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 180º (the underside of an overhang) to 90º are all strictly "cliff", whereas slope angles less that 90º 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 90º 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). Oettli (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 & Burtt 1987; Hammer 1993; Van Jaarsveld 1991b, 1994a,b; Retief & Herman 1997; Goldblatt & Manning 2000; Eggli 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.

Cremnophyte: 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 cremnophytes can also be classified as chasmophytes, but not all chasmophytes are cremnophytes (cliff-dwelling). Obligate succulent cremnophytes 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]).
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> **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]).
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> **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].

Amphicarpy: The term amphicarpy was reviewed by Barker (2005). 'Amphi' is a prefix pertaining to two types, systems or sides. According to Cheplick (1987), amphicarpy 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 an 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 amphicarpy and geocarpy in plants growing on cliff faces adapted from Barker (2005)

Terminology	Type	Subtype	Species
Active cremnocarpy	subterranean (crevice) fruiting from aerial flowers	aerial flowering and subsequent burial in cliff crevice by active growth	*Colpias mollis*, *Stemodiopsis rivae* [222]
Cremno-amphicarpy	two different floral and fruiting modes (crevice cleistogamy and aerial chasmogamy)	flowers and fruits produced above and in cliff crevices	*Dewinteria petrophila* [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 Egosa 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 cm^2. Igneous rocks had values ranging from 500–3 000 kg cm^2 and tertiary sedimentary rocks 300–1 600 kg cm^2. Lavas have a much lower value, namely 200–400 kg cm^2.

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], *Lavrania 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 schuldtianus* 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 flanaganii* [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 cremnophytes 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 form 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 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-richer 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 cremnophytes 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 cremnophytes) 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 *Anacampseros 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, sometimes10–20 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 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 spathulate 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 *Lavrania* 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 *Lavrania 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 cremnophilous 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 reseeding (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. Cremnophytes 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 cremnophytes 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 cremnophytes. *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. Cremnophytes 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 cremnophytes 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 cremnophytes 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 cremnophytes 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 a 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 *Scopelogena* (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 badspoortense* [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 muirii* [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. *Lavrania* *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. Cremnophytes 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 cremnophytes

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 cremnophyte 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 cremnophytes 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 cremnophila* [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 badspoortense* [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. badspoortense* [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). Cremnophytes with cylindrical assimilating branches have been dealt with above. Many succulent cremnophytes 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 cremnophytes; leaf and bulb scales

Cremnophilous 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).

Cremnophilous 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 whither, 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. venteri* [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 flatted 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. gariepensis* (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 & Burtt 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. schuldtianus* 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 muirii* [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. Cremnophytes 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 cremnophytes (*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 became 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 challisii* [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*).