CHAPTER 5

REPRODUCTION ON THE CLIFF

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

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

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

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

5.1 Sexual reproduction

5.1.1 Pollination

Gene exchange is vital for sexual reproduction and necessitates an effective pollination strategy. Most pollinators of cremnophytes are free flying, and consequently effective in accomplishing pollination. However, the fact that cliffs are often large and very sparsely populated with plants demands an effective advertisement strategy. Attracting the right pollinator is accomplished by either sight or aroma (or both). These mechanisms include special adaptations for pollinator attraction, seed dispersal and vegetative reproduction.

5.1.1.1 Insect pollination

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

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

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

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

5.1.1.2 Bird pollination

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

5.1.1.3 Rich flowering

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

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

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

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

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

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

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

5.1.2 Dispersal

5.1.2.1 Seed

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

5.1.2.1.1 Wind (anemochorous diaspores)

Owing to their vertical orientation, cliffs often experience turbulence and updrafts of rising warm air that help to carry light seeds upwards. This is a very effective way of dispersal and, depending on the wind or storm, seeds can be carried to adjacent cliff faces. The author has experienced strong winds on cliffs at various sites and intervals. However, various potential problems are involved in the dispersal of seed on the cliffs. The seeds have to be effectively trapped and anchored in crevices—but they fall at random. Small wonder that most cremnophytes (in fact 162 or 74%) rely on the wind to disperse their diaspores, especially members of the Asphodelaceae, Crassulaceae, Asclepiadaceae, Hyacinthaceae and Asteraceae (Table 5.5). This is in agreement with the findings of Müller (1955) that the seeds of about 60% of alpine flora and 50% of the Mediterranean garigue are wind-dispersed. Flattish or winged seeds are more buoyant. Size is also important and owing to the haphazard nature of wind and the limited habitat, investment in numbers is crucial. Most of the disk-like airborne seeds of the Asphodelaceae are relatively small (2–3 mm in diameter) and, together with the dust diaspores, these tiny seeds are the prevailing state in most cremnophytes.

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

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

5.1.2.1.1.1 Flattish or disk-like winged diaspores

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

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

5.1.2.1.1.2 Diaspores with a single lateral wing

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

5.1.2.1.1.3 Seed with a parachute (plumed diaspores)

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

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

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

5.1.2.1.1.4 Dust diaspores

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

5.1.2.1.1.5 Wind-ballists (anemoballists)

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

5.1.2.1.2 Water dispersal (hydrochory)

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

5.1.2.1.2.1 Wash-out dispersal

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

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

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

5.1.2.1.3 Bird-dispersed diaspores

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

5.1.2.1.4 Autochory (*in situ* dispersal)

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

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

5.1.2.1.5 Dimorphic dispersal strategy (amphicarpy) of semisucculent cremnophytes

The terms amphicarpy and geocarpy are defined in Chapter 2.

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

Dewinteria petrophila [221] is a remarkable chasmo-cremnophyte displaying a unique dimorphic facultative reproduction strategy (Van Jaarsveld & Van Wyk 2007a; Van Jaarsveld *et al.* 2009). It is a semisucculent biennial (rarely annual) or weak perennial. It grows under desert and semidesert conditions on the Otjihipa Mountains in the northern Namibia. In addition to its conventional aerial branches with insect-pollinated flowers and wind-dispersed seed, it produces specialised shoots that are negatively phototropic and enter crevices. These shoots bear small cleistogamous flowers developing heart-shaped capsules with fewer but large, differently shaped seeds (*in situ* dispersal) (Van Jaarsveld *et al.* 2009).

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

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

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

5.2 Vegetative (asexual) reproduction

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

5.2.1 Bulbil propagules

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

5.2.2 Winged bulbils

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

5.2.3 Inflorescence propagules

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

5.2.4 Leaf propagules

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

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

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

5.2.5 Bulb scale propagules

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

5.2.6 Dividing or proliferating clusters

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

5.2.7 Active growth

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

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

5.3 Establishment

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

5.3.1 Crevices

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

5.3.2 Cliff-face lichen fields

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

5.3.3 Germination

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

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

Taxon	Flower segments (mm)	Pollinator	Cremnophyte	Non-cremnophyte
C. flammosus [3]	40–50 × 30–35	*Meneris tulbaghia*	×	
C. elatus	35–45 × 20–30	*Meneris tulbaghia*		×
C. sanguineus	40 × 18	*Meneris tulbaghia*	×	
C. guthrieae	43 × 19	*Meneris tulbaghia*		×
C. galpinii	20 × 7–9	?		×

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

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

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

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

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

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

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

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

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

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

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

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

CHAPTER 6

PHYTOGEOGRAPHY OF OBLIGATE SUCCULENT AND BULBOUS CREMNOPHYTES

6.1 Background

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

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

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

6.2 Size of the cliff face

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

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

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

6.3 Plant size

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

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

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

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

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

6.4 Endemism

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

6.5 South African and Namibian cliff faces

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

i Great Escarpment.

ii Inland mountains on the plateau.

iii Marginal zone (between the Great Escarpment and the coast, such as the Cape Fold Belt mountains and other mountains).

iv Riverine cliffs (along larger drainage lines; found essentially throughout the region, though more abundantly in the marginal zone).

v Inselbergs (isolated mountains such as the Brandberg and Blouberg).

vi Coastal cliffs (wave or river action).

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

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

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

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

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

6.5.1 The cliffs of the Great Escarpment and inland

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

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

6.5.1.1 Cliffs of Mpumalanga Drakensberg (northeastern Great Escarpment)

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

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

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

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

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

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

6.5.1.3 Nuweveld and Roggeveld Mountains (southern Great Escarpment)

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

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

6.5.1.4 Kamiesberg

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

6.5.1.5 Namibia

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

Obligate succulent cremnophytes include *Aloe pavelkae* [26], *Conophytum ricardianum* [189], *C. taylorianum* subsp. *ernianum* [192], *Tylecodon bruynsii* [151], *T. singularis* [158] and *Cyrtanthus herrei* [5]. No obligate cremnophytes have been identified from the central part of Namibia. To the north, the Baynes Mountains (sandstone) support populations of *Aloe omavandae* [25] and *Tetradenia kaokoensis* [173]. The status of *Haemanthus avasmontana*, a possible obligate cremnophyte from the central part of Namibia, is uncertain. In spite of three expeditions, this plant of the mountains just south of Windhoek could not be relocated and was therefore omitted from the study.

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

6.5.2 Cliffs of the marginal zone

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

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

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

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

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

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

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

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

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

6.5.2.2 Greater Namaqualand zone

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

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

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

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

6.5.2.3 Kaoko marginal zone

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

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

6.5.2.4 Limpopo zone

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

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

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

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

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

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

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

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

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

Sandstone outcrops of the Msikaba Formation and Natal Group are prominent at Port St Johns (Mount Thesiger) and further north. The various rivers draining the southern Drakensberg have dissected impressive gorges in the region and they are the habitat for a number of cliff-face endemics, all associated with river gorges and discussed below (6.5.2.7). The climate is subtropical, with Indian Ocean Coastal Belt vegetation. Inland parts are mainly underlain by shale of the Ecca and Beaufort Groups (Karoo Supergroup). Cremnophilous species include *Drimia flagellaris* [70], *Gasteria croucheri* subsp. *pendulifolia* [43] and *Plectranthus purpuratus* [171].

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

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

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

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

6.5.2.7.1 Levuvu Gorge (Savanna)

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

6.5.2.7.2 Olifants River (Savanna)

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

6.5.2.7.3 The Kaap River (Savanna)

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

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

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

6.5.2.7.5 Thukela River (Savanna)

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

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

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

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

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

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

6.5.2.7.8 Mzimvubu River (Eastern Cape) (Valley Bushveld)

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

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

6.5.2.7.9 Mbashe River (Eastern Cape) (Valley Bushveld)

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

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

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

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

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

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

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

Obligate cremnophytes (31 taxa) present along all the tributaries include *Adromischus cristatus* var. *zeyheri* [98], *A. cristatus* var. *schonlandii* [97], *Albuca cremnophila* [64], *Bulbine latifolia* var. *curvata* [32], *B. natalensis* [34], *Cotyledon tomentosa* subsp. *tomentosa* [109], *Crassula capitella* subsp. *thyrsiflora* [115] (cliff form), *Cyrtanthus labiatus* [8], *C. montanus* [9], *Delosperma esterhuyseniae* [196], *Drimia uniflora* [73], *Haemanthus albiflos* [10], *Haworthia gracilis* var. *picturata* [55], *Lampranthus affinis* [212], *Ornithogalum longibracteatum* [78], *Othonna capensis* [87], *O. triplinervia* [89] (cliff form), *Schizobasis intricata* [80] and *Tromotriche baylissii* [83]. The Kouga tributary (seven taxa) has *Crassula cremnophila* [116], *Cyrtanthus flammosus* [3], *Gasteria glomerata* [46], *G. glauca*, [45], *Aloe* *pictifolia* [27], *Crassula perforata* subsp. *kougaensis* [131] and *Bulbine retinens* [37]. The Baviaanskloof tributary (four taxa) has *Adromischus subdistichus* [104], *Bulbine cremnophila* [31], *B. rupicola* [38] and *Gasteria rawlinsonii* [48].

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

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

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

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

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

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

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

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

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

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

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

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

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

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

6.5.2.7.17 Kunene River (Desert and Savanna)

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

6.5.3 Inselberg cliffs

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

6.5.4 Coastal cliffs

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

Dolphin Head is a clear promontory or peninsula in the Namib Desert. *Jensenobotrya lossowiana* [211] is restricted to these south-facing cliffs and adjacent territory. Owing to its isolation from herbivores, plants of this species could establish on non-cliff terrain in some parts of the peninsula. The fragile, pendent habit is typical of an obligate cremnophyte.

6.6 Representation of obligate succulent cremnophytes in biomes

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

6.6.1 Winter rainfall

6.1.1.1 Fynbos Biome

(6.6% of land surface area of South Africa)

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

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

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

Area cover: 71 339 km^2

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

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

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

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

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

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

Number of taxa: More than 9 000 taxa.

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

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

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

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

Geomorphology: Cape Fold Belt mountains.

Topography: 0–2400 m a.s.l.

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

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

6.6.1.2 Succulent Karoo Biome

(6.5% of land surface area of South Africa)

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

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

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

Area cover: 100 250 km^2 of the study area (83 075 km^2, Namibia; 17 175 km^2, South Africa).

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

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

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

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

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

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

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

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

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

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

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

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

Topography: 0–800 (1000) m a.s.l.

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

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

6.6.2 Rainfall in summer and winter

6.6.2.1 Desert Biome

(0.5% of land surface area of South Africa)

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

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

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

Area cover: 111 152 km^2 (110 598 km^2, Namibia; 554 km^2, South Africa).

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

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

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

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

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

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

Number of taxa: 1 200 taxa.

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

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

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

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

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

Topography: 0–800(–1500) m a.s.l.

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

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

6.6.2.2 Albany Thicket Biome

(2.2% of land surface area of South Africa)

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

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

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

Area cover: 26 000 km^2.

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

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

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

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

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

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

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

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

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

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

Geomorphology: Diverse, flat to very mountainous or hilly.

Topography: 0–1000(–1500) m a.s.l.

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

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

6.6.3 Summer rainfall

6.6.3.1 Nama-Karoo Biome

(19.5% of land surface area of South Africa)

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

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

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

Area cover: 575 437 km^2 (360 029 km^2, South Africa; 215 408 km^2, Namibia).

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

Main environmental driving forces: Winter aridity, sparse summer rainfall and extreme sun radiation. Disturbances by various larger and smaller mammals and also by other animal species.
Precipitation: (75–)100–300(–500) mm per annum (mainly convectional, and less often cyclonic). Cool to cold nights with heavy dew and regular frost in winter.
Temperature: Average daily maximum 20–24°C. Frost severe in winter, days warm. Summer temperatures high (up to 40°C on hot days).
Main bioregions: Bushmanland Bioregion, Upper Karoo Bioregion and Lower Karoo Bioregion.
Composition of vegetation: Sparse open terrain, rich in dwarf shrublets with xeromorphic characteristics, few annual and stem succulents. Smaller trees and shrubs are sparse and confined to rock outcrops (Asteraceae, Meliaceae, Euphorbiaceae, Fabaceae, Capparaceae, Poaceae). Endemism low. Characteristic shrubs include *Searsia erosa*, *S. undulata* and *S. pyroides*.
Number of taxa: 2 147 taxa.
Characteristics: Open, sandy to hilly, rocky deserts sparsely vegetated. Moderate grass and dwarf shrubby cover (grass especially after rain), moderate in spinescence.
Main adaptations: Xeromorphism, with dwarf shrubs and leathery leaves, sparse occurrence of leaf and stem succulents. Geophytes fairly common. Annuals rare. Many plants deciduous under dry conditions. Seed dispersal mainly by wind. Defence characteristics consist of chemical defence (*Euphorbia*) and armour (spinescence) or camouflage (resembling stony background).
Main succulent plant families represented: Asteraceae, Asclepiadaceae, Asphodelaceae, Crassulaceae, Euphorbiaceae, Mesembryanthemaceae and Portulacaceae.
Geology: Diverse, sand, gravel, calcrete, sedimentary (sandstone, Shale Karoo and Cape Supergroup) or dolerite intrusions (volcanic). Soils consist of rich sedimentary deposits.
Geomorphology: Flat with hills, and mountainous towards the escarpment. Characteristic karoo koppies (dolerite).
Topography: 800–1500(–2500) m a.s.l.
Cliffs: Scattered mainly along the southern and western parts of the Great Escarpment. Cliff outliers sparsely scattered and associated with inland mountains.
Obligate succulent and bulbous cremnophytes: Only one obligate cremnophyte, *Crassula tabularis*.

6.6.3.2 Grassland Biome

(27.9% of land surface area of South Africa)

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

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

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

Area cover: 349 180 km^2.

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

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

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

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

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

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

Number of taxa: 3 788 taxa.

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

Main adaptations: Annual fires during the dry winter months. *Cussonia paniculata* has a corky bark. Grazing by various antelopes. Geophytes and succulent grassland species are fairly common. Many plants are deciduous during the dry winter period. Seed mainly wind-dispersed. Many of the grasses palatable, offering good grazing, also some with defence characteristics such as tannins.

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

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

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

Topography: 800–3000 m a.s.l.

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

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

6.3.3.3 Savanna Biome

(32.5% of land surface area of South Africa)

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

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

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

Area cover: 888 208 km^2 (485 246 km^2, Namibia; 402 962 km^2, South Africa).

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

Main environmental driving forces: Winter aridity, regular fires (winter), summer moisture, sun radiation. Convectional storms with high incidence of lightning and hail. Disturbances by various larger and smaller mammals and also other animal species.
Precipitation: (200–)500–1 000(–1 200) mm per annum (mainly convectional thundershowers from moisture-laden, warm air).
Temperature: Average daily maximum 25–30°C (daily minimum 15–17°C). Frost is absent or mild in winter, with warm pleasant days. Summer temperatures are high (38–47°C on hot days).
Main bioregions: Central Bushveld Bioregion, Mopane Bioregion, Lowveld Bioregion, Sub-Escarpment Bioregion, Eastern Kalahari Bushveld Bioregion and the Kalahari Duneveld Bioregion.
Composition of vegetation: Mainly grassland with trees, shrubs and smaller succulent plants, geophytes and other herbs. Typical savanna trees include members of *Acacia*, *Combretum*, *Terminalia, Euphorbia, Colophospermum*, *Commiphora* and *Ficus*. Grasses include Panicoideae such as *Panicum*, *Andropogon*, *Trachypogon*, *Heteropogon*, *Cymbopogon*, *Themeda* and *Hyparrhenia*. The biome is also rich in herbaceous plants (*Barleria* and *Petalidium*) and succulent chamaephytes (*Aloe Cotyledon*, *Kalanchoe, Kleinia, Sansevieria* and *Eulophia*), with scattered small trees.
Number of taxa: 5 788 taxa.
Characteristics: Open to dense parkland vegetation dominated by a tree and shrub layer and grass species (Poaceae). Also with a fairly high percentage of succulent plants, often shrubby stem succulents (*Euphorbia*, *Monadenium*). Terrain diverse, from open flat to hilly terrain.
Main adaptations: Short dry winters (little frost), annual fires in the dry winter months. *Erythrina latissima* and *Cussonia natalensis* with corky bark serving as insulation against fire. Many re-sprouting species. Disturbances by big game a major driving force (elephant, buffalo, rhino). Stolons of *Sansevieria* remain behind after grazed by rhino. Grazing by various antelopes. Many plants deciduous under dry winter conditions. Seed mainly wind- and animal-dispersed. Many grasses palatable, offering good grazing, but with defence mechanisms such as tannins on dystrophic soils.
Main succulent plant families represented: Asphodelaceae (*Aloe*), Asteraceae (*Kleinia*), Crassulaceae (*Kalanchoe*, *Crassula*, *Cotyledon*), Euphorbiaceae (*Euphorbia*, *Monadenia*) and Lamiaceae (*Plectranthus, Aeollanthus, Tetradenia*).

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

Geomorphology: Diverse, flat to very mountainous or hilly.

Topography: 0–1000(–1500) m a.s.l.

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

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

6.6.3.4 Indian Ocean Coastal Belt

(1.1% of land surface area of South Africa)

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

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

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

Area cover: 12 000 km^2.

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

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

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

Temperature: Average daily maximum is 22–25°C (daily minimum 14–16°C). Frost absent or mild in winter, with warm pleasant days. Summer temperatures 35–40°C during heat waves.
Main bioregions: Divided into five units: Maputaland Coastal Belt, Maputaland Wooded Grassland, KwaZulu-Natal Coastal Belt, Pondoland-Ugu Sandstone Coastal Sourveld and the Transkei Coastal Belt.
Composition of vegetation: Mainly a mosaic of grassland, dense shrubby thicket, forest and savanna. The flora is rich in endemism, especially the sandstone of the Msikaba Formation (Cape Supergroup). Characteristic species include *Strelitzia nicolai*, *Allophylus natalensis*, *Mimusops obovata*, *M. caffra* and *Ficus burkei*. Some endemics include *Searsia acocksii*, *Leucadendron pondoensis*, *Leucospermum innovans* and *Raspalia trigyna.* Succulents and bulbous plants are also fairly well represented (*Aloe*, *Ledebouria*) and other herbs (*Blepharis*, *Barleria*).
Number of taxa: Fairy high levels of endemism, especially the sandstone parts and shale parts (Cape Supergroup, Karoo Supergroup and KwaZulu-Natal Supergroup).
Characteristics: Varied, ranging from open grassland to forest and elements of Cape fynbos vegetation on sheltered slopes and dunes.
Main adaptations: High and evenly spread rainfall, but more in summer. Winters are warm, short and mild, without frost. Many re-sprouting species in response to fire or herbivory. Fairly high representation of succulent plants and with vegetative regeneration backup. Seed dispersal mainly by wind and birds. Disturbances from big game a major driving force (elephant, buffalo, rhino). The vegetation palatable in parts, offering good grazing to game.
Main succulent plant families represented: Asphodelaceae (*Aloe*), Asteraceae (Senecio, *Kleinia*), Crassulaceae (*Kalanchoe*, *Crassula*, *Cotyledon*), Euphorbiaceae (*Euphorbia*) and Lamiaceae (*Plectranthus*, *Aeollanthus*).
Geology: Diverse, aeolian sand to Mokolian-age granites as well as sandstone of the Natal Group (Cape Supergroup, Msikaba Formation) and shale and mudstone (Karoo Supergroup). Soils include loam, sandy to clay soils (sedimentary and volcanic), sandstone, Shale Karoo or dolerite intrusions. Soils variable, from very sandy to loam, clay-loam to mineral-deprived (Msikaba Formation Cape Supergroup).
Geomorphology: Hilly terrain and wide river valleys. The vegetation consists of subtropical and Cape elements.
Topography: 0–450(–600) m a.s.l.
Cliffs: Well represented along the Transkei (Eastern Cape) coast, as well as by the coastal cliffs between the Mboyeti and Luputana Rivers. Also the quartzitic sandstone of the Msikaba Formation (Cape Supergroup) and sandstone of the Natal Group.

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

6.6.3.5 Forest Biome

(0.08% of land surface area of South Africa)

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

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

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

Area cover: 0.08% of South Africa's land surface area (568 km^2).

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

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

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

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

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

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

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

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

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

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

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

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

Topography: 0–2800 m a.s.l.

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

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

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

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

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

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

CHAPTER 7

EVOLUTION OF CREMNOPHYTES

7.1 Introduction

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

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

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

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

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

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

7.2 Evolution of cremnophytes

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

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

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

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

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

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

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

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

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

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

7.3 Adaptive trends

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

To summarise the recorded adaptive trends in cremnophytes:

Morphological adaptation

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

Reduction in defence mechanisms

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

Reproductive adaptation

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

Growth vigour

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

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

7.4 Convergence of cremnophytes

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

7.5 Distribution patterns (historical and present)

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

7.5.1 Distribution and representation

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

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

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

7.6 Evolutionary history and origin of southern African cremnophytes

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

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

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

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

7.6.1 Uplift events and the creation of cliffs during the Neogene

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

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

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

7.6.2 Origin of Albany Thicket

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

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

CHAPTER 8

CONSERVATION OF CLIFFS AND SUCCULENT CREMNOPHYTES IN SOUTH AFRICA AND NAMIBIA

8.1 Introduction

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

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

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

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

8.2 Why cliffs should be protected

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

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

8.3 Threats to obligate cremnophilous succulent plants in the study area

8.3.1 Habitat loss

8.3.1.1 Dam construction

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

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

8.3.1.2 Mining

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

8.3.1.3 Recreation

8.3.1.3.1 Hikers and climbers

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

8.3.1.3.2 Plant collectors

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

8.3.1.3.2.1 Gathering of medicinal plants

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

8.3.1.3.2.2 Plant enthusiast collectors

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

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

8.4 Natural disturbances on the cliff face

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

8.4.1 Rock falls

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

8.4.2 Fire

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

8.4.3 Storm damage

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

8.4.4 Mammals

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

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

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

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

8.5 *Ex situ* conservation

8.5.1 Propagation in botanical gardens and other institutions

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

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

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

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

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

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

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

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

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

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

CHAPTER 9

COMPENDIUM OF SUCCULENT CREMNOPHYTES AND THEIR FEATURES

9.1 Diagram (dendrogram) of obligate succulent cremnophyte growth forms

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

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

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

9.1.1 Cliff growth form formula

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

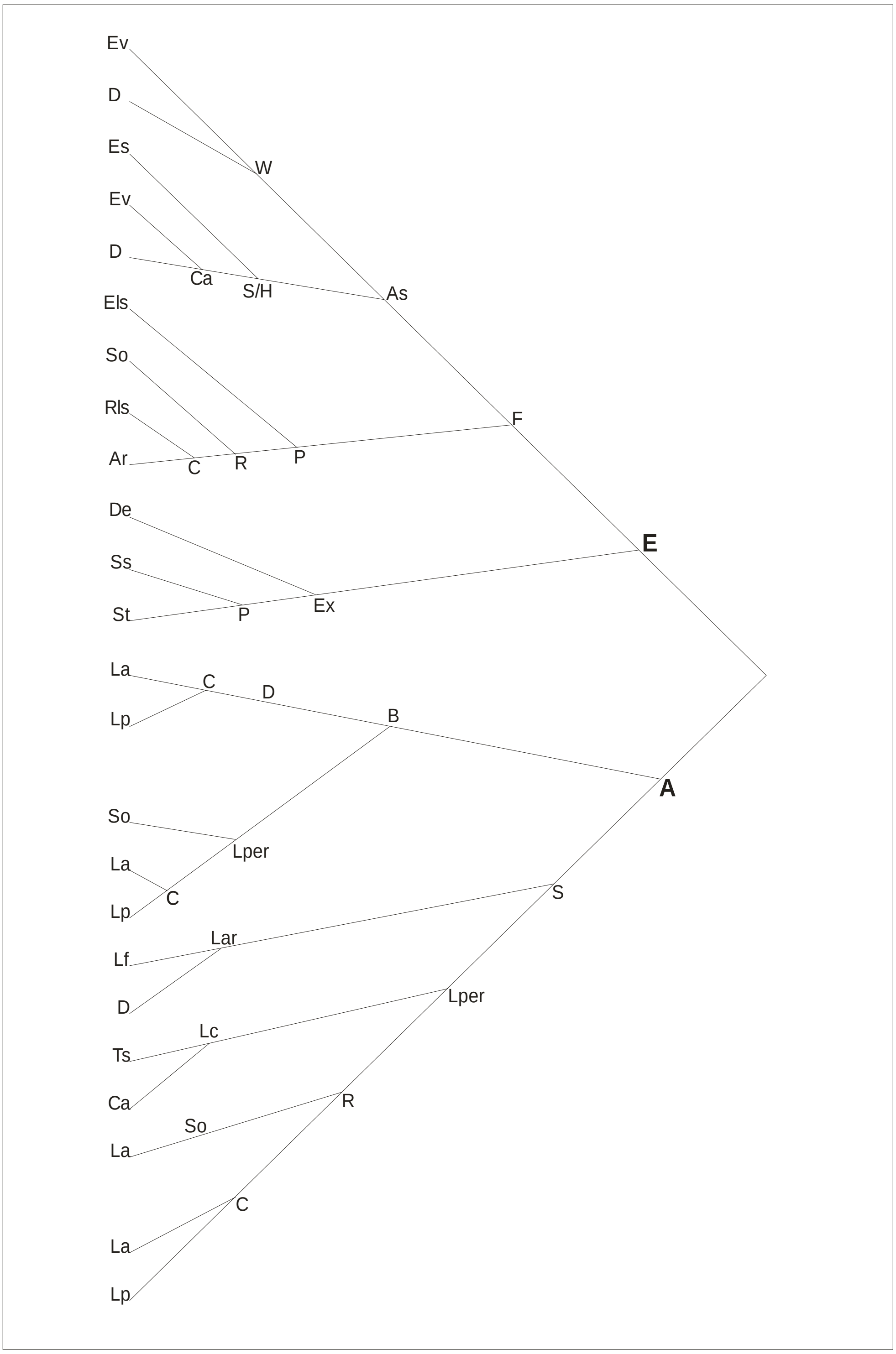

DIAGRAM 9.1. Schematic representation of the obligate or near-obligate growth forms (symbols explained in 9.1.2). The two main subdivisions are **A:** abbreviated stems, and **E:** extended stems. The diagram depicts the adaptive pathways of the 220 cremnophytes identified in this study.

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

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

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

9.1.2 Explanation of symbols

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

A = Abbreviated growth, plants with shortened internodes, resulting in compact clusters.
Ar = Apical rosette, as in *Aloe dabenorisana* [17].
As = Ascending growth.
B = Bulbous or geophytic.
C = Clustered growth.
Ca = Caudiciform or swollen stem base.
D = Deciduous.
De = Decumbent.
E = Extended branch growth, including plants with extended internodes, thus lengthening.
(e) = Bulb epigeous.
(eg) = Epinastic growth.

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

Es = Evergreen succulent stems.

Ev = Evergreen.

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

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

(fn) = Inflorescence negatively phototropic.

(ft) = Fog-trapping.

H = Herbaceous growth.

La = Leaves ascending.

Lar = Leaves annually replaced.

Lc = Leaves crowded.

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

Lp = Leaves pendent.

Lper = Leaves perennial.

P = Pendent growth.

(p) = Semi-poikilohydric.

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

(r) = Rich flowering.

(rd) = Reduction in camouflage.

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

S = Non-bulbous succulents.

So = Solitary growth.

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

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

Ts = Thin stems.

(vb) = Vegetative backup.

W = Woody growth.

9.1.3 Descriptive dichotomous key to the schematic Diagram 9.1

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

- 1a Extended growth ... **E (94)**
  - 2a Stems with rudimentary foliage, succulent ... **Ex (5)**
    - 3a Stems pendent ... **P (51)**
      - 4a Stems square ... **Ss (2)**
      - 4a Stems terete ... **St (2)**
    - 3b Stem ascending (decumbent) ... **As (36)**
  - 2b Stems foliated ... **F (88)**
    - 5a Stems pendent ... **P (51)**
      - 6a Rosulate ... **R (14)**
        - 7a Solitary growth ... **So (1)**
        - 7b Clustered growth ... **C (14)**
          - 8a Rosette apical ... **Ar (10)**
          - 8b Rosette extended into leafy stem ... **Rls (3)**
      - 6b Extended leafy stems (not rosulate) ... **Els (37)**
        - 9a Deciduous ... **De (1)**
        - 9b Evergreen ... **Ev (36)**
    - 5b Stems ascending or decumbent ... **As (36)**
      - 10a Stems succulent/herbaceous ... **S (29)**
        - 11a Stems caudiciform ... **Ca (12)**
          - 12a Evergreen ... **Ev (2)**
          - 12b Deciduous ... **De (10)**
        - 11b Stems succulent, foliate ... **Es (17)**
      - 10b Stems woody ... **W (7)**
        - 13a Deciduous ... **De (1)**
        - 13b Evergreen ... **Ev (6)**

- 1b Abbreviated (truncated) growth ... **A (126)**
  - 14a Succulent (not bulbous) ... **S (96)**
    - 15a Leaves annually replaced ... **Lar (27)**
      - 16a Leaves fused, persistent (thin stem) ... **Lf (19)**
      - 16b Leaves deciduous (thick stem) ... **D (8)**
    - 15b Leaves perennial ... **Lper (96)**
      - 17a Leaves rosulate ... **R (59)**
        - 18a Solitary growth ... **So (3)**
          - 19a Leaves pendent ... **Lp (6)**
          - 19b Leaves ascending ... **La (50)**
        - 18b Clustered growth ... **C (56)**
      - 17b Leaves crowded ... **Lc (10)**
        - 20a Stem base caudiciform ... **Ca (2)**
        - 20b Branches thin ... **Ts (8)**
  - 14b Bulbous ... **B (30)**
    - 21a Leaves perennial ... **Lper (21)**
      - 22a Solitary growth ... **So (1)**
      - 22b Clustered growth ... **C (20)**
        - 23a Leaves pendent ... **Lp (7)**
        - 23b Leaves ascending ... **La (13)**
    - 21b Leaves deciduous ... **D (9)**
      - 24a Clustered growth ... **C (9)**
        - 25a Leaves pendent ... **Lp (4)**
        - 25b Leaves ascending ... **La (5)**
      - 24b Solitary growth ... **So (1)**

9.2 Descriptions of growth forms according to Diagram 9.1

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

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

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

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

The second group (longer well developed stems, three groups) of 94 taxa (43%) are the cliff hangers and cliff squatters—plants with extended internodes and their growth orthotropous (erect trees or woody or herbaceous, erect to decumbent, squat shrublets), plagiotropous (procumbent) or becoming pendent. The group includes mostly dicotyledonous plants but also some monocotyledons such as the long-stemmed pendent members of *Aloe* and *Bulbine*. Most taxa (55) in this group have pendent stems and come from the southern and eastern parts of South Africa where summer rainfall has some influence and the rainfall is much higher. The pendent growth is due to gravity (plant growing on a vertical plane) or epinastic growth (genetic); 29 taxa with epinastic stem growth have been identified. Plants in this group are, with a few exceptions, evergreen.

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

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

9.2.1 Extended stem growth (E, 94 taxa)

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

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

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

9.2.1.1. 1 Decumbent growth (E:Ex:De, 1 taxon)

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

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

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

9.2.1.2 Foliated cremnophytes (F, 88 taxa)

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

9.2.1.2.1 Trees and shrubs (facultative cremnophytes, 8 species)

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

9.2.1.2.2 Ascending herbaceous and succulent-stemmed foliated shrubs or shrublets (E:F:As:S/H, 29 taxa)

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

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

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

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

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

9.2.1.2.4.1 Pendent rosettes (E:F:P:R, 14 taxa)

Included here are mainly monocotyledons, especially Asphodelaceae with representatives such as *Aloe* (11 species), *Bulbine suurbergensis* [39] and *Gasteria rawlinsonii* [48]. Plants are either solitary with long stems (bare or covered in dry leaves) and apical rosettes (*A. hardyi* [20], **E:F:R:Ar**), or drooping clusters (11 taxa) or shrubs with rosettes but extending into foliated stems as in *A. catengiana* [14], *A. meyeri* [22] and *Gasteria rawlinsonii*, **E:F:P:R:C:Rls**.

9.2.1.2.4.2 Pendent leafy stems (E:F:P:Els, 39 taxa)

This is a large group (39 dicotyledonous taxa) consisting of plants with leafy plagiotropous stems becoming drooping on a vertical plane. Many are actively (vegetatively) increasing their growth size, forming dense to loose mats. Plants are often rooting at the nodes, thus forming extensive clones. This group is not always clear cut, some leaning towards plants with abbreviated growth, depending on the crevice and availability of solar radiation. Compared to counterparts growing in non-cliff habitats, there is an increase in succulence and reduction in size, thus a combination of drought- and cliff-adapted features. Forms of *Crassula perforata* [131, 132] usually have shorter internodes, together with its leaves resulting in almost cylindrical bodies. The largest plant in this group is *Jensenobotrya lossowiana* [211]. This amazing species has dense clusters of club-shaped leaves on stems up to 1 m long. The main branch can be as thick as a man’s arm.

9.2.2 Abbreviated or truncated stem growth (A, 126 taxa)

The cliff huggers are clearly the largest group, with two clear-cut subgroups—the bulbous succulent plants of 30 taxa (**A:B**), and the 96 (44% of total) non-bulbous succulent cliff huggers (**A:S**). Although they display a compact growth, some bulbous species bear long, pendent leaves. The plants have shortened stems with a compact growth hugging the cliff.

9.2.2.1 Bulbous cremnophilous succulent plants (A:B, 30 taxa)

The bulbous component (30, 14%) consists mostly of plants with epigeous bulb growth, with one or two exceptions from the Drakensberg and adjacent regions. In size they range from the miniature *Drimia uniflora* [73], probably the world's smallest bulbous species occurring from almost sea level to 3000 m, to the large robust *Cyrtanthus herrei* [5] of the Richtersveld and southern Namibia. Most bulbous species on terrestrial habitats have bulbs that are located below ground. Cremnophilous bulbous taxa usually grow in dense rounded clusters, with the exception of one that is solitary. Their bulbs (storage, fleshy scales) vary from loose bulb scales (*D. cremnophila* [69]) to well tunicated (*Haemanthus albiflos* [10]), sometimes covered with dried bulb scales (*C. flammosus* [3], *C. montanus* [9] and *C. labiatus* [8]). There are two groups, evergreen and deciduous plants.

9.2.2.1.1 Bulbs with perennial leaves (A:B:Lper, 21 taxa)

There are 21 bulbous taxa with evergreen leaves. Most of them form dense clusters (*Cyrtanthus herrei* [5], *C. montanus* [9], *C. labiatus* [8], *Haemanthus albiflos* [10] and *H. pauculifolius* [12]). They can be further divided into two groups—those with pendent and those with ascending leaves. Most of them are from the southeastern regions of the study area where rainfall is experienced at any time of the year and with mild winters. However, *C. herrei* from the winter-rainfall zone is an exception in that the leaves remain evergreen. *Cyrtanthus flammosus* [3] (Eastern Cape) is the only solitary bulbous species (**So** = solitary) growing with its bulb half exposed (semi-epigeous). To compensate for a lack of vegetative output, *C. flammosus* has very large, solitary flowers (rich flowering). The species mentioned above have mainly ascending leaves. Some of them have flaccid, drooping, perennial leaves, for example *Albuca cremnophila* [64] and *A. thermarum* [68]. Both are cluster-forming. *Albuca cremnophila* is a robust evergreen species confined to the Gamtoos River and its tributaries and grows horizontally to pendent along ledges. Its leaves are leathery, long-lived and also display epinastic growth. Plants do not proliferate from the base but divide to form small, dense clusters. *Albuca thermarum* from Calitzdorp Spa is the only evergreen species with drooping leaves occurring so far west (also subject to winter rainfall).

9.2.2.1.2 Bulbs with leaves that are deciduous or replaced annually (A:B:D, 9 taxa)

There are a number of cremnophilous bulbs with deciduous leaves. Those from the Drakensberg become dormant during cold winters. *Cyrtanthus falcatus* [2] is well adapted to cliffs and apart from the epinastic growth of its leaves, the bulb presentation is also often horizontal to pendent. *Albuca crudenii* [65] from the Grahamstown region is a winter-growing taxon (summer-deciduous) and in spite of summer rain, it remains deciduous during this period. *Albuca kirstenii* [66] (Gourits River and further west) is also summer-deciduous. *Albuca shawii* [67] forms dense clusters. It is widespread in the northeastern parts of South Africa and becomes deciduous where frost or snow is experienced. In warmer subtropical regions where frost is rare, it remains evergreen.

9.2.2.2 Non-bulbous succulents (A:S, 96 taxa)

This includes clearly the largest group of the obligate cremnophytes (96 taxa, 44%). It comprises both dicotyledons (e.g. Mesembryanthemaceae, Crassulaceae, Asteraceae) and monocotyledons (Asphodelaceae) that grow in dense clusters (rarely solitary) hugging the cliffs. There are two groups—plants in which the leaves are annually replaced or renewed (27 taxa; **Lar** = leaves annually replaced) and plants with long-term perennial leaves (69 taxa; **Lper** = leaves perennial).

9.2.2.2.1 Compact succulent plants, leaves annually replaced (deciduous or aestivating leaves) (A:S:Lar, 27 taxa)

Plants with leaves that are annually replaced fall in two distinct groups—those with leaves that are deciduous during the dry resting season (8 taxa) and those with leaves that are summer-aestivating (19 taxa). The latter group is represented by members of the genus *Conophytum* and, although the leaves are evergreen, moisture is annually translocated or recycled to a young new pair, the old leaves remaining intact as a dry skin enveloping the young pair.

9.2.2.2.1.1 Compact growth with fused leaves, the genus *Conophytum* (A:S:Lar:Lf, 19 taxa)

These 19 taxa all belong to the genus *Conophytum*. Plants are usually short-stemmed and grow in tight mats or clusters (shady south-facing cliffs) and the leaves are fused (**Lf** = leaves fused) into a characteristic club-shaped body, flat or lobed at the top. In the centre is a small orifice or opening from where the flower appears. During the dry summer season, plants aestivate and the body is gradually replaced by a new young pair of leaves. Although the cluster type can also be found on quartz flats and in other habitats in the Succulent Karoo, the cliff huggers tend to be more fragile (sometimes bearing fog-trapping hairs or papillae) than the non-cremnophytes. Some non-cremnophilous species of *Conophytum* have a solitary growth form or are deeply sunken in the ground (only apical windows visible).

9.2.2.2.1.2 Compact cluster, succulent-stemmed, leaves deciduous during the long dry summer season, the genera *Tylecodon* and *Othonna* (A:S:Lper:D, 8 taxa)

This group represents plants like compact clusters in the genus *Tylecodon* of which the leaves become deciduous towards the summer months (**A:S:Lar:D**). The stems of these plants are succulent and compact. This includes species such as *T. longipes* [156], *T. ellaphieae* [155], *T. decipiens* [154], *T. singularis* [158] and *Othonna armiana* [86]. These taxa are mostly confined to crevices and ledges on shady south-facing aspects.

9.2.2.2.1.3 Compact succulent plants with perennial leaves (clustered, crowded leaves, or in dense rosettes) (A:S:Lper, 69 taxa)

This includes two groups, both evergreen—those with the leaves in clusters (*Adromischus* spp.) and those with distinct tight rosettes (*Haworthia* spp. and many *Crassula* spp.). They are mostly from an all-year- or summer-rainfall region, usually confined to south-facing cliffs.

9.2.2.2.2 Compact succulent plants with leaves crowded, the genera *Adromischus*, *Pyrrosia* and *Streptocarpus* (A:S:Lper:Lc, 10 taxa)

This group includes ten taxa, some members of the genus *Adromischus*, *Streptocarpus* and *Pyrrosia*. It comprises two groups—one with a caudex (**Ca**) and the other with thin succulent stems (**Ts**). *Streptocarpus kentaniensis* [164] has ascending leaves that become pendent on the cliffs (summer rainfall, Eastern Cape). *Pyrrosia schimperiana* [1] has short procumbent stems and ascending leaves that can become pendent. Members of *Adromischus* have crowded leaves. The caudiciform group (**Lc:Ca**) includes the dwarf *Anacampseros scopata* [220] and *Adromischus schuldtianus* subsp. *brandbergensis* [103]. Both have a swollen caudiciform base. The stems of *Anacampseros scopata* are densely covered with long hairs with fog-trapping abilities—the species occurs within the fog range (Vyftienmyl se Berge, Port Nolloth).

9.2.2.3 Plants with leaves in tight (rarely loose) rosettes (A:S:Lper:R, 59 taxa)

There are 59 taxa, and two groups have been identified—those usually with a solitary or sparsely branched rosette (three taxa) and the other (56 taxa) with rosettes in tight to loose clusters.

9.2.2.3.1 Plants with solitary rosettes (A:S:Lper:R:So, 3 taxa)

It includes three species, *Aloe dewinteri* [18] (summer rainfall), *A. kouebokkeveldensis* [21] (winter rainfall) and *Bulbine natalensis* [34] (summer rainfall) (**A:S:Lper:R:So**). The aloes are quite large, rosulate plants and the *Bulbine* is smaller.

9.2.2.3.2 Plants with leaves in a tight rosette in dense to loose clusters (A:S:Lper:R:C, 56 taxa)

These plants (56 taxa) can also be divided into two groups—those (50 taxa) with ascending and those (six taxa) with pendent leaves. The first group consists of the compact cluster-forming members of *Haworthia*, *Gasteria* and *Crassula*, all with short ascending to spreading leaves. The second group is the smallest and often displays epinastic growth, as in *G. croucheri* subsp. *pendulifolia* [43]. Other examples include *Aloe soutpansbergensis* [29], *Bulbine cremnophila* [31], *B. meiringii* [33], *B. thomasii* [40] and *Trachyandra tabularis* [62]. Most of them (except *Trachyandra*) originate from summer-rainfall regions.