublets ('cliff squatters') and pendent plants ('cliff hangers'). The compact growth (often tight clusters or mats) is mainly associated with the winter-rainfall Succulent Karoo and Thicket regions and especially Namaqualand. However, further north the same compact growth forms are associated with an increase in altitude such as the Drakensberg Escarpment and other northern mountains. Most pendent growth forms are associated with the eastern and southeastern summer-rainfall regions; there are also a number of smaller pendent shrublets from the high quartzitic sandstone mountains of the Western Cape.

The degree of specialisation varies from highly adapted (smaller percentage) to less specialist (often eco-forms), while some taxa have no obvious adaptations. This study revealed a general increase in succulence in most obligate cremnophilous succulent plant species (compared to closely related species in other habitats), a reflection of their xeric habitat. The plants furthermore tend to be more compact (leaves crowded or in a tight rosette).

Owing to an absence of larger herbivores that can cause disturbances on cliffs, cremnophytes display a relaxation in defence mechanisms. There is a general decrease in mechanical, chemical and camouflage defence mechanisms, but with a few exceptions.

There is furthermore a shift in reproductive output, including an increase in vegetative reproduction (backup), wind-dispersed seed and rich flowering associated with certain species. Most obligate cremnophilous succulent plants in the study area have cliff-adapted features (morphology and reproductive output) that ensure their long-term survival.

Compared to the rich variety of obligate cremnophilous succulents (and succulent bulbous plants) found on cliffs in South Africa and Namibia, there are relatively few non-succulent obligate cremnophytes. The extreme run-off in this environment makes it necessary for plants to store water. This is virtually impossible for non-succulent plants and without some additional adaptation, they cannot survive in the cliff habitat. Poikilohydric plants such as lichens, ferns and mosses, on the other hand, are often found on cliffs. Lithophytic members of *Ficus* are well adapted, starting off as a succulent lithophyte but their wandering roots ensuring a normal tree in adulthood.

The few remaining herbaceous elements are highly specialised. They include the three chasmophytes *Dewinteria petrophila* [221], *Colpias mollis* and *Stemodiopsis rivae* [222]. *Dewinteria petrophila* (Kaokoveld) is a semisucculent annual or a weak perennial, depending on follow-up rains. It has a unique amphicarpic seed dispersal strategy (backup). The *in situ* self-sown, larger seed (from cleistogamous flowers and protected until germination) together with its dispersal of normal smaller aerial seed (smaller size but larger numbers) is an effective survival strategy. *Stemodiopsis rivae* (Limpopo Province) and *Colpias mollis* (Namaqualand) have peduncles that bend towards the dark crevices (where seeds are deposited) after fertilisation (local dispersal). Although not very succulent, *Dewinteria petrophila* and *Stemodiopsis rivae* were included in this study to demonstrate that without succulence (or additional vegetative backup dispersal), some form of reproductive specialisation is necessary for the long-term survival of non-succulent species in the cliff habitat.

OPSOMMING

Die vertikale krans-habitat is bekend vir talle spesifiek aangepaste plantsoorte en vertoon 'n hoë graad van endemisme. Oor die afgelope nege jaar is slegs die sukkulente en bolplant-sukkulente kremnofiete van Suid-Afrika en Namibië sistematies ondersoek en gedokumenteer. Onderskeiding is gemaak tussen sukkulente wat op kranse groei as deel van 'n groter habitat, en dié wat kransegebonde is en slegs op kranse groei. Die meeste belangrike kranse-habitats in die studiegebied is besoek en alle plante wat daar groei, is gedokumenteer. 'n Kontrolelys van die 220 kransegebonde taksons asook 'n beskrywing (ook aanpassingskenmerke) van elke sukkulente kremnofiele takson word verskaf.

Gedurende die studie is sowat 45 nuwe kranstaksons benaam, wat om en by 20% van die totaal insluit, 'n bewys dat kranse-habitats een van die onbekendste studieterreine verteenwoordig, nie net in Suid-Afrika nie maar wêreldwyd. Onder die nuut beskrewe kranstaksons (sien ook Appendix 1) is die genus *Dewinteria*. Nuwe taksons is ook in die volgende genusse benaam: *Adromischus* (2 taksons), *Aeollanthus* (1 takson), *Albuca* (2 taksons), *Aloe* (4 taksons), *Bulbine* (7 taksons), *Cotyledon* (3 taksons), *Crassula* (4 taksons), *Drimia* (2 taksons), *Drosanthemum* (1 takson), *Esterhuysenia* (1 takson), *Gasteria* (3 taksons), *Ornithogalum* (1 takson), *Plectranthus* (1 takson), *Senecio* (1 takson), *Tetradenia* (1 takson) en *Tylecodon* (4 taksons). 'n Verrassende herontdekking was dié van *Crassula cymbiformis* [117] in die Limpopo Provinsie. Nadat dit vir die eerste keer in Ränkinspas in die Waterberg deur Dave Hardy versamel is, is dit nie weer gevind is nie, ten spyte van verskeie soektogte. 'n Groot populasie egter is onlangs op die nabygeleë Kransberg (Marakele Nasionale Park) ontdek, waar groot getalle van hierdie plante teen kranse met 'n suidelike aansig voorkom.

Waarnemings wat tydens die huidige studie gedoen is, ondersteun vroeëre verklarings dat kranse van die mees verwaarloosde habitats op aarde verteenwoordig. Ontdekkingstogte in die Baynes- en Otjihipa-gebergtes in Namibië het *Aloe catengiana* [14] en *Schizostephanus gossweileri* opgelewer, die eerste keer dat hierdie plante in Namibië aangeteken is. Suid-Afrika en Namibië het 'n ryk en unieke kranseflora en nuwe inligting oor die verspreiding van talle kranseplante het met die studie aan die lig gekom.

Die onderskeie kransaanangepaste groeivorms word ook beskryf, bespreek en met verwante nie-kransgebonde plante vergelyk. Drie basiese kransgroeivorms kon op grond van stingellengte, geïdentifiseer word: kompakte of polvormende plante ('kransomhelsers'), kransstruikies ('kransplakkers') en hangende groeivorms ('kranshangers'). Die kompakte groeivorms (dikwels digte polle of matte) word meestal met winterreënstreke in Sukkulente Karoo en Ruigte, en veral Namakwaland, geassosieer. Verder noord kom dieselfde kompakte groeivorms voor, maar hier met groter hoogtes bo seespieël geassosieer, soos die Drakensberg Platorand en ander noordelike bergreekse. Die meeste hangende groeivorms word met die oostelike en suidoostelike somerreëngebiede geassosieer; daar is ook 'n aantal kleiner hangende struikies van die hoë kwartsitiese sandsteenberge van die Wes-Kaap.

Die graad van spesialisasie varieer van hoogs aangepas (kleiner persentasie) tot minder gespesialiseer (dikwels ekotipes), met sommige taksons sonder enige noemenswaardige aanpassings. Hierdie studie dui op 'n algemene toename in sukkulensie by die meeste kransgebonde sukkulente kremnofiete (in vergelyking met naby verwante soorte in ander habitats), 'n weerspieëling van hulle dor habitat. Die plante toon verder 'n meer kompakte groeiwyse (blare gedronge of in digte rosette).

Weens die afwesigheid van groter roofvryande wat versteuring op kranse kan veroorsaak, is daar 'n verslapping in verdedigingsmeganismes. Daar is 'n algemene afname in meganiese, chemiese en kamoefleringsaanpassings by kransgebonde sukkulente kremnofiete, alhoewel met enkele uitsonderings.

Daar is verder 'n verskuiwing in voortplantingstrategieë, waaronder 'n verhoging in vegetatiewe voortplanting (rugsteun), windverspreide saad en die vorming van groot blomme ('*rich flowering*') wat met sommige soorte geassosieer word. Die meeste kransgebonde sukkulente in die studiegebied toon kransaanangepaste eienskappe (morfologies en voortplantingsvermoë) wat oorlewing oor die lang termyn verseker.

In vergelyking met die ryk verskeidenheid kransgebonde kremnofiete (en bolsukkulente) wat in Suid-Afrika en Namibië aangetref word, is daar betreklik min nie-sukkulente kransgebonde plante. Die ekstreme vertikale terrein en afloop vereis dat plante water berg, maar dit is feitlik onmoontlik vir 'n nie-sukkulente en sonder 'n vorm van bykomende aanpassing kan so 'n plant nie in die krans-habitat oorleef nie. Poikilohidriese plante soos

korsmosse, varings en mosse, aan die ander kant, word dikwels op kranse aangetref. Litofitiese lede van *Ficus* is baie goed by kranse aangepas, aanvanklik met 'n vlesige stingel maar die dwalende wortels verseker 'n normale boom in die volwasse stadium.

Die paar oorblywende kruidagtige elemente op kranse is hoogs gespesialiseerd. Onder hulle is die drie chasmofiete *Dewinteria petrophila* [221], *Colpias mollis* en *Stemodiopsis rivae* [222]. *Dewinteria petrophila* (Kaokoveld) is 'n halvesukkulente eenjarige of 'n swak meerjarige, afhangend van opvolgreën. Dit het 'n unieke amfikarpiese saadverspreidingstrategie (rugsteun). Die *in situ*-selfgesaaide groter saad (van kleistogame blomme en beskerm totdat dit ontkiem) tesame met die verspreiding van normale kleiner bogrondse saad (kleiner maar groter hoeveelhede) is 'n doeltreffende oorlewingstrategie. *Stemodiopsis rivae* (Limpopo Provinsie) en *Colpias mollis* (Namakwaland) het bloeistele wat ná bevrugting na die donker klipskeure groei waar die saad dan neergelê word (plaaslike verspreiding). Hoewel nie baie sukkulent nie, is *Dewinteria petrophila* en *Stemodiopsis rivae* by hierdie studie ingesluit om te toon dat sonder sukkulensie (of bykomende vegetatiewe voortplanting as rugsteun), een of ander vorm van voortplantingspesialisasie nodig is vir die langtermynoorlewing van nie-sukkulente plante in die kranse-habitat.

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CURRICULUM VITAE

Ernst Jacobus van Jaarsveld

Ernst Jacobus van Jaarsveld was born in 1953 in Johannesburg, South Africa. He matriculated at Hoërskool Linden in 1971 and then studied at the Pretoria Technikon where he received his National Diploma in Horticulture in 1975. In 1988 he enrolled as M.Sc. student (Systematics) at Natal University and successfully completed the course in March 1990.

Employed by the National Botanic Gardens (today the South African National Biodiversity Institute), he initially spent two years at the Lowveld National Botanical Garden in Nelspruit and then in 1976 took up the position of Horticulturist at Kirstenbosch National Botanical Garden where he is still employed. His experience includes ornamental horticulture, botany and botanical exploration.

The horticultural component is mainly by way of ecological gardening with and promotion of South African plants, especially drought-resistant (xerophytic) flora, with the emphasis on succulent plants, both in the Kirstenbosch Conservatory and Matthews Rockery. At Kirstenbosch he specialises mainly in succulents and other xerophytic plants. He is in charge of the Botanical Society Conservatory (opened in September 1996) and has planned it to represent all the major arid biomes of South Africa and Namibia. For a holistic approach, he also introduced the various geological formations, with the emphasis on the great diversity of succulents in the region, their adaptations and ethnic uses. He received a Chairman's Award from his employer in recognition of these undertakings.

Ernst has travelled widely and has collected plants with potential ornamental use throughout Southern Africa, many of which have been successfully introduced into cultivation. He has been invited abroad several times to address various congresses and meetings on the subject of succulent plants. He is a member of the International Organization of Succulent Plant Study (IOS) and has also served as Co-ordinator of the Aloaceae section of the IOS.

Botanical exploration has been conducted in various parts of southern Africa (South Africa, Namibia, Lesotho and Swaziland). An expedition to Madagascar was undertaken on invitation of President Marc Ravalomanana. Apart from general collecting and exploration of succulent plants, his investigations also include expeditions in search of cremnophilous bulbous and succulent plants.

Ernst van Jaarsveld is the author or co-author of more than 200 popular, semi-scientific or scientific articles and various books, which include the following:

- *A revision of the genus Gasteria* (Fernwood, 1994).
- *Flowers of southern Africa: the Sappi selection* by Thalia Lincoln (co-authors J.P. Rourke & G. Duncan) (Sappi, 1995).
- *List of southern African succulent plants* (participated as co-author with various others) (Umdaus, 1997).
- *Mesembs of the world* (participated as co-author with various others) (Briza, 1998).
- *Succulents of South Africa, a guide to their regional diversity* (co-authors B-E. van Wyk & G.F. Smith) (Tafelberg, 2000).
- *Vygies, gems of the veld* (co-author U. de V. Pienaar) (Cactus & Co. Libri, 2000).
- *Wonderful waterwise gardening* (Tafelberg, 2000).
- *Gerhard Dreyer's Wild flowers* (Sunbird, 2003).
- *Cotyledon and Tylecodon* (co-author D. Koutnik) (Umdaus, 2004).
- *Plectranthus in South Africa and Namibia and the art of turning shade into glade* (Fernwood, 2006).
- *Waterwise gardening* (Struik, 2010).

Ernst is also the author of two soft-cover booklets, *Plectranthus Handbook* (National Botanic Gardens, 1984) and *Eastern Transvaal splendour* (Caltex South Africa, 1995). In 1995 he gave a series of 45 radio talks on invitation of the South African Broadcasting Corporation.

He has written parts of three volumes of the *IOS Illustrated handbook of succulent plants* (editor U. Egli): *Monocotyledons* (Springer, 2001), *Dicotyledons* (Springer, 2002) and *Crassulaceae* (Springer, 2003).

Ernst van Jaarsveld is the author or co-author of the names of more than 95 plant taxa described as new to science, three of them with distributions that extend into Namibia and one in Angola.

He has been a member of the *Species Survival Commission* of the IUCN. In this capacity he was involved in drawing up a strategic succulent conservation plan for the Aloaceae, South African subregion, and provided guidance on the conservation of the following threatened species: *Saphesia flaccida*, *Freylinia visseri* (became extinct in habitat but was replanted), *Jordaaniella anemoniflora* and *Gasteria baylissiana*.

In September 1996 he was made a fellow of the American Succulent and Cactus Society. In October 2003 he was awarded three medals: the Senior Captain Scott Medal by the Suid-Afrikaanse Akademie vir Wetenskap en Kuns for his research on South African plants, the Dudley D'Ewes Medal by the Botanical Society for the promotion of South African plants, and the Hans Herre Medal by the Succulent Society of South Africa.

He has written a series of monthly articles on indigenous plants for various magazines such as *Sarie*, *SA Gardening* and *Vrouekeur*, and publishes regularly in *Veld & Flora*, *Aloe* and other succulent journals (American and British). He has had a weekly column, *Vra vir Ernst*, in the *Buite Burger* (formerly *Kultuurkroniek*) (*Die Burger*, Western Cape Region, Tuesdays) and in *Huisgids* (*Die Beeld*, Gauteng Region, Fridays) since 1996. Since 2010 the column appears weekly in *By* (*Beeld*, *Die Burger*).

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- 1974–1976: Horticulturist, Lowveld Botanical Garden (National Botanic Gardens).
- 1976–currently: Horticulturist, Kirstenbosch National Botanical Garden (National Botanical Gardens, National Botanical Institute and South African National Biodiversity Institute).

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APPENDIX 1

DISCOVERY OF OBLIGATE CREMNOPHYTES NEW TO SCIENCE ON EXPEDITIONS BY THE AUTHOR AND COLLEAGUES

Collaborators on expeditions: Steven Carrs (Windhoek), Anton Cilliers, James Deacon, Paul Ems (SANBI), Adam Harrower (SANBI), Tielman Haumann, Gregory Nicolson, Wessel Swanepoel (Windhoek), Werner Voigt (SANBI), Rob Welsch and Phakhamani Xaba.

28 taxa new to science

Aeollanthus rydingianus [166]
Albuca cremnophila [64]
Albuca thermarum [68]
Aloe omavandae [25]
Anacampseros scopata [220]
Bulbine cremnophila [31]
Bulbine pendens [35]
Bulbine thomasiae [40]
Bulbine retinens [37]
Bulbine suurbergensis [39]
Conophytum ernstii [179]
Conophytum taylorianum subsp. *rosynense* [193]
Crassula badspoortense [113]
Cyrtanthus flammosus [3]
Drimia cremnophila [69]
Drimia mzimvubuensis [72]
Drosanthemum anemophilum [206]
Gasteria glauca [45]
Gasteria glomerata [46]
Gasteria tukhelensis [49]
Ornithogalum pendens [79]
Othonna cremnophila [88]
Plectranthus dolomiticus [167]
Plectranthus ernstii [168]
Plectranthus mzimvubuensis [170]
Tetradenia kaokoensis [173]
Tylecodon longipes [156]
Tylecodon petrophilus [157]

One new record for Namibia

Aloe catengiana [14] (formerly known only from southern Angola)

Two new records for Angola

Tetradenia kaokoensis [173]
Aloe omavandae [25]

APPENDIX 2

NEW CREMNOPHILOUS PLANT TAXA IN SOUTH AFRICA AND NAMIBIA DESCRIBED BY THE AUTHOR OR IN COLLABORATION WITH OTHER AUTHORS

(55 taxa described and one awaiting formal description. *Plants named before 2000.)

- Adromischus cristatus* (Haw.) Lem. var. *mzimvubuensis* Van Jaarsv. [96]
Adromischus liebenbergii Hutchison subsp. *orientalis* Van Jaarsv. [102]
Adromischus schuldianus (Poelln.) Poelln. subsp. *brandbergensis* B.Nord. & Van Jaarsv. [103]
Aeollanthus haumannii Van Jaarsv. [165]
Aeollanthus rydingianus Van Jaarsv. & A.E.van Wyk [166]
Albuca thermarum Van Jaarsv. [68]
Albuca cremnophila Van Jaarsv. & A.E.van Wyk [64]
Aloe arborescens Mill. subsp. *mzimnyati* Van Jaarsv. & A.E.van Wyk [13]
Aloe challisii Van Jaarsv. & A.E.van Wyk [15]
Aloe dabenorisana Van Jaarsv. [17]*
Aloe kouebokkeveldensis Van Jaarsv. & A.B.Low [21]
Aloe meyeri Van Jaarsv. [22]*
Aloe omavandae Van Jaarsv. [25]
Aloe pavelkae Van Jaarsv., Swanepoel, A.E.van Wyk & Lavranos [26]
Bulbine cremnophila Van Jaarsv. [31]
Bulbine latifolia (L.f.) Schult. & Schult.f. var. *curvata* Van Jaarsv. [32]
Bulbine meiringii Van Jaarsv. [33]
Bulbine ramosa Van Jaarsv. [36]
Bulbine suurbergensis Van Jaarsv. & A.E.van Wyk [39]
Bulbine thomasiae Van Jaarsv. [40]
Cotyledon elisae Van Jaarsv. [107]
Cotyledon pendens Van Jaarsv. [108]
Crassula badspoortense Van Jaarsv. [113]
Crassula cremnophila Van Jaarsv. & A.E.van Wyk [116]
Crassula foveata Van Jaarsv. [122]
Crassula smithii Van Jaarsv., D.G.A.Styles & G.McDonald [143]
Cyrtanthus flammosus Snijman & Van Jaarsv. [3]*

- Drimia cremnophila* Van Jaarsv. [69]
Drimia loedolffiae Van Jaarsv. [71]
Drimia mzimvubuensis Van Jaarsv. [72]
Drosanthemum anemophilum Van Jaarsv. & S.A.Hammer [206]
Drosanthemum sp. nov. (awaiting description)
Gasteria batesiana G.D.Rowley var. *dolomitica* Van Jaarsv. & A.E.van Wyk [42]
Gasteria croucheri (Hook.f.) Baker subsp. *pendulifolia* (Van Jaarsv.) Zonn. [43]
Gasteria doreeniae Van Jaarsv. & A.E.van Wyk [44]
Gasteria glauca Van Jaarsv. [45]*
Gasteria glomerata Van Jaarsv. [46]*
Gasteria tukhelensis Van Jaarsv. [49]
Ledebouria cremnophila S.Venter & Van Jaarsv. [75]
Ledebouria venterii Van Jaarsv. & A.E.van Wyk [76]
Ornithogalum juncifolium Jacq. var. *emsii* Van Jaarsv. & A.E.van Wyk [77]
Ornithogalum pendens Van Jaarsv. [79]
Oscularia cremnophila Van Jaarsv., Desmet & A.E.van Wyk [214]
Othonna armiana Van Jaarsv. [86]
Othonna cremnophila B.Nord. & Van Jaarsv. [88]
Pelargonium vanderwaltii Van Jaarsv. [163]
Plectranthus mzimvubuensis Van Jaarsv. [170]
Plectranthus saccatus Benth. subsp. *pondoensis* Van Jaarsv. & Milstein [172]
Senecio pondoensis Van Jaarsv. & A.E.van Wyk [92]
Tetradenia kaokoensis Van Jaarsv. & A.E.van Wyk [173]
Tylecodon bodleyae Van Jaarsv. [150]*
Tylecodon bruynsii Van Jaarsv. & S.A.Hammer [151]
Tylecodon ellaphieae Van Jaarsv. [155]*
Tylecodon longipes Van Jaarsv. & G.Will. [156]*
Tylecodon petrophilus Van Jaarsv. & A.E.van Wyk [157]
Tylecodon sulphureus (Toelken) Toelken var. *armianus* Van Jaarsv. [159]*

APPENDIX 3

LIST OF PUBLICATIONS ON SUCCULENT AND BULBOUS SUCCULENT CREMNOPHYTES AS WELL AS ON OTHER SUCCULENT PLANT TAXA BY THE AUTHOR OR IN COLLABORATION WITH OTHER AUTHORS

1. Articles

- MOLL, E. & VAN JAARSVELD, E.J. 2007. Table Mountain's cliff-face flora. *Veld & Flora* 93,4: 226–227.
- NORDENSTAM, B. & VAN JAARSVELD, E.J. 2005. *Othonna cremnophila*, a new species of the Asteraceae-Senecioneae from the Richtersveld, Northern Cape Province, South Africa. *Aloe* 42,1 & 2: 4–7.
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- VAN JAARSVELD, E.J. 1988. Kirstenbosch Botanical Gardens with specific reference to *Cotyledon tomentosa* and the succulent collection. *National Cactus and Succulent Journal (U.S.)* 60: 252–257.

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- VAN JAARVELD, E.J., DESMET, P. & VAN WYK, A.E. 2005. *Oscularia cremnophila*, a rare new species from Western Cape, South Africa. *Bothalia* 35: 160–163.
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- VAN JAARVELD, E.J. & VAN WYK, A.E. 2004. *Gasteria doreeniae*, a new species from the Eastern Cape. *Aloe* 41,4: 81–83.
- VAN JAARVELD, E.J. & VAN WYK, A.E. 2004. *Plectranthus mzimvubuensis*, a new species from eastern Cape, South Africa. *Bothalia* 34: 30–32.
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- VAN JAARVELD, E.J. & VAN WYK, A.E. 2005. *Aeollanthus rydingianus*, a new species from northern Namibia and southern Angola. *Bothalia* 35: 157–160.

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- VAN JAARVELD, E.J. & VAN WYK, A.E. 2005. *Ornithogalum juncifolium* var. *emsii*, a new cliff-dwelling *Ornithogalum* from Eastern Cape, South Africa. *Bothalia* 35: 82–84.
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