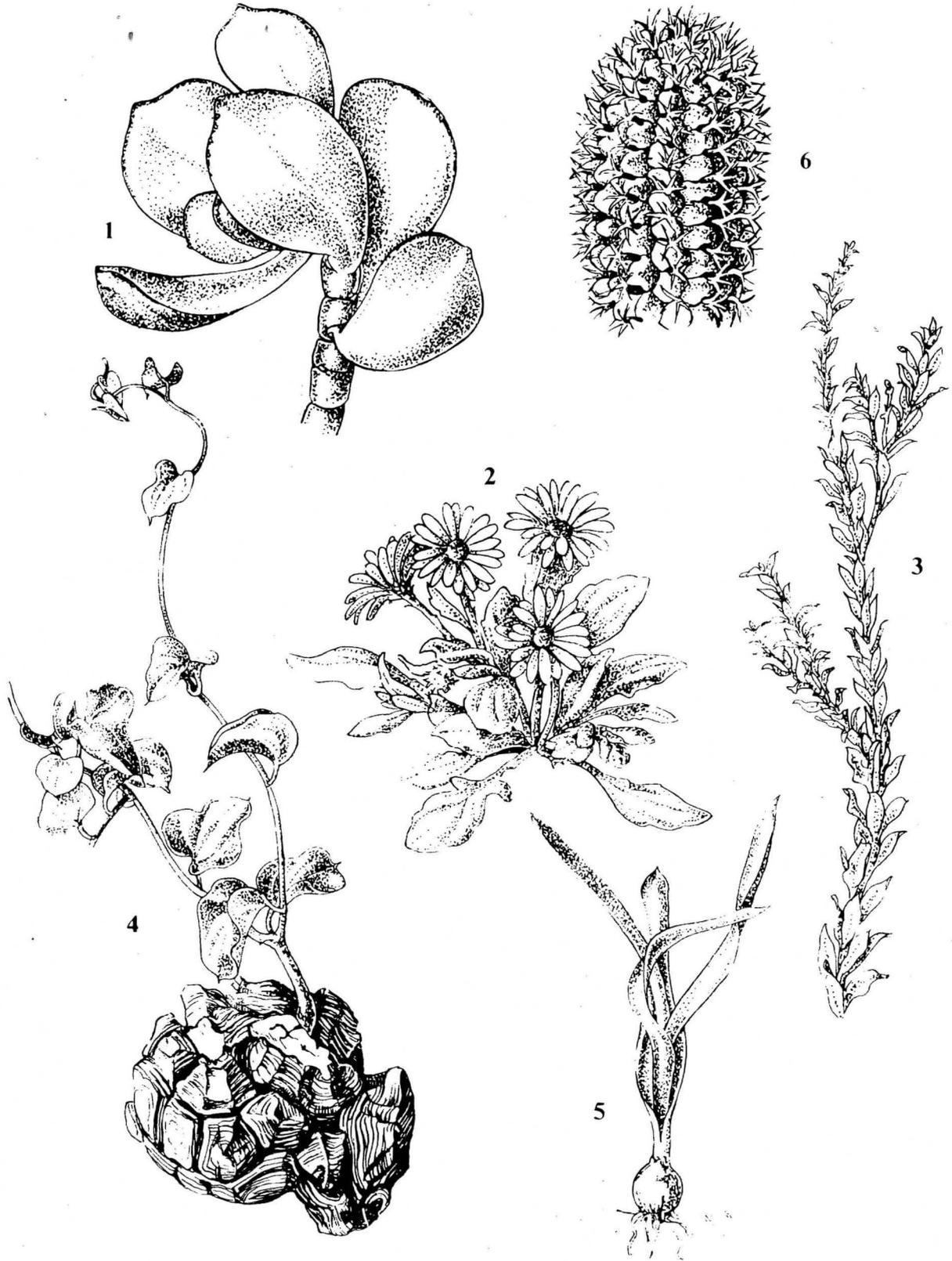


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Plant life forms from arid regions. (1) LEAF SUCCULENTS (*Cotyledon orbiculata*). (2) ANNUALS (DROUGHT EVADERS) (*Ursinia nana*). (3) KAROO SHRUBS (*Freylina undulata*). (4) PLANTS WITH CAUDEX (*Dioscorea elephantipes*). (5) GEOPHYTES (*Ornithogalum maculatum*). (6) STEM SUCCULENTS (*Euphorbia stellaespina*). Illustration by Ellaphie Ward-Hillhorst

The Succulent riches of South Africa and Namibia and their adaptive strategies

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1. Introduction

South Africa is well-known for its richness in succulent plants. Of the world's approximately 10 000 succulent plant species, more than a third originate from Southern Africa (36%). There are some 23 000 indigenous plant species in South Africa of which 3 693 species are succulent, making up 16% of our total flora. This reflects a long history of aridity. The 3 693 succulent species are represented by about 30 families. More than half the species belong to the family Mesembryanthemaceae, which is at present the world's largest family of succulent plants and is dominant in large areas in the dry winter rainfall areas of the Western and Southern Cape. Ironically, although it is the third largest plant family in South Africa and the largest of the winter rainfall biome, it is at present the most neglected by local botanists. The highest concentration of endemic genera occurs in the winter rainfall or Succulent Karoo which is situated in the southern and western parts of Southern Africa. With an area of about 2,5 million square kilometres, two-thirds is under water stress as it receives less than 500 mm of rain per annum, with droughts often ravaging the rest of the area.

Table I: The plant riches of South Africa compared to the rest of the world

	World Flora	S.A. Flora	World Succulents	S.A. Succulents
Species total	250,000 ¹	23,000 ²	10,000 ³	3 693
Families	250-350 ⁴	207 ⁵	32	32
Species % of world flora		8%	4%	1,4%

(1,4) Heywood (1978) (2,5) Gibbs Russel (1984) (3) Rowley (1978)



The Richtersveld is one of the driest parts in South Africa, and one of the world's richest succulent plant regions. Taken from the top of the Richtersberg looking south towards the Rosyntjieberg. The small xerophytic tree is the Kringboom, *Maerua schinzii*



Although large parts of the arid regions of South Africa appear to be devoid of life, on closer inspection it becomes clear that it is rich in a very specialized flora and fauna. The Pellaberg, North-western Cape, has a very interesting flora, some of which is endemic

2. What is a succulent?

Succulents are xerophytes. The ecological term xerophyte is derived from the Greek word *xeros* which means dry and refers here to plants adapted to grow and reproduce successfully in a dry climate. According to their main adaptive strategies South African xerophytes can roughly be divided into four groups.

(i) **Succulents** consisting of plants with fleshy leaves, branches, or caudiciform bases. The shape of these natural plant reservoirs justifies the Afrikaans name 'vetplant' (fat plant). Some succulents also have succulent roots.

(ii) **Karoo shrubs** are non-succulent herbaceous or woody plants with small leathery leaves and well-developed taproots. Some Karoo shrubs are deciduous in the dry season. The Karoo shrubs are represented by various families, of which the Asteraceae are the most prominent.

(iii) **Geophytes** are plants with subterranean water storage organs such as bulbs, corms, etc., including a few succulent species e.g. *Bulbine striata*. During the dry season the plant rests with its growing part at or below ground level.

(iv) **Annuals** (Therophytes) are drought evaders, which means they complete their life cycle within the rainy season. The plants survive the dry season as seeds which germinate with the onset of the next rainy season.

In this article the emphasis is on the succulent plants indigenous to Southern Africa, the reasons for such a rich succulent flora, and their adaptive strategies to cope with the dry climate. Succulents also occur in high rainfall areas but usually in habitats where the water drains away very rapidly. *Aloe alooides* from Sabie is an excellent example. It occurs on steep well-drained dolomitic outcrops in a high rainfall region. The first succulent ancestors perhaps had their origin in a relatively high rainfall climate during the Cretaceous (about 100 million years ago) and they later spread with the onset of favourable drier conditions. Water is a very scarce



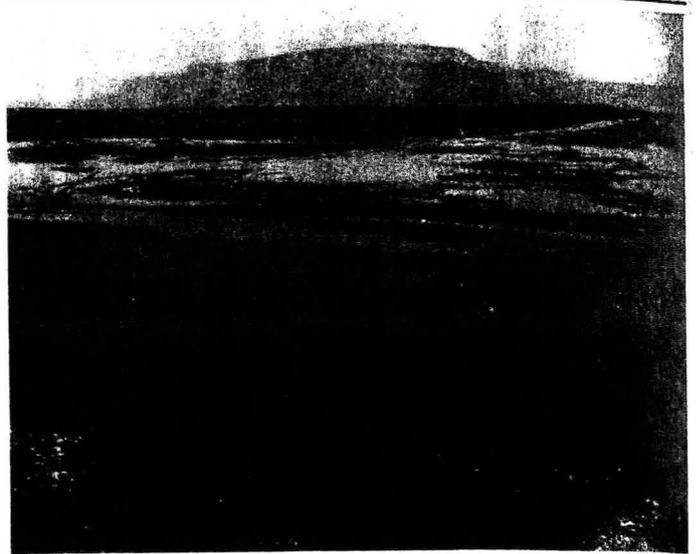
Aloe bainesii also occurs in a high rainfall region in the eastern parts of Southern Africa. It is Africa's second largest succulent plant species and the largest of the Monocotyledons

commodity in deserts and is the most important factor determining the survival of succulents. However, it is the prolonged lack of sufficient water which is the main reason for their succulent nature, although other factors also had an important effect on their present morphology (shape and structure). It is the interdependence between life forms, climate and time (spanning millions of years), and diversity in soil and terrain which was responsible for their present variety of interesting shapes. We also have to bear in mind that it is an ongoing process; plants re-adapt to changes in climate. In a wet climate, present succulents could even evolve into mesophytes (non-succulent plants).

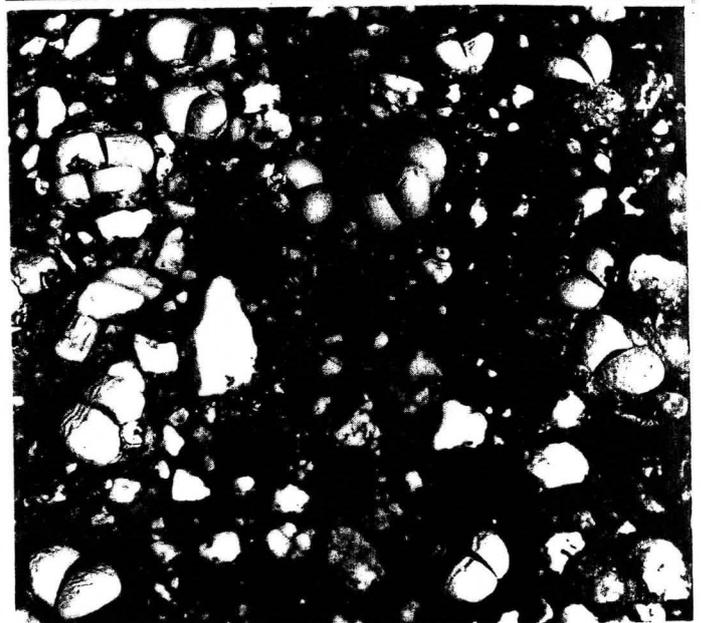
In comparison with other dry areas of the world South Africa has an exceptionally rich succulent flora. This can be partly explained by its present climate, its long history of aridity and its physical features and geology.

3. Distribution of succulents in Southern Africa

Succulents are distributed throughout South Africa, even in the high rainfall forest regions. Their distribution density, however, varies greatly. There is no doubt that the majority of the South African succulent taxa are confined to the southern and western winter rainfall areas below the inland escarpment, especially the families *Mesembryanthemaceae*, *Crassulaceae* and *Portulacaceae*. There is a gradual decrease in the density of succulent species from west to east in the north-west, and from the south to the north-east. The density remains more or less constant over the north-eastern escarp-



There is a high concentration of succulent species in the winter rainfall Karoo regions of South Africa. The Knersvlakte has a very rich succulent flora, especially in the families *Mesembryanthemaceae*, *Euphorbiaceae* and *Asclepiadaceae*. Note the quartz flats in the background



The genus *Argyroderma* is endemic to the Knersvlakte. *Argyroderma delaetii* resembles the quartz pebbles. Note the closed hygrochastical fruit capsules. The quartz flats carry a rich succulent flora. The white pebbles reflect the sun

ment and highveld but there is an increase again in the eastern, dry river valleys of the Northern Natal and Eastern Transvaal, especially the latter in which the greatest concentration of *Aloe* species occurs (the centre of highest endemism in the world). As will be seen later, the climate, geology and physical features play a very important role in their distribution.

4. Physical features and geology

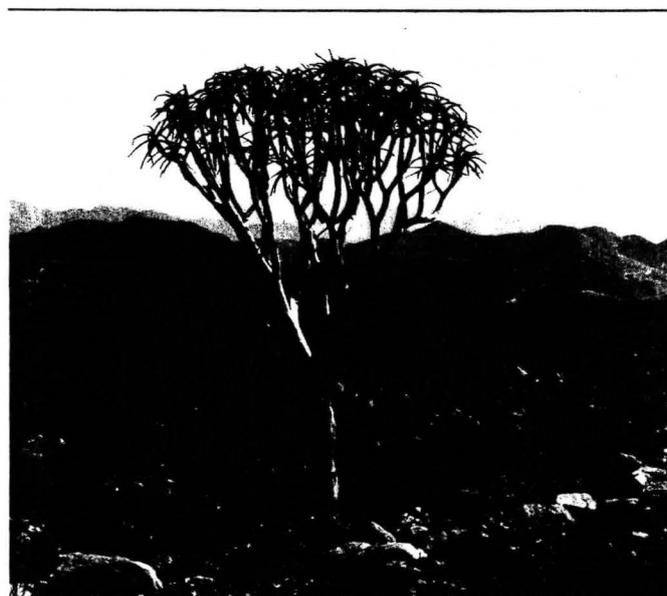
The Southern African subcontinent tapers towards the south, terminating where the warm Indian Ocean of the east coast and the cold Atlantic Ocean of the west coast meet. It varies greatly in altitude. There are three major physical features which characterize the subcontinent and play an important role in the distribution of succulents; firstly, the narrow

Table II: South African regions of high succulent concentration (centres of endemism) and the associated veld types

Region	Dominant succulent plant families	Veld type according to Acocks (1975)	No	Rainfall		Annual amount in mm	
				Winter	Summer		
1. WESTERN CAPE							
a. The lower Orange River valley and adjacent regions	MCSE	Namaqualand Broken Veld	33	×	×	150–300	
		Succulent Karoo	31	×		50–200	
b. Namaqualand Coast		Strandveld	34	×		50–300	
c. The Knersvlakte		Succulent Karoo	31	×	×	50–200	
d. Loeriesfontein and southern Bushmanland		Western Mountain Karoo	28	×	×	150–200	
e. Tanqua Karoo		Succulent Karoo	31	×	×	50–200	
f. Robertson and Worcester Karoo	Karrold Broken Veld	26	×	×	150–300		
2. SOUTHERN CAPE							
a. The Little Karoo							
	MCS E	Succulent Karoo	31	×	×	50–200	
		Spekboomveld	25	×	×	250–300	
		Karrold Broken Veld	26	×	×	150–300	
b. Lower Breede, Gouritz and Brak Rivers							
	MC	Noorsveld	24	×	×	250	
		Valley Bushveld	23	×	×	500–900	
		Renosterveld	46	×	×	300–500	
c. Northern foothills of the Swartberg and adjacent regions							
	MC PE MC	Spekboomveld	25	×	×	250–300	
		Succulent Karoo	31	×	×	50–200	
		Karrold Broken Veld	26	×	×	150–300	
d. Baviaanskloof, Steyterville and Klipplaat region							
	MCE	Succulent Karoo	31	×	×	50–200	
		Noorsveld	24	×	×	250	
		Spekboomveld	25	×	×	250–300	
3. EASTERN CAPE							
Port Elizabeth region which includes the adjacent dry river valleys and the region extending northwards to the Somerset-East district							
	MCEP	Valley Bushveld	23	×	×	500–900	
		False Karrold Broken Veld	37		×	150–300	
4. TRANSKEI AND NATAL							
Low lying river valleys of the Transkei and Natal regions							
	AEC	Valley Bushveld	23		×	500–900	
5. EASTERN TRANSVAAL AND SWAZILAND REGION							
a. Lowveld							
	AE	Lowveld	10		×	500–570	
b. Olifants River and Steelpoort Valley							
		Mixed Bushveld	18		×	350–650	
c. Zoutpansberg and Western Transvaal regions							
	AE	Mixed Bushveld	18		×	350–650	
		Arid Sweet Bushveld	14			350–500	

M = Mesembryanthemaceae C = Crassulaceae S = Asclepiadaceae E = Euphorbiaceae A = Asphodelaceae P = Portulacaceae

coastal belt of the south, east and west coasts; secondly the interior Great Escarpment, and thirdly the coastal mountains of the Western, Southern and Eastern Cape. Geologically, South Africa is very complex, an important factor regarding its diverse succulent flora. The higher ground of the climatically severe inland escarpment consists mainly of the 200–345 million year old shale, mudstone and sandstone formations of the Karoo sequence. In the east, the Karoo sequence is overtopped by Basalt, the lava flow of the Jurassic period (about 180 million years ago) which resulted in the Lesotho highlands. The escarpment gradually slopes towards the west and south-west where it terminates in the Langeberg and Roggeveld mountains in the west, and the Nuweveld, Sneeu-berg and Winterberg mountains in the south. The fringe of the western and southern escarpment averages about 1 000 metres in height. The Great Escarpment's highest part is in the east, the Drakensberg, which is South Africa's highest mountain range. The Drakensberg range runs relatively close to the east coast in Natal and Transkei. It averages about 2 500 to 3 500 metres here. Its northernmost point is in the North-eastern Transvaal. This high-lying ground of the escarpment, especially in the western half, is very dry. Although very arid and comprising the larger part of the Great Karoo, it is poor in succulent flora as compared to the



The interior mountains of the North-western Richtersveld consist mainly of lava and are relatively poor in succulent species. This region lies in a rain shadow caused by the Kuboesberg and its climate is very arid. *Aloe dichotoma* is in the foreground



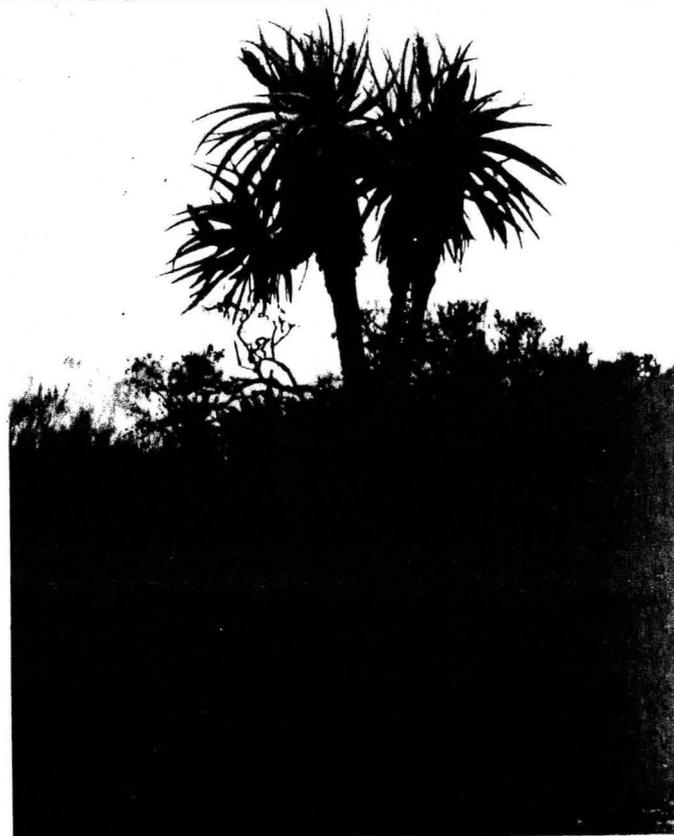
Aloe plicatilis is endemic to the quartzitic sandstone mountains of the Table Mountain group. The soils are poor in nutrients (Dystrophic) (Goudini, Worcester) and the rainfall occurs mainly in winter

low-lying western and southern parts. Characteristic of the escarpment is the intrusive dolerite koppies and dykes so frequently encountered in the Karoo, and which date from 150–195 million years ago.

Apart from this inner high-lying plateau which encompasses two-thirds of South Africa, there are the true mountains of the Cape Supergroup which run close and parallel to the south and south-west coast of South Africa, known as the Cape Folded Mountains. These coastal mountains which cause rain shadows, play an important role in the distribution of succulents. They consist of hard quartzitic sandstone which average about 1 000–1 500 metres in altitude.

The Cape Folded Mountains in the south are surrounded by the succulent-rich, low coastal plains and lower inland Karoo regions. These consist in the south of recent alluvium, calcrete and sands, and also of shales and sandstones of the Cape Supergroup. Other prominent formations in the south, rich in succulent flora, include sandstones and calcrete of the Malmesbury group as well as granites of the Cape granite suite and cretaceous conglomerates. The lower inland Karoo region to the north of the Cape Folded Mountains is very rich in succulent flora, especially *Mesembryanthemaceae* and *Crassulaceae*. It consists mainly of sandstones, shales and mudstones of the Karoo sequence.

The Little Karoo which lies between the Cape folded Mountains, is also one of the succulent treasure houses of South Africa. It consists of shales, sandstone and limestone of the Kango group, Cretaceous conglomerates and sandstone of the Uitenhage group as well as recent alluvium, sand and calcrete. The geology of the west coast is complex and some formations carry vegetation dominant in succulents. The coastal areas consist of coastal sands and alluvium soils. Inland towards the Namaqualand escarpment they consist of granites of the Little Namaqualand suite as well as diorite and gneiss of the O'okiep formations. The well-known Richtersveld



Aloe speciosa and *Euphorbia enopla* on a shale bank near the Breede river. The shale formations are rich in nutrients (Eutrophic) and rich in succulent species (Malgas district, Southern Cape)

in the north-west is very mountainous. Its central mountain range and northern parts consist of rock formations of the Gariiep complex and Orange River group, of which quartz forms an important component. Other succulent-rich formations of this area include the granodiorite of the northern and north-western parts, recent granites of the Tatasberg complex and Cape Granite Suite (Kuboos formation).

The Olifants River valley in Eastern Transvaal is another low-lying area rich in succulent flora. It is situated between the Strydpoort Mountains in the north to the Bankenveld in the south and the Eastern Transvaal Drakensberg in the north-east. Geologically it is complex, with very old Precambrian rocks of the Transvaal sequence. As was previously mentioned, this area has the richest diversity of *Aloe* species.

5. Climate

South Africa has an interesting climate. It lies between two diverse climatic regions, the tropics to the north and the temperate zone to the south. It is often very unpredictable, with abundant climatic conflict between the two regimes. In winter, the "Ferrel westerlies" (see Section 5.2) manage to extend to the Southern Cape, fighting off the South Atlantic high pressure, forcing it to the north, and in summer the South Atlantic and South Indian winds counter by deflecting the cold fronts to the south.

Because climate plays such an important role in the distribution of succulents, some background is necessary. Climate whether in South Africa or any part of the world, is influenced by three important factors: Firstly the latitude (distance from the tropics) which determines the amount of radiation secondly the position of the area in relation to the sea, and thirdly the altitude, which has a very important influence on the temperature, rainfall etc. Apart from these three most important factors, secondary factors such as the air circulation

of the atmosphere, ocean currents and mountains also have an important role to play.

Arid climates such as those found in South Africa are caused by the following factors: A prevailing high pressure system that prevents the inflow of moist air; land adjacent to a cold ocean, and mountain barriers. Our climate is the result of two major air circulation patterns (see Section 5.1): The Hadley Cell that brings the prevailing high pressure, and the Ferrel westerly winds causing the characteristic low pressure systems and cyclonic cold fronts in winters. The country is situated along the fringe of the tropics between 22 and 35 degrees latitude with a strong maritime influence. It is washed by the warm south-flowing Mozambique current in the east and the cold north-flowing Benguela current in the west.

The major features causing the dry weather pattern are as follows:

5.1 High pressure system causing prevailing aridity

Between the tropics and the temperate climates of the world there exists a prevailing high pressure system caused by the circulation of two large cells of rotating air on both sides of the equator, namely the Hadley Cell. It is driven by convection; hot air rises over the equator or tropics, then moves in a southerly and northerly direction respectively. In the southern hemisphere, while moving southwards, it loses most of its moisture, cools and descends at about 30° latitude (Durban to Springbok). This results in the characteristic high pressure belt preventing cloud formation over South Africa and its adjacent oceans.

This causes the south Atlantic high pressure system along the west coast, and the south-east trade winds, so charac-



The Boegoeberg (Richtersveld coast) is adjacent to the cold Benguela current on the west coast. The area is subject to regular fog on which the dominant succulent vegetation thrives. *Crassula brevifolia* ssp. *psammophila*, *Senecio phonoliticus*, *Conophytum saxetanum* and *Tylecodon schaeferanus* on the sheer eastern slope of the Boegoeberg

teristic of the summer months along the Cape coast. These strong south-easterly winds have a very important influence on the Benguela current as will be explained a little later. The south Indian high pressure system in summer causes the moisture-bearing north-easterly winds to enter over the escarpment as the high pressure belt weakens in summer over the interior. This results in thunder showers and other convective rain typical of the escarpment and interior. In winter the high pressure cell over the interior intensifies, and moisture-bearing winds cannot penetrate, resulting in winter aridity.



Crassula nudicaulis var. *herrei*, *Adromischus montium-klinghardtii*, *Crassula columella* and *Conophytum meyerae* on the farm Gembokvlei (Ograbies mountains, Richtersveld)



Senecio phonoliticus and *Conophytum saxetanum* on the Boegoeberg

5.2 The Ferrel westerlies which bring winter rainfall

The Ferrel westerlies are prevailing winds that are situated between the Hadley Cell to the north and the Polar Cell in the south. These Ferrel westerly winds spiral eastwards around the globe and result in the characteristic low pressure systems which bring the cyclonic winter rainfall and cold fronts, on which the winter rainfall Karoo flora is so dependent for its survival.

5.3 Influence of the cold Benguela current

The Benguela current flows in a northerly direction along the west coast. Strong prevailing south-east trade winds caused by the South Atlantic high pressure cell (Hadley Cell) cause the upwelling of very nutrient-rich deep-lying cold water along the shores of the west coast and it has an influence along the west coast as far as Southern Angola. This cold ocean (10°–14°C) cools the air and prevents the uptake of water in sufficient quantities; instead it brings to the region regular fog and heavy dew so important to the succulent vegetation of the west coast and the Namib.

5.4 Influence of the mountains on the distribution of rainfall

The influence of the Escarpment on the entrance of moisture-bearing winds has already been discussed. In the south the Cape Folded Mountains form a natural barrier and as a result moist air reaches the inland parts in limited quantities only. Examples include the Little Karoo and Tanqua Karoo; the latter receives less than 25 mm per annum in parts. Certain areas are almost devoid of vegetation. The winter rainfall is blocked off by the Cedarberg in the west, and summer rainfall is blocked by the Roggeveld mountains in the east.



The Tanqua Karoo lies in a rain shadow with parts receiving less than 25 mm per annum. The winter rainfall is blocked off by the Cedarberg in the west and the summer rainfall is blocked by the Roggeveld mountains in the east. It is the habitat of *Lithops comptonii*, *Tanquana prismaticus* and *Didymaotus lapidiformis*

5.5 Climatological advantages for succulents in the winter rainfall area

These are as follows:

(a) Precipitation occurs during the cool season. (May–September) when less evaporation takes place. Succulent species in this area actually grow in the cool season and most species are inactive or deciduous in summer.

(b) Frost is uncommon or mild.

By contrast, the Great Karoo has poor succulent flora compared to the winter rainfall Karoo regions. It receives higher rainfall, mainly in summer (September to April). However

(a) the downpour is of high intensity, thus producing a high runoff,

(b) precipitation occurs in summer when evaporation is high, (c) the high altitudes of the inland escarpment have extremely dry and cold winters with sub-zero temperatures during the night. Hot dry winds are frequent during the growing season.

6. The origin of succulent plants and the influence of animals on their present shapes

6.1 Why plants are more specialized in dry climates

In a high rainfall climate where the terrain allows, almost every square metre is covered with a dense plant growth consisting mainly of mesophytic plants. Usually this is a closed community and the main competition is for light and space. The plants most often have dorsiventrally compressed (flat) leaves which enable them to expose a greater surface to

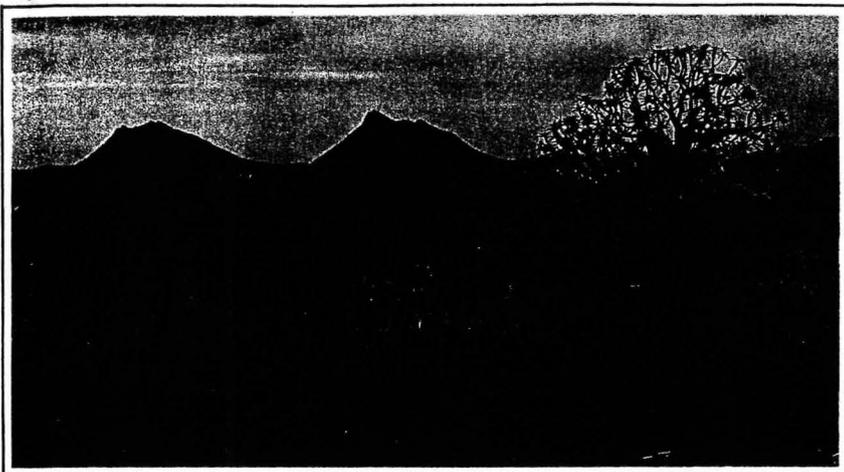


Tylecodon schaeferanus on a sheer south slope of the Boegoeberg

Table III: Geological time scale showing major features in earth's history with specific reference to Southern Africa and the evolution of succulent plants

Millions of years	Era	Period	Epoch	Rock Formation (1) in Southern Africa (Group)	Major Features in Earth's History (2)							
0	CENOZOIC	Quaternary	Holocene	Sand, alluvium, limestone	Evolution of many neo-endemic succulent taxa							
0,01			Pleistocene									
1,6		Tertiary	Pliocene	Alluvium sands, Kalahari sands	Great fluctuations in climate, glacials and interglacials. Succulents become abundant in arid regions throughout Southern Africa							
5						Miocene	Formation of Antarctic ice sheet. Semi-deserts develop along African west coast					
26			Oligocene	Uplift of E. African coast	Succulents become more widespread. High pressure cells become more intense. Forerunner of cold Benguela current. Great climatic fluctuations. Evolution of herbaceous plants. Cooling of earth's surface. Formation of cold Antarctic bottom water							
38						Eocene	First succulents. Ice-free earth					
54						Palaeocene	Early grasses and herbaceous perennials					
65	MESOZOIC	Cretaceous	(Enon conglomerates) Uitenhage Cape Palaeolatitude 50°-55°S	Flowering plants become dominant. Gondwanaland separated into Africa, India, Australia, South America and Antarctica. Extinction of dinosaurs								
140					Jurassic	Lebombo Dolerite intrusions Major volcanic eruption	Large widespread cosmopolitan flora. Ginkgo, cycads, ferns, conifers. Evolution of birds, mammals, social insects					
210								Triassic	Karoo Sequence (Great Escarpment)	Age of Dinosaurs. Conifers dominate vegetation		
245	PALAEOZOIC	Permian			Reptiles become abundant. Conifers become widespread							
290						Carboniferous			Insects become widespread. Primitive woody trees, cycads, ferns			
365										Devonian		
413						Silurian	Cape supergroup (Cape folded mountains)	First primitive vascular land plants				
441									Ordovician			
464						Cambrian	Cape granite suite	Invertebratae				
570	PRECAMBRIAN		Malmesbury Vanrhynsdorp Gariiep complex O'Kiep Soutpansberg Waterberg Orange River Transvaal sequence	Primitive Invertebratae Oxygen producing algae become widespread Oxygen levels rise								
2 500					Central Rand West Rand Beit Bridge complex (Northern Transvaal) Oldest known South African Rocks	Fossil bacteria (Barberton rocks) Atmosphere containing high levels of nitrogen & carbon dioxide Estimated Age of Earth						
3 000												
3 860												
4 600												

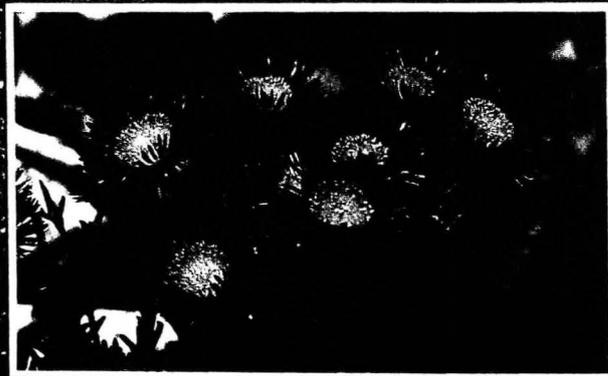
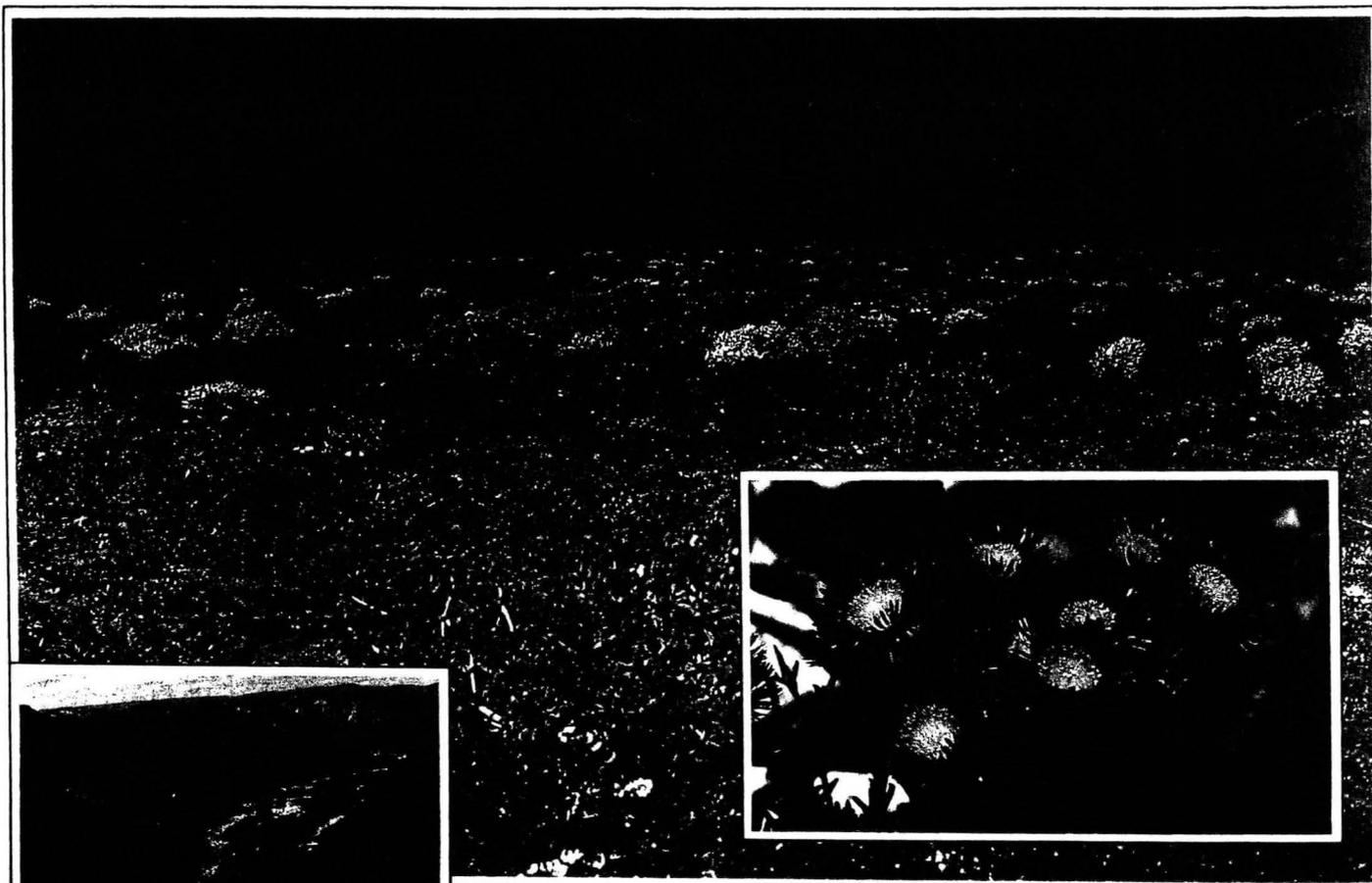
1. Visser 1984
2. Deacon 1982, Goldblatt 1978, Holland 1978, van Zinderen Bakker 1975



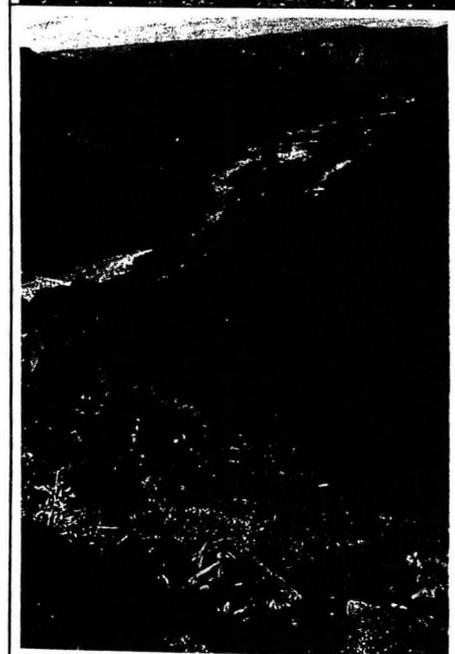
Aloe dichotoma from Pella. The succulent vegetation is a reflection of the long history of aridity



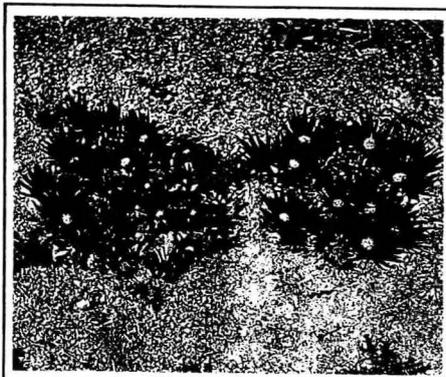
South Africa has a very rich and peculiar succulent flora. *Cheiridopsis peculiaris* in the dry summer season. Note the dry sheath that protects the plant from the hot sun (Steinkopf, Richtersveld)



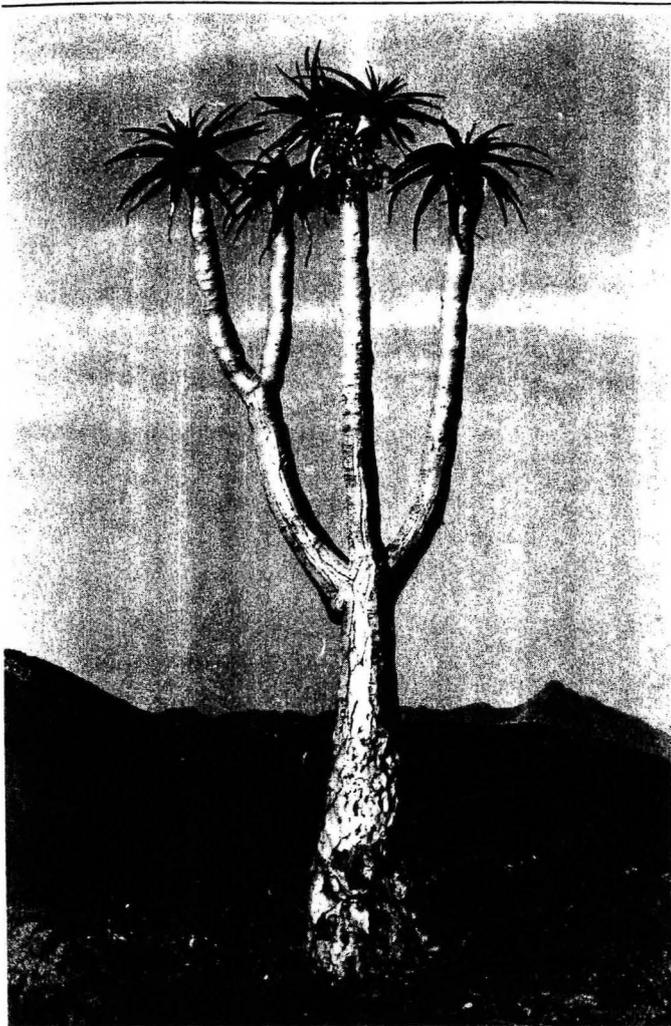
The family Mesembryanthemaceae is the succulent plant family with the most species. It is also one of the world's most colourful plant groups. *Lampranthus aurantiacus* and *Eberlanzia* sp. in flower east of Prince Albert



The arid regions of the North-western Cape are rich in succulent species. *Aloe gariensis* in the foreground (Rooiberg, Richtersveld)

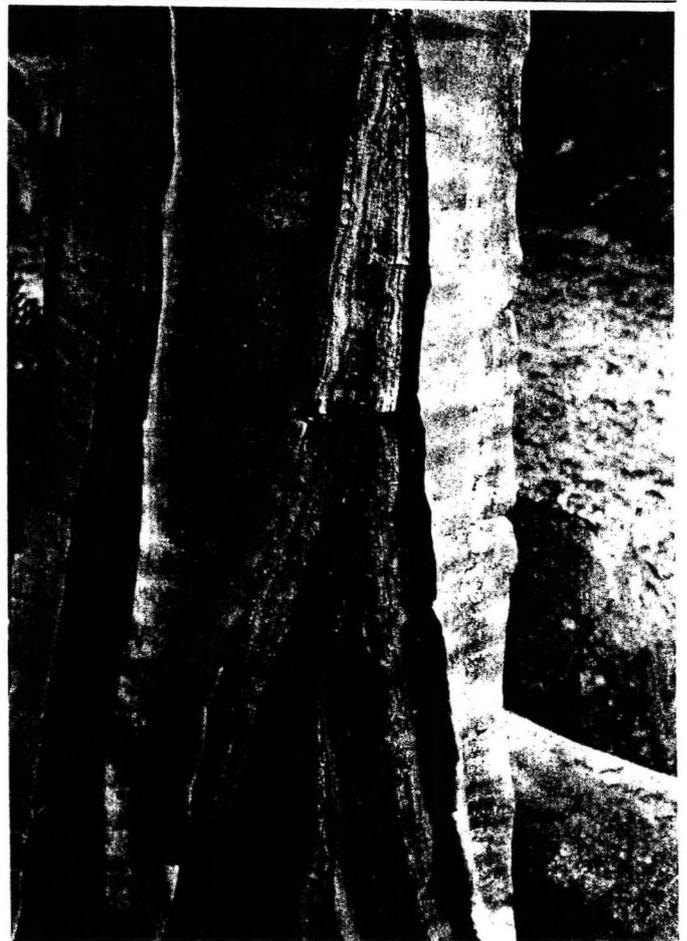


Dorotheanthus rourkei from Rietputz and *Hymenogone glabra* from Yzerfontein are two annual succulents. These are drought evaders which survive the long dry summer as seeds, only to germinate with the onset of the cool wet winters



Aloe pillansii from Paradysberg (Richtersveld). Note the damaged bark on the lower stems caused by goats in times of severe drought

light for the vital process of photosynthesis. In such a climate the pressure of animal predation in the community is not severe. As one moves towards a drier region there is a drastic decrease in plant cover, and an increase in xerophytes (Fig. 2). The plant concentration becomes more sparse and simultaneously pressure from animal predation increases. The plant community has to develop or evolve mechanisms, on the one hand, to cope with the drought, and on the other hand to avoid predators. At the same time these plants also have to find successful ways of reproduction. With time, as a result of the above-mentioned environmental pressures, many of these plants have developed peculiar shapes, sizes and self-protective mechanisms which allow survival under great pressure. This is in contrast to mesophytic plants which under favourable climatic and environmental conditions do not need to make such adaptations. Succulents are thus among the most specialized plants in the world. Stebbins (1952) and Axelrod (1972) draw attention to three important reasons why evolution accelerates in a dry climate. Firstly, in a dry climate the diversity of geology and topography has a much greater effect on plants than in a high rainfall climate. Secondly, the broken geological formation of a locally dry site tends to break up populations into smaller units, each of which is still able to interbreed and eventually give rise to new taxa (species). Thirdly, these taxa develop specialized xeromorphic structures (of which succulents are a good example) to cope with the dry conditions. There are many good examples to illustrate this, e.g. the widespread *Aloe arborescens* with its genetic variability and all the existing local forms, each adapted to its specific area, which perhaps in future could give rise to new species.



The bark of *Aloe dichotoma* and *Aloe pillansii* has sharp ridges which make it unpleasant to climb with bare feet (mechanical defence)



6.2 How succulent plants evolve

The question that arises is how succulents come into existence and why some look alike although they are not related. The answer lies in the phenomenon that life forms strive to be in harmony with their environment. When climatic and environmental conditions change, for instance when the climate becomes drier, these plants have to adapt, or die as was the case with the Dinosaurs 80–100 million years ago. All life forms came into existence by the creative power of our Creator. The process by which it happened can be partly explained by natural selection. How does this happen? The ability of a life form to take a particular shape or size stimulates the imagination. The reproductive and self-preserving urges are the strongest urges that exist among living things. Without it life would cease. This urge to live is a grace placed by our Creator in the genetic make-up of all living things. The genetic material or building plan of life is carried by all living beings. A basic genetic variability is inherent in all plant populations. This variability ensures that some members of the population will probably survive when changes in the regular climate occur. This genetic variability includes a built-in stability, but also flexibility. The built-in stability ensures that a plant remains unchanged and can survive a long-term stable climatic condition which could stretch over millions of years; the flexibility of some plants ensures that a plant can adapt to continual change in climate. Whilst the Palaeoendemic (Palaeo = ancient) *Welwitschia mirabilis* may possess the genetic stability to survive a long-term climatic condition, this may not enable it to survive a sudden change in climate. By contrast the neoendemic genera (neo = recent) *Gasteria* and *Haworthia* exhibit extreme genetic variability (flexibility) and could easily adapt to climatic changes. In order to survive, plants produce seeds. The seedlings dispose of variability, and although the offspring may look alike, there are slight differences. Mutations caused by natural radiation, including permanent changes in the genetic material, as well as hybridization, cause changes in the offspring. Only if these changes cause descendants to be more successful, will their chances of survival be better. We can illustrate this by means of the following example: A population of *Lithops meyeri* occurs amongst quartz pebbles in the South-western Richtersveld. The leaves are more or less the same size and colour as the stones and superficially they look alike. Those offspring which are different in colour would be spotted very soon by predators and eaten; their chances of survival are thus very small. Other examples include our vegetables and fruits in which our human species used the natural variability of species to select, hybridize and thus breed better quality plants.



Long term environmental pressures, especially those caused by animal species, have resulted in the peculiar defence strategies of succulent plants. *Pachypodium namaquanum* (Rosyntjieberg) has a thorny stem (mechanical defence) which is also poisonous (chemical defence). *Aloe ferox* (Malgas) has bitter sap and thorny leaves. *Conophytum burgeri* (Aggeneys) is well camouflaged





Lithops meyeri from Lekkersing

6.3 Main adaptive strategies which succulent plants follow to avoid animals

Ancestral man and beast who also dwelt where succulents grew were partly responsible for the plants evolving means of protecting themselves:

i. Defence

a. Mechanical. These plants are normally large, conspicuous and have thorny leaves or stems. *Aloe marlothii* and *Euphorbia grandicornis* are examples.

b. Chemical. This includes plants with a bitter and/or poisonous sap; *Adenia*, *Aloe* and *Euphorbia* species are good examples. Animals avoid these plants because of their inedibility.

c. Camouflage. This includes a great number of smaller species which resemble their surroundings and are thus difficult to see. *Lithops*, *Argyroderma* etc. are examples.

ii. Species density

Some members of the Mesembryanthemaceae are often the dominating plant group, especially in the winter rainfall Karoo, hence the Afrikaans name 'Vygieveld'. The ability to remain the dominant vegetation is part of their survival strategy. *Ruschia frutescens*, *R. utilis* and *Portulacaria afra* are good examples. The grazing animals therefore have a much smaller effect in the veld.

iii. Mimicry

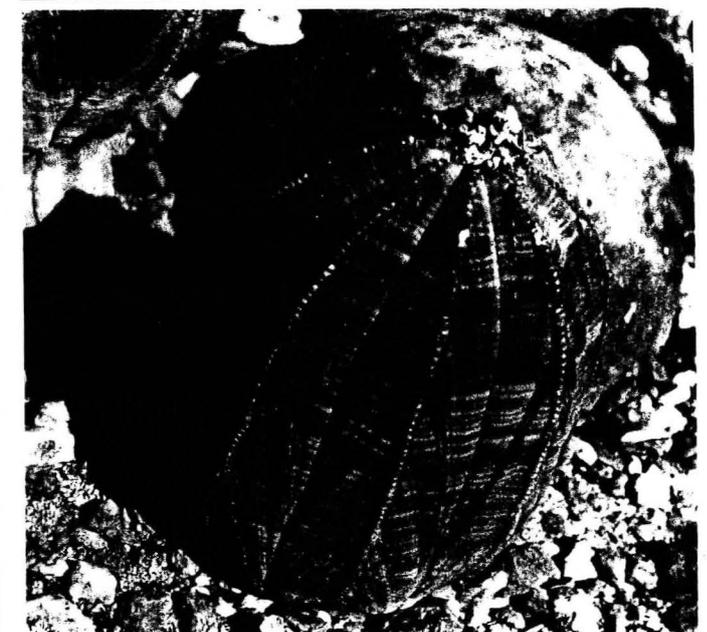
There are a number of cases where non-poisonous plant species resemble poisonous species with the result that animals would perhaps avoid such a plant, considering it to be poisonous. *Senecio ficoides* in certain parts of the Eastern Karoo resembles the inedible *Encephalartos lehmanii*. *Pelargonium crithmifolium* resembles the poisonous *Tylecodon reticulatus* and *Pelargonium tetragonum* resembles *Euphorbia mauritanica*.

6.4 Convergence

Convergence is a term used when one life form resembles another superficially because of similar environmental conditions that caused similar appearance etc. Some of the South African Euphorbiaceae resemble American Cactaceae, although they belong to totally different families.



The Naboom (*Euphorbia ingens*) has a toxic white sap (Chemical defence). It occurs in the subtropical and tropical eastern parts of Africa and is avoided by animals



Euphorbia obesa is difficult to spot in its natural habitat. It is another example of a plant resembling a rock



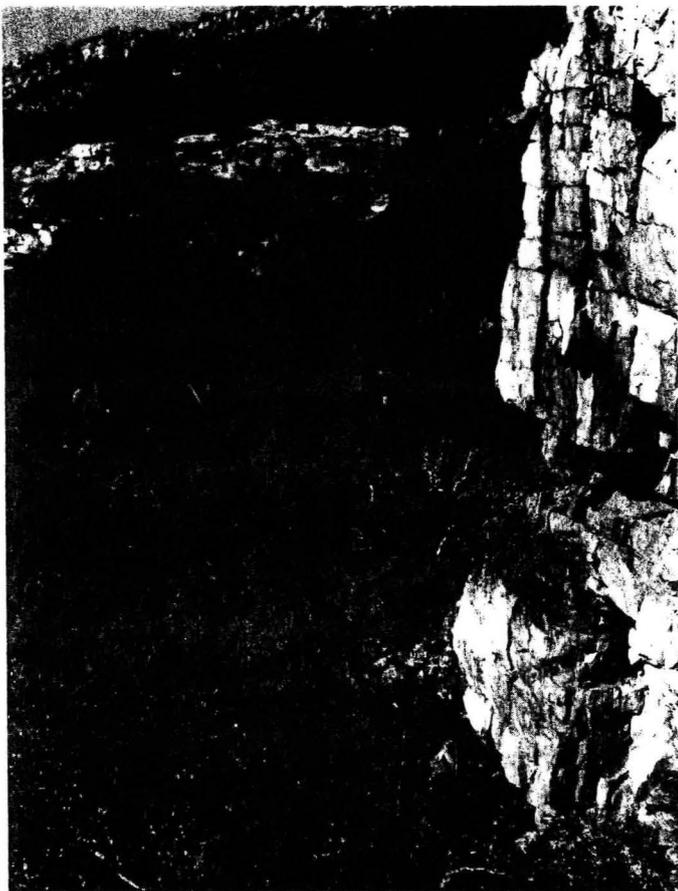
Note how well this seedling of *Gasteria acinacifolia* blends in with the decaying leaves



Gasteria obliqua is well camouflaged amongst the vegetation (Hankey)



The genus *Commiphora* (Burseraceae) is represented by 32 species in the arid subtropical regions of Southern Africa. *Commiphora gracilifrons* occurs in the North-western Cape and is highly aromatic



Portulacaria afra is dominant on the western slopes of Swartwaterspoort. Although the plants are frequently grazed, the ability to remain dominant is their main survival strategy



The South-eastern Cape is rich in succulent flora. Note the *Euphorbia grandidens*, *Senecio ficoides*, *Crassula lactea* and *Gasteria maculata* var. *liliputana*

7. Why Southern Africa is so rich in succulent flora

7.1 The evolutionary history of Southern African succulents

The subject of palaeobotany is important in our search for answers to the question of why Southern Africa has such a rich and diverse succulent flora. It throws some light on the past history of the world's climate and physical features which played a major role in the evolution of succulents. Although only a fragmentary record of succulent plant fossils exists, Speirs (1980) points out that certain facts on succulent plant evolution can be established without having any fossilized succulent on record, of which the following is the most significant. Succulents are flowering plants (Angiosperms) which evolved only during the early Cretaceous (140 to 65 million years ago), a geological period during the Mesozoic. In relation to the world's estimated age of 4 600 million years this is comparatively recent. We also know that the world's climate was warm and moist, and arid climates were uncommon from the time when the angiosperms evolved until about the Oligocene (38–26 million years ago). It thus seems that succulents evolved fairly recently compared to the time of appearance of the first plants 400 million years ago. But before I embark further on the subject, it is necessary to provide some background on non-flowering plants, from which flowering plants were derived, as well as to mention some animal life which evolved with the plants and which were partly responsible for the present shapes and sizes of our succulent plants.

The earth's estimated geological age is 4 600 million years. The earliest life forms known were the fossilized bacteria formed about 3 500 million years ago. Oxygen-producing algae became widespread 2 300 million years ago, with the result that the earth's oxygen levels rose dramatically, which enhanced the evolution of other primitive life forms which preceded the first plants. The Cape Folded Mountains date from about 360–450 million years ago (Ordovician–Devonian), a result of the deposits of sandy soil on a prehistoric seashore. By 350 million years ago primitive woody trees, ferns and primitive cycads evolved which became widespread during the Carboniferous period (365–290 million years ago). Our



Although in a high rainfall region at Cala pass, Transkei, the habitat is well-drained. Situated on a sheer eastern slope are the succulent species *Crassula orbicularis*, *C. parvula*, *Delosperma* sp. and *Gasteria excelsa*. Note *Selaginella*, a xerophytic fern species as well as the geophytic orchid (*Holothrix* sp.) It is thought that all our present succulent species evolved after the Cretaceous period (65–140 million years ago)



Kentsia pillansii occurs in poor (dystrophic) quartzitic sandstone soils of the Cape Supergroup



Aloe dichotoma from north of the Hantam. Note the juvenile, adult and dead plants. To date no fossil record of a succulent has been found

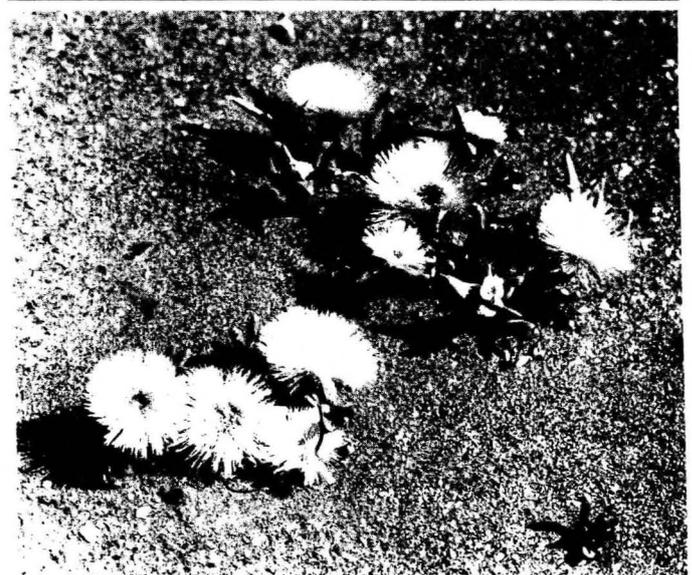
present coal and oil fields date from this period which is also when amphibians and the first reptiles appeared. The Mesozoic era (245–65 million years ago) was still very moist and hot. During this time the giant reptiles dominated the earth. Also the first primitive mammals made their appearance. By 180 million years ago there was a very widespread cosmopolitan flora consisting of ginkos, cycads, conifers and ferns. Flowering plants from which our present succulent plants evolved during the early Cretaceous, about 140 million years ago, at a time prior to the breakup of Gondwanaland, the giant 'supercontinent' of which Africa was part. About 100 million years ago it began to separate into the present Africa, South America, Australia, India and Antarctica. All this time, flowering plants were in an active state of evolution but only became widespread and dominant about 90 million years after the separation. It is also estimated that during the Cretaceous Africa was situated 15 degrees south of its present position, and Southern Africa lay in cooler latitudes (Goldblatt 1978). The continents were densely forested during this period with temperate Podocarpus forests in the South. Since

the early Tertiary, about 65 million years ago, pockets of aridity probably existed along the fringe of the tropics, caused by the prevailing high pressure systems (Goldblatt 1978). It is presumed that the first ancestral succulents made their appearance at this time, perhaps on local dry slopes which later, with the onset of drier conditions, became more widespread. Holland (1978) in a very interesting article on the evolutionary biogeography of the genus *Aloe* suggested that aloes originated during the Tertiary along the Highlands of South-eastern Africa. We must again bear in mind that there is no definite evidence. Another possibility that should not be ruled out is that during this period some succulents occurred as epiphytes on trees which provided local dry habitats. *Peperomia* and some epiphytic *Cactaceae* are present-day examples. These plants occur in warm tropical rain forests. The slopes of mountains or volcanoes in moist areas could also have provided local dry sites where succulent ancestors (Axelrod 1972, Speirs 1980) could have evolved.

It appears from this that it is not impossible that some of the first succulents date from the Cretaceous era. The Oligocene, (26–38 million years ago) is, however, the time when succulent flora began to evolve and radiate extensively. The Oligocene was an epoch characterized by the cooling of the earth's surface, which had a dramatic effect on the plant and animal life, and especially on the evolution of succulents. The possible reasons for the evolution of succulents from this period are as follows. Firstly the formation of cold antarctic bottom water resulted in the forerunner of the Benguela current (Van Zinderen Bakker 1975) which had a cooling and drying effect on the western and southern coasts of South Africa. Secondly the uplift of the East African coast which resulted in further mountain building, causing diversity in terrain, dry sites as well as rain shadows (Goldblatt 1978). Thirdly the high pressure systems on the fringes of the tropics which became now more intense resulting in further dryness. These conditions had a dramatic effect on the world's flora as there was an increased selection pressure for drought resistant species (Deacon 1983, Goldblatt 1978). The large evergreen forests that stretched across Africa partly declined, evolving into an open savannah woodland, and herbaceous plants appeared. The Oligocene is thus the period during which it is assumed that ancestral succulents evolved and became widespread as open drier habitats became established. An increase in animal predation pressure in dry habitats most likely caused succulents to develop their two main defensive strategies, namely mechanical defence and camouflage,

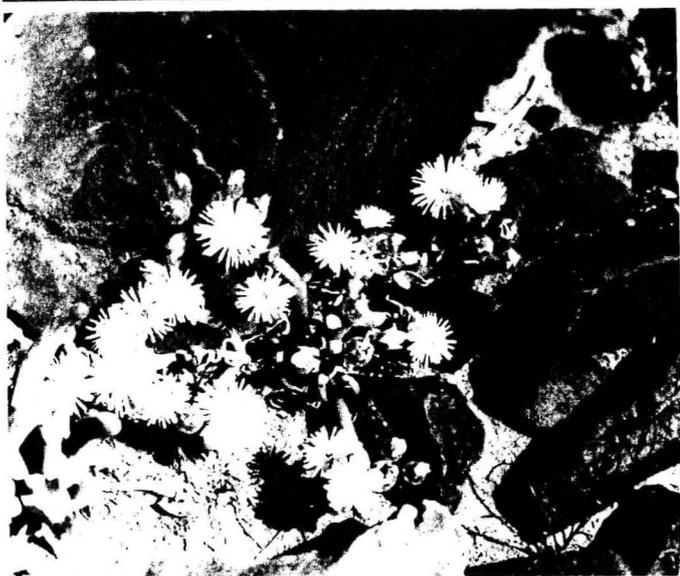


The Pellaberg consists of hard quartzitic sandstones. Winter rainfall flora as well as tropical summer rainfall flora occur here. It receives winter and summer rainfall

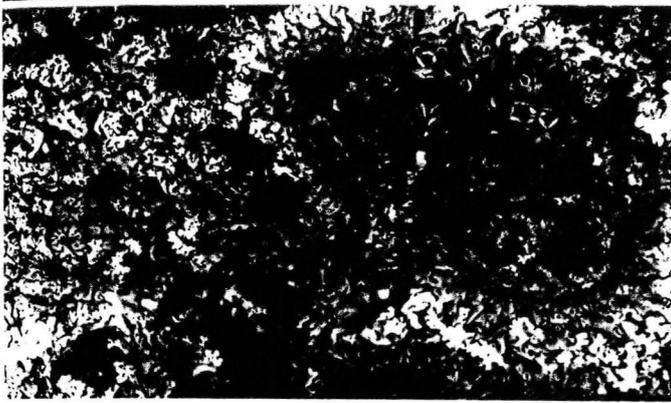


Eurystigma clavatum, (Heuningslaai) is endemic to the Ceres Karoo. It has attractive straw-coloured flowers

resulting in their peculiar shapes, sizes etc. We must also remember that, during the Oligocene, there existed two diverse floral kingdoms in Southern Africa which both contributed to our present rich succulent flora. Firstly the Cape Floral Kingdom from Southern Africa which consisted of a cool temperate forest flora, perhaps similar to the Knysna forests, as well as a sclerophyll vegetation in drier open areas and forest clearings (Deacon 1983), and secondly the tropical flora from Central and Northern Africa. Fossil records from Banke, in the North-western Cape, revealed a sclerophyll vegetation (Deacon 1983, Goldblatt 1978). Thus one can presume that our present-day winter rainfall Cape succulents evolved from the flora of the cooler temperate Cape. The eastern and northern tropical vegetation gave rise to succulents of tropical or subtropical origin. The presence of two diverse floral kingdoms, each evolving succulent flora in their region, adapting to a drier Africa, is thus an important reason for the richness of the succulent flora in Southern Africa. During the Oligocene there occurred great climatic fluctuations presumably caused by fluctuation in the sun's temperature. This period was characterized by cooler and drier periods as well as hotter and moister periods, but during the wetter periods succulents could survive in dry sheltered pockets in the mountainous regions both in Southern and Eastern Africa.



Mesembryanthemum nodiflorum from McDougal's Bay. This species occurs in the Western Cape as well as in North Africa. It is an annual or biennial



Conophytum obcordellum growing well camouflaged amongst lichens (Clanwilliam). Most of the Mesembryanthemaceae belong to the warm temperate winter rainfall flora

When favourable drier conditions recurred, succulents again migrated from their "shelters" to the surrounding areas. The Miocene (26–5 million years ago) which followed the Oligocene was characterized by further drastic change in climate which came closer to our present situation. The antarctic ice sheet formed and grew, cold water due to the Benguela current caused semi-desert areas to spread along the west coast (Deacon 1983), stimulating the spread of succulents in that area. According to Van Zinderen Bakker the Cape cyclonic winter rainfall is about the same age as the Namib as it was influenced by the same source, the cold antarctic climate. The late Pliocene, about 2 million years ago, resulted in further coastal uplift, causing more terrain diversity, further promoting the speciation of new succulent plants. During this period there was much fluctuation in the world's climate with glacials (ice ages) and warmer interglacials. During the glacials the polar ice sheets grew and the sea levels dropped. Van Zinderen Bakker suggested that during the ice ages the Benguela current had a drying effect on the west coast right up to the Congo, which further extended the migration and evolution of drought resistant plants and also resulted in the extinction of others. During interglacials the tropical flora moved southwards and the karroid flora of the Cape Floral Kingdom retreated to their present sites. We also see here that there was much climatic as well as floral conflict between the two climatic and floral kingdoms but together with terrain and geological diversity this resulted in the birth of many new succulent taxa (species). A good example is our present Eastern Cape where climatic and vegetation conflict occurs, resulting in the speciation of *Gasteria*, *Haworthia*, *Bulbine*, *Crassula* etc. During the last 1,7 million years, the earth was subject to 17 glacials of cooler and drier weather with the last glacial lasting from 70 000 to 10 000 years ago (Deacon 1983). The climate during the last glacial had a cooling and drying effect on Southern Africa, with the Karoo stretching perhaps to the Northern Transvaal or Zimbabwe. The cyclonic winter rains perhaps then stretched to the mentioned area. Succulents of the Cape Floral Kingdom could have occurred over a much wider range and recently became extinct, or now exist as a few remnants in the Transvaal, restricted to dry pockets. In drier areas the occurrence of *Frithia pulchra*, *Khadia* spp., *Gasteria batesiana*, *Haworthia*, *Portulacaria* as well as other typical Cape flora are good examples.

Our present succulent flora tells us a story of the long struggle for existence in an unstable dry climate within a very diverse terrain as well as severe animal predation. As was mentioned before, our present succulents derive from two floristic kingdoms, the flora of the warm temperate Cape and the flora of subtropical East Africa, of which the former is by far the richest.



Crassula nudicaulis is a very widespread species. Here it is photographed on the farm Kwaggaskop in the Knersvlakte



Conophytum bilobum

7.2 Southern African succulents of tropical origin

The subtropical succulents probably had their origin along the mountain ranges in East Africa and in West Africa, probably on the fringe of the tropics in the late Cretaceous, but became widespread during the Tertiary, with the onset of drier and cooler conditions. Succulent genera which probably originated from this area include *Aloe* (Holland 1978), *Talinum*, *Euphorbia*, *Pachypodium*, *Cyphostema*, *Cissus*, *Ceropegia*, *Sesamothamnus*, *Pterodiscus*, *Plectranthus*, *Kalanchoe*, *Adansonia*, *Thorncroftia* and *Aeolanthus*. We can safely assume that these succulents existed before or close to the separation of Madagascar, since most of these genera are featured on the island as well as Africa. Along the west coast of Africa the succulent members of the genera *Cyphostemma*, *Moringa* and *Commiphora* evolved which also migrated southwards, the latter only just entering the North-western Cape. *Welwitschia*, although not a succulent, seems to be a palaeoendemic which probably had its origin in tropical or subtropical West Africa and later, with the development of the Benguela



The genus *Portulacaria* has a disjunct distribution. It occurs in the southern and eastern parts of South Africa and then again in the arid western part. *Portulacaria armiana* from Sandberg (Southern Namib)

current, became widespread along the fog belts of Southern Angola and the Central and Northern Namib. The juvenile phase of *Welwitschia* develops a distinct cork layer suggesting a past adaptation to fire. This substantiates the fact that the Namib had a grass cover in the past. Thus it becomes clear that the Namib is without doubt one of the richest and oldest deserts in the world, with succulent xerophytes representing two diverse floral kingdoms which both contributed to its present make-up and richness. Present centres of speciation and evolution in the summer rainfall subtropical parts include the Eastern Transvaal and Swaziland, to a lesser extent the dry river valleys of Southern Natal and Kaokoland in the west.

7.3 Southern African succulents of warm temperate winter rainfall origin

The richest succulent flora in the world occurs and had its origin in the cooler, warm temperate South Africa. The Cape succulents probably evolved during the early tertiary on locally dry montane sites in Southern Africa, and became widespread during the cooler and drier Oligocene with the depletion of the temperate forest that existed in the area. But it was only the formation of the Antarctic ice sheet in the Miocene, we presume, that caused active speciation. *Aloe*, as Holland suggested, had its origin in the highlands of South-eastern Africa, and became widespread during the tertiary. However, *Aloe* must have entered the temperate south Cape flora very early, probably in the early Tertiary. This seems likely because of the distinctive and evolved *Aloe* taxa found in the winter rainfall region. Examples include *A. plicatilis*, *A. haemanthifolia*, *A. dichotoma* and *A. pillansii*. Succulent families and genera which are part of the temperate Cape flora include Mesembryanthemaceae, the majority of South African Crassulaceae (*Tylecodon*, *Adromischus*, *Cotyledon*, *Crassula*), Portulacaceae (*Portulacaria*, *Anacampseros*), succulent *Senecio*, *Othonna*, Zygophyllaceae, Aizoaceae and some Euphorbiaceae and succulent Geraniaceae. Present centres of speciation and endemism include the Knersvlakte, Richtersveld, Little Karoo and the South-eastern Cape. (See also table II).



Oophytum oviforme from the Knersvlakte is well camouflaged amongst the quartz



Adromischus cristatus occurs in the South-eastern Cape. It receives both winter and summer rainfall

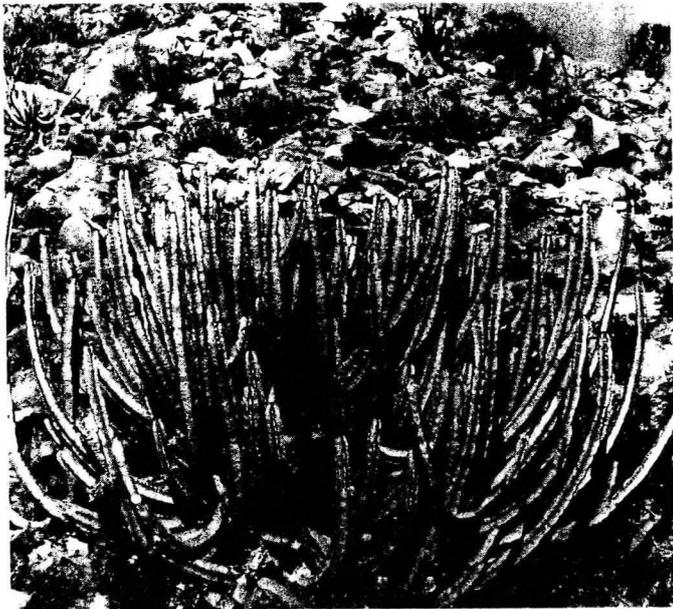
7.4 Present evolution of succulents in the intermediate zones of the South-eastern Cape

The South-eastern Cape is floristically very interesting and rich in succulent flora which exhibits a high degree of endemism (Cowling 1982). There are presently signs of active succulent speciation. *Gasteria*, *Haworthia* and *Bulbine*, *Crassula* and *Euphorbia* are examples. This active speciation of the above-mentioned genera is a result of the dry climatic conflict between the subtropical east coast climate and the temperate Cape climate together with the local diversity in terrain. It is a meeting ground of two floral kingdoms, an area shared by species of subtropical and temperate origin. Species on the border became fragmented with signs of active speciation. The above-mentioned genera together with *Faucaria*, *Bergernanthus* and *Glottiphyllum* are good examples of recent neo-endemic genera. But this climatic conflict was not always confined to the South-eastern Cape. It moves northwards during glacials, and perhaps resulted in the present rich Eastern Transvaal *Aloe* flora. Also very interesting, are the Eastern Transvaal *Aloe*, tree Euphorbias, as well as the

Namibian *Cyphostemma* species, which in cultivation do extremely well in the winter rainfall climate at Kirstenbosch, some even reproducing. By contrast *Adenia*, *Sesamothamnus*, *Pachypodium*, *Adenium* and *Adansonia* cannot be grown outdoors here. The only reason that I can think of is that *Cyphostemma*, Eastern Transvaal Aloes and *Euphorbia* species have been subject to winter rainfall during past glacials and that these plants have a built-in flexibility to cope with wet winters.

7.5 Disjunct distribution of our present succulent flora

Another interesting phenomenon found amongst our succulent flora is the existence of disjunct distribution patterns. The genera *Portulacaria* and *Bowiea* are examples. *Portulacaria afra* occurs widespread in the South-eastern karroid regions, going up along the east coast to the dry Northern and North-eastern Transvaal river valleys. Two related species *P. armiana* and *P. pygmaeum* re-appear in the Richtersveld.



Euphorbia hottentotta from Kuboes, Richtersveld



Bulbine latifolia, *Crassula capitella* ssp. *thyrsiflora* and a *Gasteria obliqua* juvenile growing below the thorny Eastern Cape Valley Bushveld (Hankey). The thorny cover provides shelter. There is a marked increase of *Gasteria* species in the all year rainfall regions of the Eastern Cape

Bowiea also has an interesting distribution, occurring in Eastern South Africa (*B. volubilis*) and suddenly re-appearing in the lower Orange River valley in the west. *Gasteria* section *longiflorae* has a similar distribution pattern and there are also many non-succulent xerophytic examples, for instance *Erytrophysa*, *Euclea linearis*, *Heteromorpha aborescens* and *Azima tetraantha*. These examples also suggest that the South African climate during past glacials was more uniformly dry and that our xerophytic flora, having a much wider northern distribution, and with unfavourable severe conditions, became restricted to milder arid pockets where it survived.

7.6 Summary of reasons for the rich and diverse succulent flora of Southern Africa

The rich diversity of South Africa's succulent flora is the result of the long history of aridity in the region, with the first succulents appearing on local dry sites dating perhaps from the end of the Cretaceous (about 80 million years ago) as well the past climatic instability characterized by severe climatic fluctuations, in which the climate gradually became drier and cooler. The present dry climatic situation is caused by:

- Upwelling of cold water along the west coast resulting in a stable aridifying effect on the west coast with occasional dense fog belts;
- The high pressure system on the fringe of the southern tropics which has a general drying effect over Southern Africa;
- Rain shadows caused by mountain ranges, of which the Ceres and Little Karoo are good examples.

Physical features (mountain ranges) and geological diversity result in local dry sites and diversity in soil types, which in turn result in the fragmentation of populations into smaller units. The mountain ranges provide arid pockets where succulents can survive the climatic onslaught.

Animal pressure led to their present main adaptative strategies of armour (structural and chemical) and camouflage.

South Africa is enriched by the occurrence of succulents from two distinct floral kingdoms i.e. the richer flora of the warm temperate Cape and the subtropical flora.



Gasteria maculata, *Crassula cordata* and *C. capitella* ssp. *thyrsiflora* growing below a *Euphorbia curvirama* (Alicedale)

8. Xeromorphic adaptations of Southern African succulent plant families

(Technical terminology on sexual reproduction and pollination adopted from van der Pijl (1982) and Real (1983))

8.1 Mesembryanthemaceae

(124 genera, 2 316 species in South Africa and Namibia)

As mentioned, this is at present South Africa's, but also the world's largest succulent plant family. The family is extremely diverse, often dominant in the winter rainfall Karoo regions where the greatest centres of endemism and species density occurs. Mesembryanthemaceae range from a few mm tall (*Maughaniella luckhoffii*) to shrubs 3,5 m tall (*Stoeberia beetzii* var *arborescens*). The attractive shining flowers are modified stamens. Their fruit structures are among the most complicated in the plant kingdom.

Drought adaptation

Succulent leaves: The majority are leaf succulents, the leaves are normally oblong and terete. When flat they may be laterally rather than dorsiventrally compressed as found in most other mesophytic plants. In this position the rays of the sun do not fall perpendicularly on the leaves at midday. (*Leipoldtia grandifolia*). *Cheiridopsis* and *Argyroderma* have thick cuticula. The annual species have big shiny watery cells on the leaf surface. The leaves of *Monilaria* and *Amoebophyllum* wither during the dry summer months. *Conophytum stephanii* and *C. pubicalyx* have hairy leaves; both occur in an area where coastal fog is frequent. Water condensates on the leaves and ensures extra moisture. *Conophytum*, *Mitrophyllum* and many other genera use the pair of old withered leaves as a protective sheath to cover the new pair during the dry resting season. This protecting "armour" also wards off insects, and protects the plant from excessive water loss. The light-coloured grey leaves of *Argyroderma* and *Schlecteranthus* reflect the sun.

Stem succulents: *Psilocaulon* (Psilo – bare; Caulon – stem), or "scorpion vygie", as the local name implies, has succulent stems. The leaves are early deciduous.

Shallow root system: Most Mesembryanthemaceae are shallow rooted and can make very effective use of light showers.

Pachycauls, geophytes and succulent roots. *Mestoklema* and *Sphalmanthus* have a succulent caudex which is in most cases underground. The roots of *Trichodiadema pomeridiana* are succulent.

Leaf Orientation: The orientation of the terete leaves of *Cephalophyllum ceresianum* is always towards the sun. In the early mornings they point towards the east, midday almost erect and in the afternoon they point towards the west.



Pherolobus maughanii is an annual from the Calvinia district. Note the large club shaped stigmas and large epidermis cells



Prenia sladenii, growing near the confluence of the Fish and Orange rivers, has compact leaves which prevent excessive water loss



Juttadinteria tetrasepala is a compact tufted succulent of the southern Namib (Kortdoringberg)



The family Mesembryanthemaceae is at present the world's largest succulent plant family. It is also one of the most diverse families represented by about 120 genera. This is *Herreanthus meyeri*, a monotypic genus from Rooiberg (southern Richtersveld)

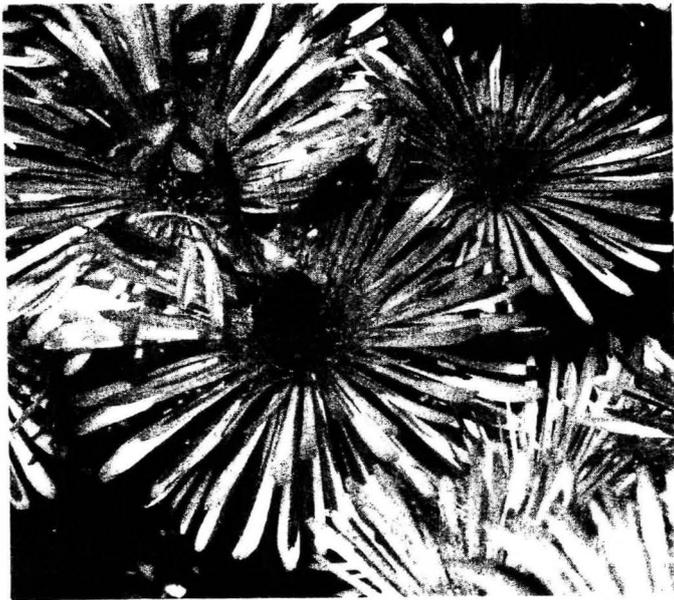
Reproductive adaptation

Sexual: Insects (bees, flies, wasps and moths) are the main pollinating agents attracted by the large shiny flowers. The petals are modified staminodes. *Stomatium*, *Neohenrichia* and *Mossia* have scented flowers which open during late afternoon and night to attract moths. *Dorotheanthus apetalus* and *Micropterum pappulosum* are self-pollinated; both have very small inconspicuous flowers.

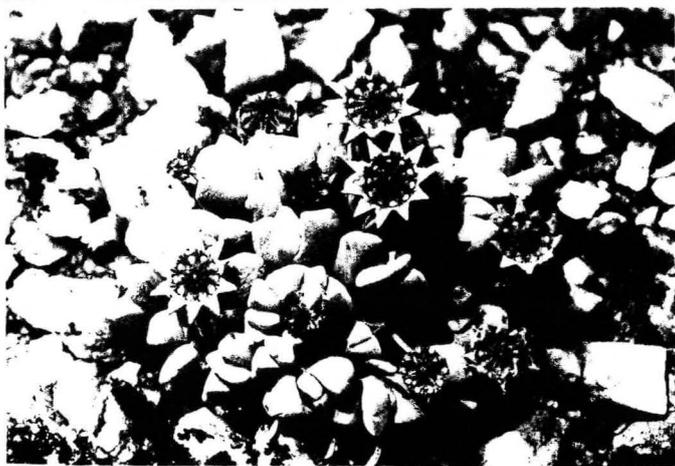
Seed Dispersal:

Rain: Most Mesembryanthemaceae fruits are hygrochastical (wet – open, dry – closed). Fruits open when it rains, and the velocity of the falling raindrops scatters the seeds around the plant. It is termed rain ballism (van der Pijl 1982). The fruiting capsules of the various genera vary, some have placental tubercles, cell lids etc. to ensure that not all the seeds are washed out by the first rains.

Wind: The fruit capsules of *Stoeberia* are hygroscopical (open when wet and remain open). The seeds are winged in most cases, and are wind dispersed (flyers). *Ruschianthemum* and *Hymenogone* have schizocarpic fruits, the capsules split up in various parts and are wind dispersed. *Sceletium* fruits are light when dried out and are soon detached from the mother plant. The plants have a procumbent habit and a combination of factors including the long stems as well as wind are responsible for seed dispersal.



The Mesembryanthemaceae has colourful flowers. The honeybee plays an important role as the pollinating agent for *Lampranthus multiradiatus*



Cheiridopsis herrei after a shower of rain; note the open hygrochastic capsules. The velocity of the raindrops on the capsule disperses the seed (Bloeddrif, Richtersveld)

Autochory: *Stoeberia carpii* has long weak flowering branches of up to 1 m long. The flowers are produced at the apex. The long fruiting branch leans under the weight of the heavy succulent leaves. The seeds are thus distributed by the long "arms" of the plant (blastochory). These long fruiting branches are brittle and are often detached from the mother plant, however the sufficient water supply in the leaves ensures that fruiting will take place, even if the flowering branch is detached from the mother plant. The plants are also self-fertile.

Animals: Fruits of *Carpobrotus* (Goukum, sourfig etc.) are delicious and highly prized by some humans and baboons (Mammalochory). Fruits of *Carpobrotus muirii* and *C. acinaciformis* are sold on the Cape Town fruit market. These are also popular for making jam.

Irregular seed germination: The seed germination in some species is uneven, ensuring that not all the seeds germinate after the first rains. *Caryotophora* fruits are very hard (a schizocarp), which would only disperse the seeds after several years of weathering. Recent research by Ihlenfeldt has shown that some Mesembryanthemaceae seeds, during early germination, with a sudden drought, are able to "freeze" temporarily until the right conditions occur.

Vegetative reproduction: *Jordaaniella* and *Cephalophyllum* and many other species are procumbent, and will root at several places where the stems touch the soil. *Lampranthus tenuis* has brittle side branches, these fall to the ground and root next to the mother plant. This species occurs on the fringe of low lying pans in the Cape Peninsula and during the rainy season the plants are often half submerged. *Lampranthus glaucus* reproduces itself vegetatively by the same method as above.



Skiatophytum tripolium has long trailing branches. The fruiting capsules are hygroscopical and drooping. The seeds are released when the capsule opens (blastochory)



Carpobrotus species have fleshy edible fruits. Seeds are dispersed by humans, baboons and other animal species



This sheer precipice of the Dabenorisberg is the habitat of *Conophytum fulleri*, well protected from browsing animals and plant collectors

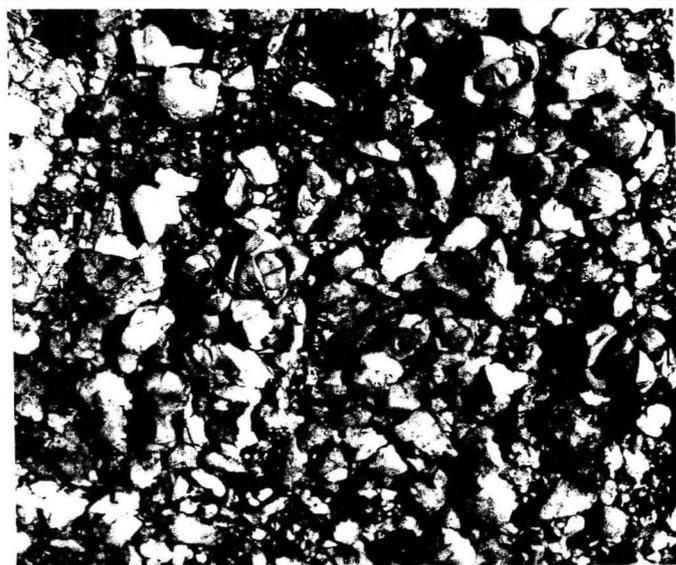
Defence

Camouflage and mimicry: Dwarf species often look like stones in their surroundings. *Lithops*, *Friithia*, *Dinteranthus*, *Gibbaeum* and *Pleiospilos* are examples. *Erepsia* occurs in Fynbos. When not in flower it is almost impossible to detect as it merges in with the sclerophyll vegetation.

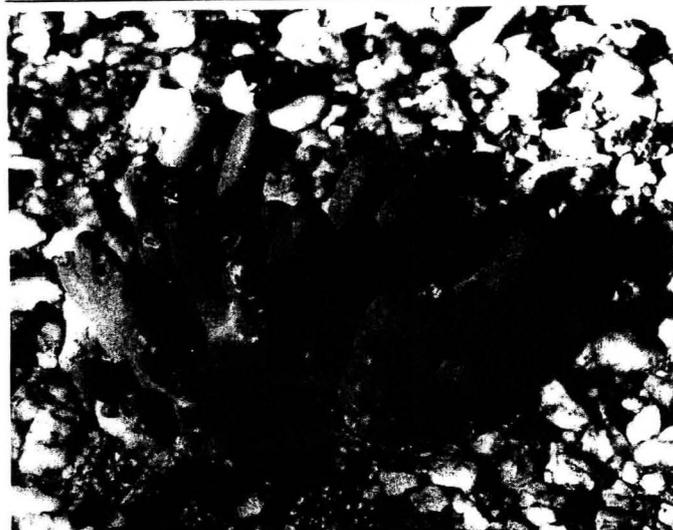
Mechanical: The spiny modified branches form an excellent protection for *Eberlanzia*. *Trichodiadema* has tufts of thorny hairs on the leaf apices. The dry fruiting capsules of *Ruschia indurata* in the Bloemfontein and Winburg districts are brittle, the capsule becomes detached from the pedicel and 3-4 thorny bristles remain on the stalk. The old inflorescence of *Ruschia pungens* is persistent and modified to a thorny protection. The stems of *Amoebophyllum* are deciduous in summer, the branch hardens and terminates into a hard sharp point. *Psammophora* and *Arenifera* have a sticky leaf surface, sand and other material sticks to the leaves which makes them difficult to see, and presumably unattractive to predators.

Chemical: Some Mesembryanthemaceae are poisonous, *Drosanthemum hispidum* and *Psilocaulon absimile* are toxic to animals. (Watt & Breyer-Brandwijk 1962).

Habitat protection: *Conophytum fulleri* and many other species occur on steep south facing rock crevices, well protected from non-flying phytophagous animals.



Lapidaria margaretae from Pella is difficult to spot amongst the quartz pebbles



The leaves of *Dactylopsis digitata* have a high salt content and are avoided by browsers (chemical defence). Note also the *Tylecodon pygmaeus* and *Oophytum nanum*

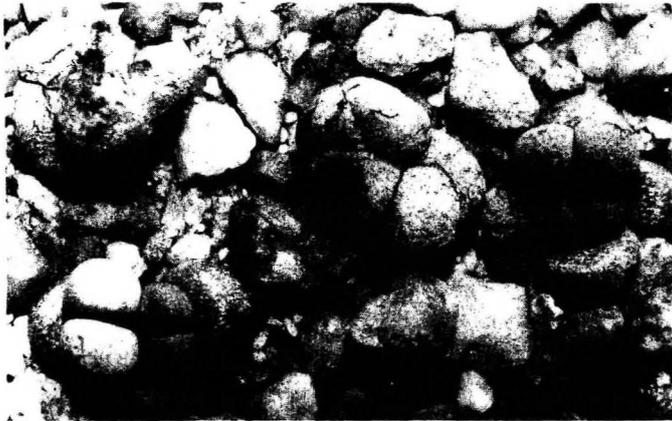
8.2 Crassulaceae

(5 genera, 280 succulent species in South Africa and Namibia)

Crassulaceae is South Africa's second largest succulent plant family. It is common in the dry winter rainfall areas. It varies from dwarf annual species (*Crassula glomerata*) to shrubs up to 2,5 m tall (*Tylecodon paniculatus*). There are four genera represented in South Africa.

Drought adaptation

The Crassulaceae are mainly leaf succulents (*Crassula*) but stem succulents (*Tylecodon*) and caudiciform plants (*Tylecodon tuberosus*) also occur. *Cotyledon tomentosa* has very hairy leaves, protecting the plants from excessive transpiration but may also play a role in warding off insect predators. *Tylecodon singularis*, as the specific epitheton implies, has a single large flat leaf. Its habitat is the mountainous terrain of the Southern Namib which is frequently subject to coastal fog. This is a possible adaptation where fog condensates on the leaf which is then either directly absorbed or drips off the plant to be used by its shallow root system. The *Tylecodons* are deciduous in the dry summer periods. The dense imbricate leaves of *Crassula teres*, *C. columella* and *C. columnaris* act as a pseudostem and only a small surface is exposed to transpiration. Some forms of *Cotyledon orbiculata* and *Kalanchoe* species have blooms covered by a white waxy powder which reflects sunlight and prevents excessive water loss. Crassulaceae are shallow-rooted, thus allowing the plant to make use of light showers. Many species have tuberous roots (*Tylecodon ventricosus*).



Crassulaceae is South Africa's second largest succulent plant family, best represented in the winter rainfall regions of South Africa. *Crassula elegans* (*C. globosa*) from the Knersvlakte is well camouflaged amongst the quartz pebbles



Crassula barklyi from Strandfontein, Namaqualand. Note the compact growth and prolific nature

Reproductive adaptation

Sexual: Pollination is mainly by insects. *Cotyledon* and some *Tylecodon* species have large colourful tubular flowers which are bird pollinated (Ornithophily). *Kalanchoe* and certain *Crassula* species have an elongated flowering branch ideal for wind dispersal. This strategy of seed dispersal is termed Anemoballism (van der Pijl 1982). Most Crassulaceae have very light small seeds which are wind-dispersed (dust diaspores).

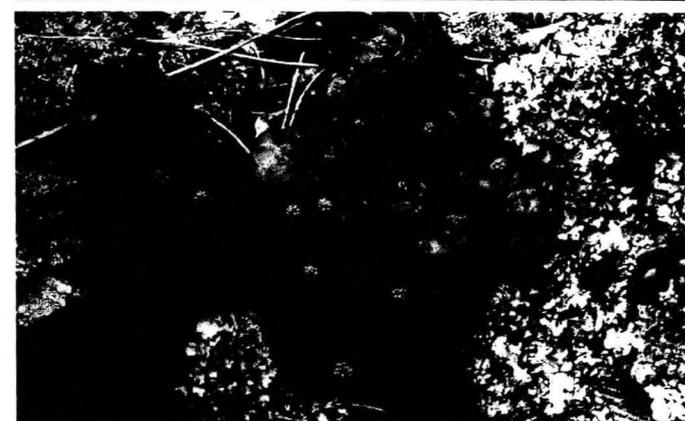
Vegetative reproduction: The leaves of *Adromischus* are brittle, and will root whenever they are detached from the mother plant. Most *Crassula* species will also root from detached leaves or stems.



Cotyledon orbiculata from Kortdoringberg, Richtersveld. Note the ovoid leaves



Adromischus alstonii from Bloeddrif. Note the vegetative reproduction from the detached leaves



Crassula orbicularis from Malgas. Note the prolific nature of the plants (vegetative reproduction)

Defence

Mechanical: *Tylecodon wallichii* have large thornlike phyllopodia (petiole bases). The old inflorescences of *Tylecodon reticulatus* are persistent and harden with age and act as a thorny armour. The old star-shaped calyxes of this and some other species become detached from the corolla but remain hanging loosely on the pedicel. When the wind blows these calyxes vibrate, resembling small living insects. *Crassula hystrix* has thornlike hairs on its leaves which offer effective protection against insect predators.

Chemical: The conspicuous larger *Cotyledon* and *Tylecodon* species are poisonous to cattle, causing Krimpsiekte in cattle (Watt & Breyer-Brandwijk 1962), hence the name Krimpsiektebossie.

Camouflage and mimicry: The small edible species are mostly well camouflaged, resembling their background (*Crassula elegans*, *C. corallina*, *Tylecodon occultans*). *Crassula streyi* resembles the aromatic *Plectranthus oertendahlia*, and the plants also occur in the same environment, both being endemic to Southern Natal, suggesting mimicry. *Othonna herrei* resembles *Tylecodon wallichii*. *Pelargonium crithmifolium* resembles *Tylecodon reticulatus* and both also occur in the same area. The stems of *T. suffultus* and *T. kritzingeri* resemble dry branches. Both are found amongst xerophytic shrubs. *T. kritzingeri* is a scandent species with curled leaves which support the weak branches amongst the karroid shrubs. It is deciduous in summer and very difficult to detect.

Habitat protection: *Adromischus diabolicus*, *Crassula exilis* subsp. *sedifolia* and *Cotyledon tomentosa* are examples found on sheer cliff faces. Many species occur in the dense eastern Cape thorn scrub community and are thus protected by the thorny larger shrubs.



Crassula capitella ssp. *thyrsoiflora* and *C. hirtipes* from Strandfontein

8.3 Asclepiadaceae

(18 genera, 250 succulent species in South Africa and Namibia)

Asclepiadaceae is S.A.'s third largest family of succulent plants. It is widespread but more common in the karroid winter rainfall areas of the Cape. It is often edible. Most members are small and inconspicuous, occurring in the protection of xerophytic herbs and shrubs. Some are twiners (*Ceropegia*) and a few are conspicuous and large (*Hoodia*). As with the Orchidaceae, the flowers are highly specialized, having a similar pollen dispersal strategy. The flowers of most of the Asclepiadaceae are large and showy.

Drought adaptation

Asclepiadaceae are mainly stem succulents, but leaf succulents (*Ceropegia*) and geophytes occur (*Brachystelma*, *Raphionacme* etc.). Leaves of most species are reduced and early deciduous or sometimes reduced to spines (*Hoodia*). Most species have shallow adventitious roots. The branches of certain species are densely hairy (*Stapelia flavirostris*), which prevents excessive transpiration. The flowers are also fleshy compared to most other succulents.



Crassula elegans and *Adromischus marianae* var. *hallii* (lefthand) from Brandkaros



Crassula capitella ssp. *thyrsoiflora* amongst quartz rocks on Kortdoringberg. The plant on the left is *Dianthus namaensis*



Trichocaulon simile from Brandkaros (Richtersveld). Water is stored in the succulent stems. Note the paired fusiform follicles

Reproductive adaptation

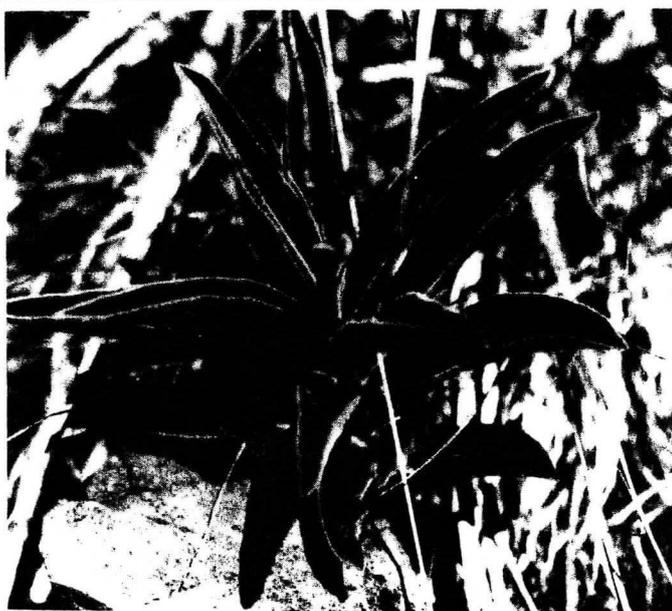
Sexual: Some Asclepiadaceae flowers are very large and smell like rotting meat, attracting bluebottles and flies (Sapromyophily). Some flowers are fringed with a hairy margin resembling a dead mammal or part of it. Although being pollinated by flies or bluebottles, these plants do not offer nectar or other rewards to the insect. These insects are thus fooled. As with the Orchidaceae the pollen is sticky, adhere to the visiting insects, and is carried off to other plants to ensure cross-pollination. *Ceropegia* has a tubular corolla with stiff hairs, their apices facing towards the corolla base, temporarily trapping the insect, which ensures cross-pollination.

Seed dispersal: Seeds are produced in paired fusiform follicles which split open longitudinally when ripe, releasing the flattish seeds attached to their silky parachutes (plumed diaspores). It is dispersed by wind.

Vegetative reproduction: The smaller species are often mat forming and will root where stems touch the soil while others are stoloniferous. Detached pieces lying on the ground could also root.



Huernia quinta in flower. Most Asclepiadaceae flowers are pollinated by flies and bluebottles. What would the pollinating agent be for this species?



Raphionachme hirsuta has a subterranean tuber. It occurs in grassveld on the Transvaal highveld (Jacanlee, Randburg)

Defence

Mechanical: The larger conspicuous species have thorny columnar stems (*Hoodia*). The spines are modified leaves. The *Quaqua* species, which are edible, are armoured with hardened phyllopodia.

Camouflage: Although it is South Africa's third largest family, most members are not at all conspicuous. The majority of taxa are edible and the plants have a camouflage existence. *Fockea*, *Piarranthus* and *Duvalia* are good examples.

Chemical: It is reported that certain strains of *Sarcostemma viminalis* are poisonous to humans and animals (Watt & Breyer-Brandwijk 1962).

Habitat protection: *Tridentia baylissii* and *Lavrani haagei* are examples found on sheer cliff faces. Many other species occur in dense thorny scrub and are thus protected.

Convergence: The spiny columnar stems of *Trichocaulon* superficially resemble some members of the Cactaceae. This cannot be regarded as a protective strategy, however, since the cacti which they resemble do not occur naturally in Southern Africa.



Quaqua mammillaris are armed with thorny phyllopodia. It is edible (Hantam)

8.4 Asphodelaceae

(6 genera, 248 succulent species in South Africa and Namibia)

The family Asphodelaceae is South Africa's fourth largest succulent plant family, but the largest of the Monocotyledonae. *Aloe* which incorporates about 150 species, are very characteristic of the South African landscape, with the greatest species density found in the North-eastern Transvaal. The Asphodelaceae range from dwarf succulent species (*Bulbine mesembryanthoides*) to succulent trees 20 m in height (*Aloe bainesii*). Asphodelaceae are widespread throughout the winter and summer rainfall areas. The family Asphodelaceae was formerly placed under the Liliaceae.

Drought adaptation

Plants are mostly leaf succulents, but *Aloe dichotoma* and a few other species also have succulent stems. A few species are geophytic (*Bulbine*) having leaves that whither during the dry season. The leaves of most *Aloe*, *Gasteria* and *Haworthia* species are leathery with a waxy layer on the epidermis. Some species have glaucous leaves. *Aloe kniphofioides* is geophytic.

Reproductive adaptation

Sexual: The large tubular-flowered species are mainly bird pollinated (*Aloe*, *Gasteria*). *Bulbine* and *Haworthia* have small white and yellow flowers which are insect pollinated. Succulent Asphodelaceae flower mostly in the dry season when there is not much competition from other flowering plants. (*Aloe*, *Haworthia* and *Gasteria*) and the seed usually ripens just in time for the coming rainy season. The inflorescence of *Aloe suffulta* is scandent and supported by the dense vegetation in its native Zululand habitat. The perianth of *Aloe* and *Gasteria* produces nectar in profusion and the flowers are pollinated mainly by sunbirds. *Aloe* flowers are protandric: when the pollen is shed the nectar is at the base of the ovary (perianth subpendulous). When the lengthened stigma ripens (perianth horizontal), nectar is guided to the perianth apex by air pressure from the desiccating corolla.

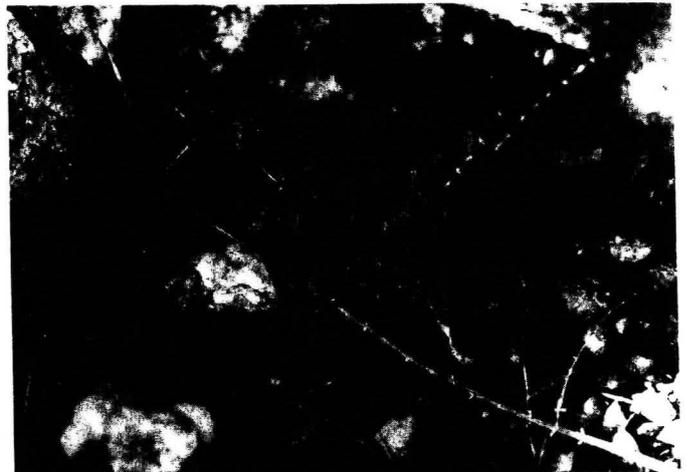


Aloe pillansii is a rare endemic of the winter rainfall southern Namib. Water is stored in the succulent leaves and stems (Cornell's kop, Richtersveld)



Aloe speciosa is a leaf succulent from the southern and eastern Cape. The leaves are bitter (chemical defence)

The nectar is often seen in the mouth of the perianth or hanging as a characteristic drop from the flower apex. This also attracts bees and other insect pollinating agents. This is very well developed in *Gasteria* flowers which remain pendulous. *Gasteria* flowers are basally inflated (Gasteriform). The perianth segments are fused into a cylindrical tube. The inner segments are fused dorsally on the outer segments. The margin of the inner segments is free, involute or canalicate for the length of the ventricose base enclosing or encircling the 3 stamens, thus forming a membranous sheath through which the nectar is projected. This distinctive feature is found in all *Gasteria* species. The inner segments in many *Aloe* species are also somewhat canalicate but not to the same extent as in *Gasteria*. Nectar is guided through the 3 inner perianth sheaths and as the desiccating corolla deflates thus pushing the nectar to the perianth apex. Most *Gasteria* and *Aloe* flowers are green- or yellow-tipped, thus making them conspicuous to insect pollinators. *Aloe*, series Saponariae also have an inflated corolla base, however the inner segments are fused to the outer ones and the perianth margins are not free. The filaments around the ovary are distinctly flattened and their margins touching. The nectar accumulates in the ventricose base and is pushed between the ovary and the flattened filaments. When the stigma ripens the base deflates, and the air pressure pushes the nectar to the perianth apex. This is a great attraction to bees which cannot penetrate the narrow perianth tube. It thus seems to be adapted to insect as well as bird pollination. The bulbous based perianths described above could perhaps also be explained functionally as a means to protect the ovary against destructive bird species.



Bulbine striata is a geophyte from the southern slopes of Pellaberg. The leaves wither during the dry hot summer months



The colourful tubular flowers of *Gasteria carinata* pollinated by sunbirds (Potberg)

Seed dispersal: The tall inflorescence, the erect capsules and the flat or winged seeds suggest an adaptation to wind dispersal (Anemochory). This is found amongst most succulent Liliaceae.

Vegetative reproduction: *Aloe variegata*, *A. grandidentata*, some *Gasteria* and *Haworthia* species are stoloniferous, and colonise small areas often forming dense groups. Leaves of the majority of *Gasteria* species are regularly grazed by cattle, especially in times of drought. The leaves are brittle and if a broken part drops to the ground, it rapidly roots and proliferates to form new plants. Young plants rarely develop on the inflorescences of *Gasteria acinacifolia*.



Aloe ferox in fruit. The erect infructescence and winged seeds are a clear adaptation to the wind dispersal (Infanta, S. Cape)



The small white flowers of *Haworthia* are pollinated by insects (*H. turgida* from Matjieskloof, Malgas)

Defence

Mechanical: Most *Aloe* species are conspicuous and the leaves armoured with thorns (*Aloe melanacantha* etc.) Old persistent leaves protect the stem of *A. ferox* and *A. marlothii* etc. The leaf margins of some *Gasteria excelsa* clines are razor sharp. The leaves of *Gasteria* and *Haworthia* are coriaceous (leathery) which makes them unpopular to most insects. The bark of *Aloe dichotoma* and *A. pillansii* have sharp vertical ridges.

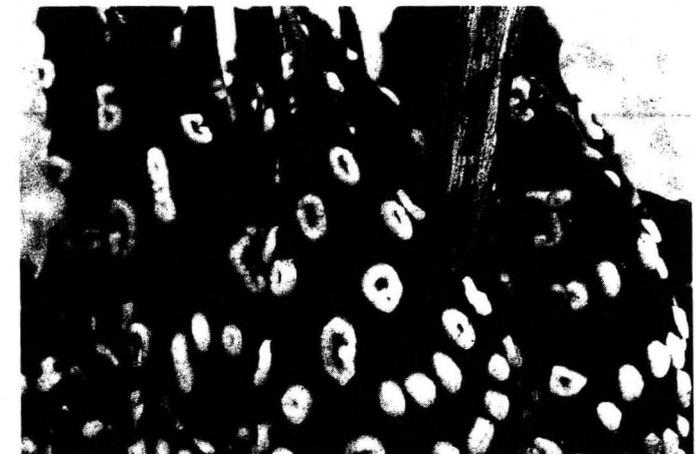
Chemical: The leaf sap of *Aloe*, although not poisonous, is very bitter and is usually avoided by cattle. *Aloe ferox* leaves are often fed to cattle in the Eastern Cape to rid them of ticks and other external parasites (Watt & Breyer-Brandwijk 1962).



Gasteria carinata proliferates from the base to form dense groups. Note the stoloniferous *Euphorbia stolonifera* (Hartenbosch, S. Cape)



When *Gasteria excelsa* are grazed by game or cattle, broken leaf pieces lying on the ground will root and proliferate to form new plants (Chalumna, E. Cape)



The coriaceous white tubercles of *Haworthia pumila* forms an effective armour (mechanical defence)



Gasteria maculata var. *liliputana* is well camouflaged below the xerophytic shrubs



Aloe dabenorisana occurs on sheer precipices, well out of reach of game and browsing stock (Pellaberg)

8.5 Euphorbiaceae

(4 genera, 210 succulent species in South Africa and Namibia)

The family Euphorbiaceae varies from dwarf geophytes (*E. tuberosa*) to large succulent trees (*E. ingens*). The species are widespread throughout South Africa with its main centre of distribution in the South-eastern Cape where plants are a conspicuous feature of the landscape.

Drought adaptation

Plants are mainly stem succulents. Leaves are small and early deciduous. *Synadenium* is a stem and leaf succulent.



The bark of *Aloe plicatilis* is corky and a good insulator. Fynbos (narrow leaved shrublands) which is subject to fire

Camouflage: *Haworthia springbokvlakensis* and many other *Haworthia* and *Gasteria* species are well camouflaged in their habitats. *Gasteria armstrongii* is well camouflaged, resembling the stony background of the habitat in the Gamtoos valley.

Habitat protection: *Gasteria rawlinsonii*, *Aloe meyeri* and *A. dabenorisana* occur on sheer cliff-faces (cremophilous) and are thus well protected from non-flying predators.

Convergence: Aloes superficially resemble the American Cactaceae.



Most Euphorbia species are stem succulents. Note the ribbed stems of *Euphorbia polygana* (Trappalanda, E. Cape). The thorny stems are avoided by browsing animals (mechanical defence). Note also the resemblance towards the Cactaceae from America

Reproductive adaptation

Sexual: Insects are the main pollinating agents. The flowers are small, yellow and often inconspicuous.

Seed dispersal: The fruit is a 3-locular capsule which is under tension and the seeds are dispersed explosively (active ballists).

Vegetative reproduction: *Euphorbia stolonifera*, as the name implies, is stoloniferous. A few species will root from branches that fall to the ground.



Synadenium cupulare is a leaf succulent from the subtropical parts of eastern South Africa. The milky sap is highly toxic (chemical defence)



Euphorbia herrei is a rare succulent from the Richtersveld. Note the articulated ribbed stems (Buffelsbank)



Euphorbia virosa from the southern Namib resembles American Cactaceae, a fine example of convergence. Note also the *Euphorbia gregaria* and *E. dregeana* (S. Namib, north of Sandberg)

Defence

Mechanical and chemical: Most conspicuous species are armoured and poisonous. Thorns are in most cases modified stipules. The leaf bases of *E. hamata* are modified to hard thorny tubercles. The side branches of *Euphorbia fasciculata* are modified spines. Most succulent euphorbias have a milky poisonous sap which sticks to the skin and often causes irritation (Watt & Breyer-Brandwijk 1962). The sap could also cause temporary or permanent eye damage. The bushmen use *E. virosa* as a substance in their arrow poison.

Convergence and camouflage: *Euphorbia globosa* is a non-thorny species which resembles stones. *Euphorbia opuntoides*, *E. virosa* strongly resemble American Cactaceae. This is an example of convergence.



Euphorbia marlothiana occurs in loose sand. It is stoloniferous and forms large clumps (Melkbosstrand)



Euphorbia ephedroides amongst quartz pebbles together with *Crassula atropurpurea* var. *cultriformis* (Kortdoringberg, Richtersveld)

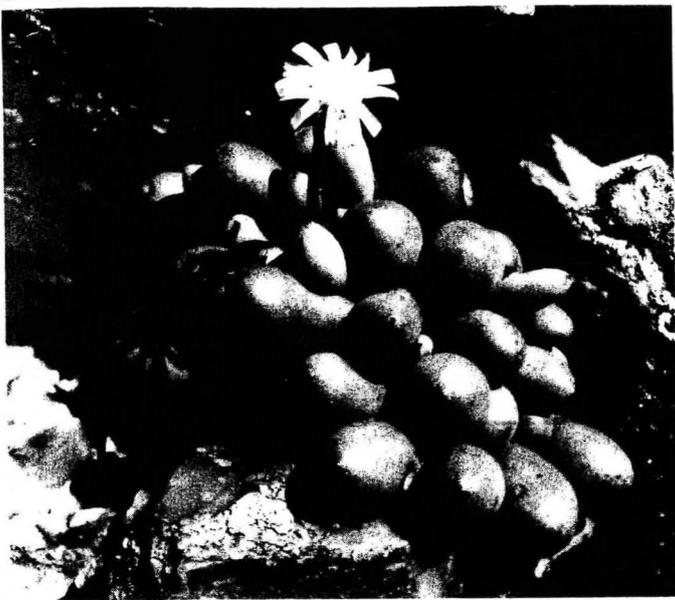
8.6 Asteraceae

(3 genera, 120 succulent species in South Africa and Namibia)

The family Asteraceae is the largest family of flowering plants in the world. Only few are succulent. Succulent Asteraceae are chiefly confined to Southern Africa and are mainly confined to the karroid winter rainfall region. The succulent *Senecio* spp. are common in areas in the South-eastern Cape. The plants vary from dwarf procumbent leaf succulents (*Senecio radicans*) to shrubs 2,5 m tall (*Othonna triplinervia*).

Drought adaptation

Most species are leaf succulents, with terete or round leaves. *Senecio articulatus* has articulated succulent stems and its succulent leaves are deciduous during the dry season. *Senecio*



Othonna clavifolia is a leaf succulent from Kortdoringberg, Richtersveld. Note the compact club shaped leaves. The yellow flowers are pollinated by insects

radicans is an evergreen procumbent mat-forming species which often develops tuberous roots. Most *Othonna* species are deciduous in the dry season and a few are geophytic (*O. hallii*). *Senecio haworthii* has a dense silver-white hair layer on its leaf-surface which also reflects sunlight. *Othonna armiana* has a caudex.

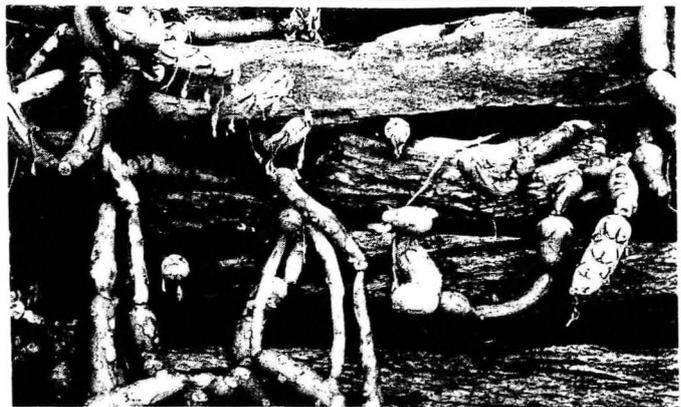
Reproductive adaptation

Sexual: Pollination is by insects. Seeds are attached to a parachute (pappus) and are wind dispersed (Plumed diaspores). The seeds of *Othonna armiana* seem to fall in van der Pijl's (1982) classification of 'creeping diaspores'. The hygroscopic bristles on the seed's surface perform a movement which leads to the penetration of the seeds into the soil.

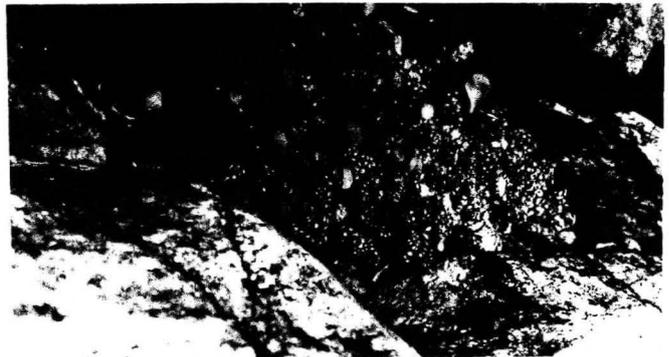
Vegetative reproduction: *Senecio radicans*, *S. rowleyanus* etc. are mat forming and will root freely. The succulent articulated stems of *S. articulatus* are brittle and will root if detached from the mother plant. *Senecio iosensis* is stoloniferous.



Note the defensive leaf stand of *Senecio orbicularis* (Jacanlee, Randburg). This species has a succulent subterranean tuber



Senecio articulatus is a deciduous stem succulent. The stems are brittle and will root when detached (Worcester)



Othonna armiana has a succulent caudex. The hardened phyllopodia forms a protection against phytophagous insects (mechanical defence)



Othonna euphorbioides from Namaqualand have thorny stipules (mechanical defence)

Defence

Mechanical and chemical: *Senecio* species are often aromatic especially in the very dry parts of the North-western Cape. *Othonna auriculifolia* is poisonous to small stock (Watt & Breyer-Brandwijk 1962). The leaf bases of *Othonna herrei* and *O. armiana* are modified to hard thorny tubercles. The old inflorescences of *O. euphorbioides* are persistent and form a thorny protection.

Camouflage and mimicry: There is a slight resemblance of *Othonna herrei* to *Tylecodon wallichii* which is probably due to mimicry. Certain forms of *Senecio ficoides* resemble *Encephalartos lehmanii*. *Senecio longiflorus* resembles the poisonous *Euphorbia mauritanica*.

Habitat protection: *Othonna cyclophylla* occurs on very steep vertical rock faces.

Convergence: *Othonna euphorbioides*, as the name implies, resembles an Euphorbia. This is an example of convergence. *Senecio stapeliiformis* which resembles a *Stapelia* is another example of convergence.

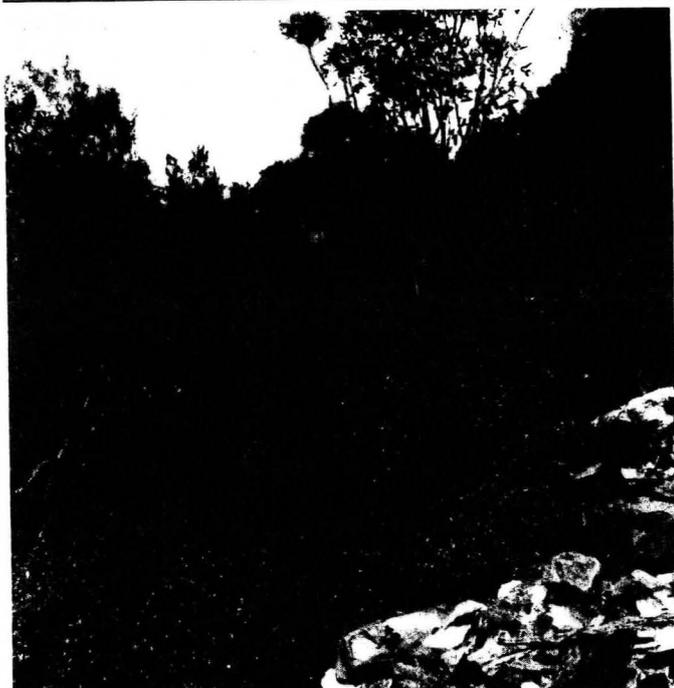
8.7 Portulacaceae

(5 genera, 53 succulent species in South Africa and Namibia)

The family Portulacaceae is extremely variable. The majority of species are dwarf perennials. *Ceraria* and *Portulacaria* are shrubs up to 3 m tall. The family is widespread in the dry parts of South Africa but with a high degree of endemism in the winter rainfall Karoo. *Portulacaria afra* is dominant in certain areas of the Southern Cape (Spekboomveld) and *P. armiana* in parts of Southern Namibia. The former is the most widespread and serves as fodder for the Addo elephants.



Ceraria namaquensis is a succulent shrub with small succulent leaves (NW. Cape)



Portulacaria afra is widespread in the arid regions of southern and eastern low lying areas of South Africa. It is a leaf and stem succulent and a valuable fodder plant (Baviaanskloof). The tall shrub in the background is *Cussonia spicata*

Drought adaptation

Most species are leaf and stem succulents with a shallow root system. *Portulacaria pygmaeum* from the Richtersveld and adjacent areas has a succulent caudex. *Anacampseros* which often has succulent roots are very interesting; it is divided into two sections. The stipules of section *Avonia* are modified to large white imbricate scales which protects the plants from direct sun. Taxa in Section *Anacampseros* is often covered with dense hairs which more or less have the same function as the last named.

Reproductive adaptation

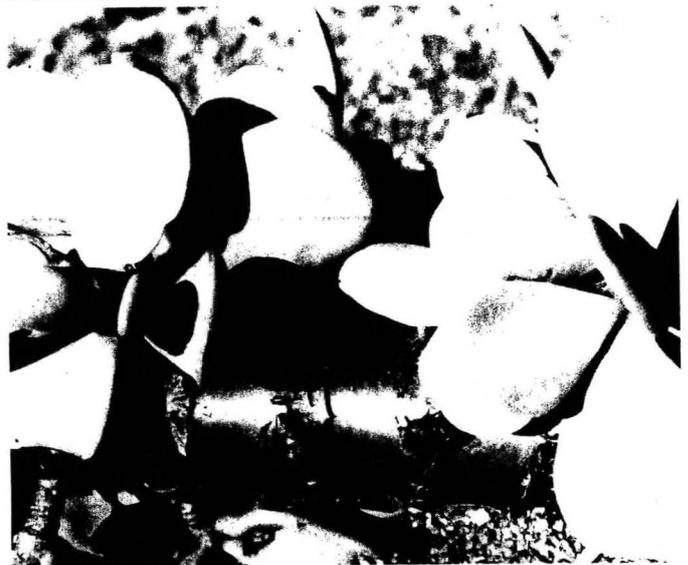
Pollination is mainly by insects. Seeds are very light and are wind dispersed (winged diaspores). The tall flowering branches of *Portulacaria armiana* (3–6,4 m) are an ideal adaptation for wind dispersal (ballistic anemochore).

Defence

Mechanical and chemical: *Portulacaria afra* is poisonous in certain areas. It is also very possible that *Portulacaria armiana* of the southern Namib is poisonous. The tall flowering branches carry dense flower clusters at their apices, out of reach to most of the grazing game that occurs in the area. The large imbricate stipules and the dense hairs of *Anacampseros* wards off predators.



Ceraria fruticulosa is usually a shrub of 1,5 m tall. This form from Brandkaros, Richtersveld is a prostrate shrub. Note the succulent leaves and main branches

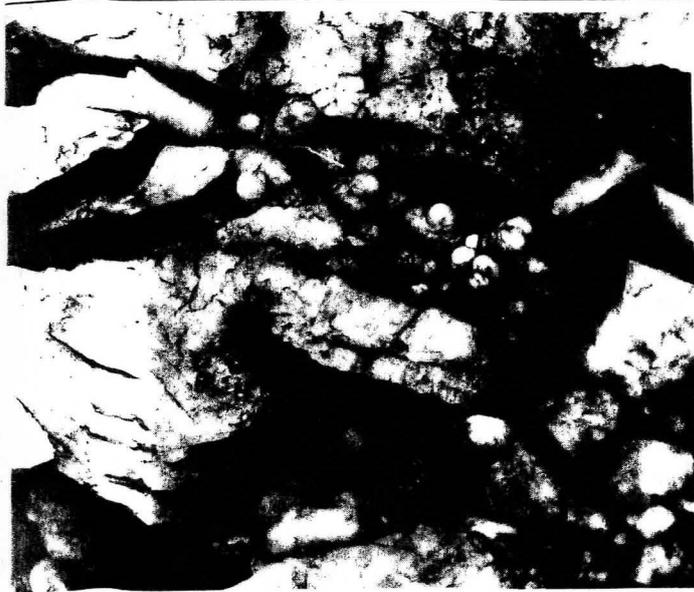


The leaves of *Portulacaria armiana* resemble a Cotyledon. It is a succulent shrub of the southern Namib and is often dominant

Camouflage and mimicry: *Anacampseros* is small and well camouflaged. Most species are edible. There is a slight resemblance of *Portulacaria armiana* to *Zygophyllum prismatocarpum* which occur in the same habitat which may be due to mimicry or convergent evolution.



Waxes on the leaves of *Anacampseros subnuda* are an ideal protection against the sun and would also play a role in warding off insects



Anacampseros meyeri is well camouflaged amongst the quartz pebbles. The dense imbricate scales (stipules) protect the plant from solar radiation and could play a role in warding off insects

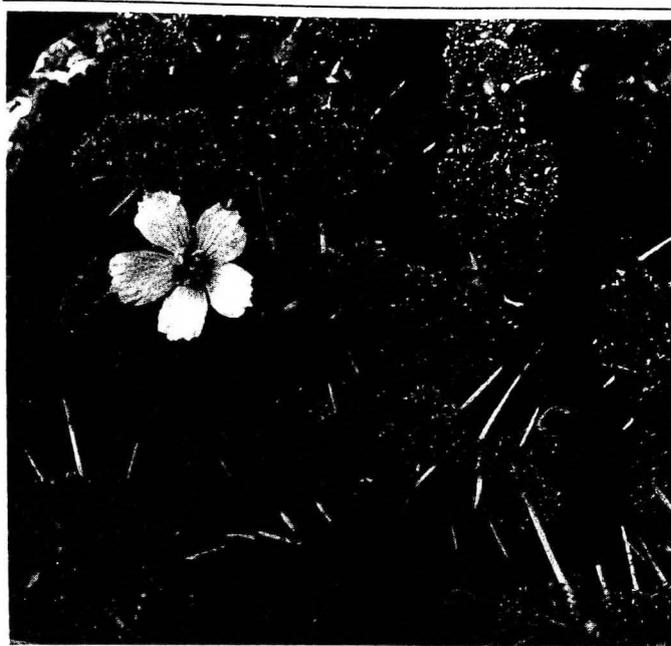
8.8 Geraniaceae

(2 genera, 40 succulent species in South Africa and Namibia)

This family consists mainly of xerophytes and it is very well represented in the South Western Cape. It varies from small geophytes (*Pelargonium sibthorpiiifolium*) or caudiciform species to shrubs 1,5 m tall (*P. paniculatum*).

Drought adaptation

Stem succulents are in the majority (*P. gibbosum*, *P. crithmifolium*, *P. canosum*). These species also have slightly succulent leaves which are thicker in winter. The Geraniaceae have shallow roots and make use of light showers. *Sarcocaulon*



Sarcocaulon crassicaule is a stem succulent with a very tough coriaceous bark. Its thorns are modified leaf petioles (mechanical defence)

(Bushman candle) has a very hard succulent stem with a thick coriaceous bark. *P. antidysentericum* has a caudex. *P. rapaceum* is a geophyte which remains in a state of dormancy during the winter months.

Reproductive adaptation

Sexual: Pollination is by insects. Seeds are wind-dispersed (plumed diaspores).

Seed dispersal: The seeds have a drilling action caused by the hygroscopic spirally twisted awn; when wet, the awn unwinds and pushes the seed by a drilling action into the soil (trypanocarpy).

Defence

Mechanical and chemical: The Geraniaceae are aromatic, which makes them unattractive to most predators. The leaf petioles of *P. spinosum*, *P. paniculatum*, *P. hystrix* and *Sarcocaulon* spp. are modified to spines. The stems of *Sarcocaulon* are hard, dry and inedible. The inflorescence of *Pelargonium crithmifolium* is persistent and thorny.

Camouflage and mimicry: *Pelargonium crithmifolium* resembles *Tylecodon reticulatus*, *P. tenuicaule* and *P. hystrix* are well camouflaged amongst the xerophytic shrubs. *P. antidysentericum* resembles *Dioscorea elephantipes*. *Pelargonium tetragonum* resembles the poisonous *Euphorbia mauritanica*.

8.9 Zygophyllaceae

(3 genera, 34 succulent species in South Africa and Namibia)

The family Zygophyllaceae is common in the dry winter rainfall Karoo and especially the Namaqualand and Southern Namib coast. It varies from small dwarf herbs to shrubs 2 m tall (*Z. prismatocarpum*). Zygophyllaceae are not frequently found in cultivation as they are difficult to propagate.

Drought adaptation

The species are leaf succulents.

Reproductive adaptation

Insects are the main pollinating agents. Seeds are winged and wind dispersed.

Defence

Chemical: The leaves of *Augea capensis* have a high salt content and are unattractive to browsers.

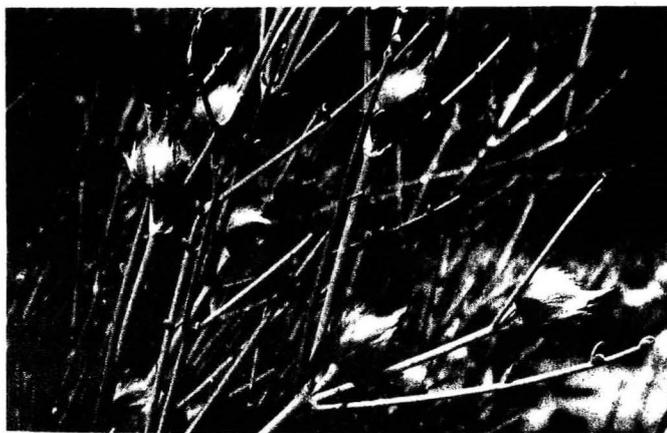
Convergence: *Augea capensis* superficially resembles members of the Mesembryanthemaceae family.



Zygophyllum prismatocarpum is a leaf succulent of the southern Namib. It superficially resembles *Portulacaria armiana* (convergence). The genus *Zygophyllum* is well represented on the south western coast of Africa



Zygophyllum stapfii from Mcdougalsbay, Port Nolloth. Note the procumbent growth and the orbicular leaves (Baboon shilling)



Sisyndite spartea is a common succulent shrub of the dry river beds in the North-western Cape and Namibia

8.10 Lamiaceae

(3 genera, 23 succulent species in South Africa and Namibia)

The succulent Lamiaceae occur in the subtropical eastern and northern regions of South Africa. The succulents vary from dwarf succulent herbs (*Plectranthus purpuratus*) to shrubs 1 meter tall (*P. spicatus*). The majority of species are found in well-drained rocky sites.

Drought adaptation

The Lamiaceae are mainly leaf succulents (*P. neochilus*, *P. cylindraceus*, *P. spicatus*, *P. verticilatus*). *P. ernstii* is a stem succulent. *Plectranthus* have shallow root systems and the plants are adapted to remain in a semi-desiccated stage for long periods. *P. xerophilus* has horizontal tuberous roots and the leaves become deciduous in winter. *Plectranthus strigosus* has a dense, hairy leaf surface.

Reproductive adaptation

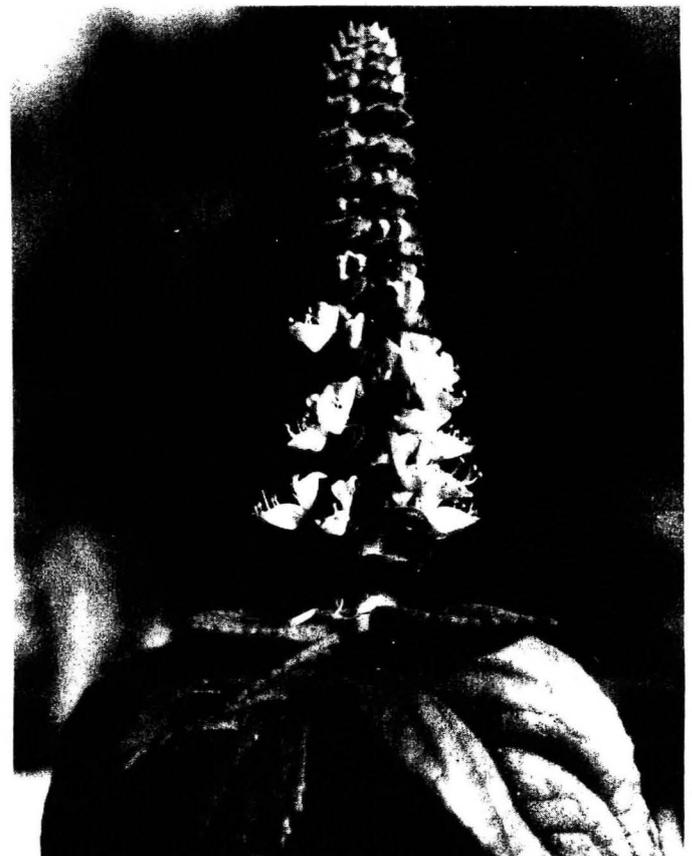
Sexual: Pollination is by insects. The stamens of *Aeolanthus canescens* are under tension and pollen is released explosively, thus covering visiting insects. (Ryding 1981). The seeds are small nutlets which are somewhat persistent to the calyx. *Plectranthus neochilus* has a hairy throat in the calyx preventing the seeds from falling out all at once.

Asexual: *Plectranthus tetensis* has very brittle side branches which detach from the mother plant, and root.

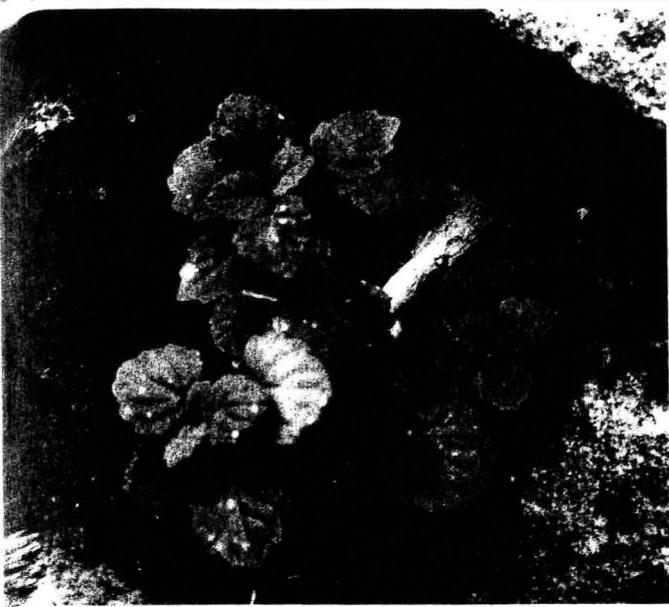
Defence

Chemical: Many members of the Lamiaceae have aromatic oils which are avoided by predators.

Habitat protection: *Plectranthus ernstii* occur on sheer south-facing cliffs. The succulent stems might be edible. *Plectranthus madagascariensis*, *P. verticilatus* and *P. strigosus* occur in very dense thorny Eastern Cape scrub.



Plectranthus coerulens from the eastern highlands of Africa. The leaves are succulent and aromatic



Plectranthus ernstii is a stem succulent. It has articulated stems and occurs on sheer quartzitic sandstone cliffs at Oribi Gorge



Plectranthus spicatus from Ubombo, Natal. Note the succulent leaves and large coarse teeth. It has a wide distribution in the subtropical eastern parts of South Africa



Plectranthus cylindricus from Wyllies Poort, N. Transvaal



Plectranthus neochilus from Siteki, Swaziland. Note the hairy succulent leaves

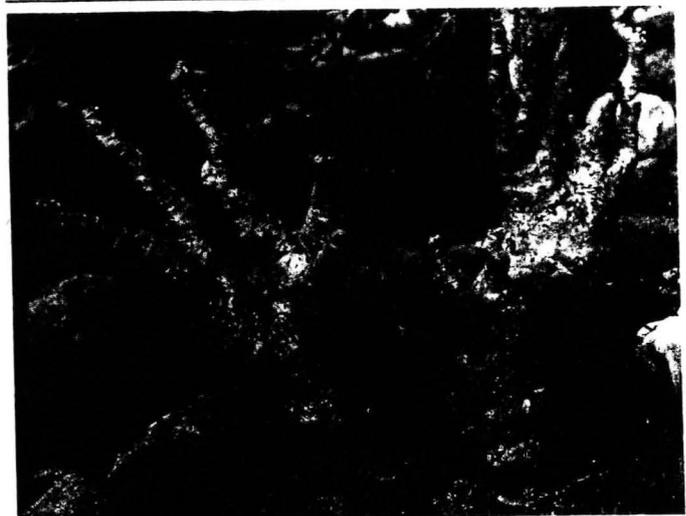


Plectranthus verticillatus is a trailing leaf succulent of the subtropical low lying eastern regions of South Africa

8.11 Vitaceae

(2 genera, about 30 succulent species in South Africa and Namibia)

Members of this family are of subtropical summer rainfall origin. Its succulent members vary from small succulent-stemmed climbers (*Cyphostemma sandersonii*) to thickset dwarf trees (*Cyphostemma currorii*). Most species occur in full sun in the northern parts of Southern Africa. *Cissus quadrangularis* resembles the South American climbing cacti. This is an example of convergence.



Cyphostemma juttae is a deciduous stem and leaf succulent. Note cryptic nature of the stems amongst the rocks

Drought adaptation

Most species are leaf and stem succulents. *Cyphostemma* species are deciduous during the dry season. *Cissus rotundifolia* is an attractive leaf succulent which occurs as a climber in dry warm bushveld areas. Most species have a shallow root system. There are also a few geophytic species.

Reproductive adaptation

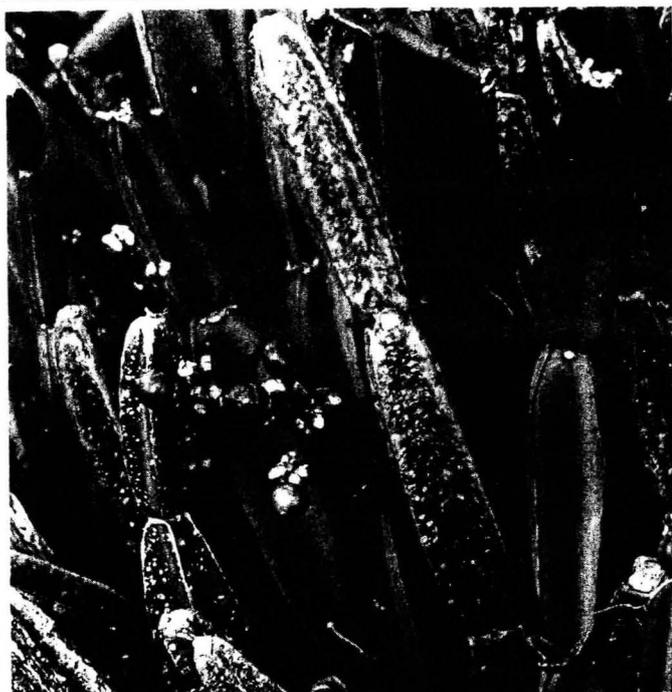
The fleshy, often red-coloured drupe is an attraction to fruit eating animal species which disperse the seeds. Pollination is by insects. Some species are slightly poisonous to humans.

Defence

Camouflage: The gnarled succulent stems resemble rocks in the surroundings. (*Cyphostemma juttae*, *C. currorii*, *C. uter* etc.)



Cissus quadrangularis is a stem succulent common in the dry subtropical eastern parts of South Africa. (The succulent leaves are early deciduous)



The red fruits of *Cissus quadrangularis* are dispersed by birds and other animals (biotic dispersal)

8.12 Dioscoreaceae

(1 genus, 18 succulent species in South Africa and Namibia)

This group of plants are caudiciform, with annual scrambling or climbing branches. It occurs in the winter and summer rainfall areas of South Africa.

Drought adaptation

The perennial succulent caudex is a water storage organ. The caudex of *Dioscorea elephantipes* could attain a height of up to 700 mm tall and about the same diameter. The bark is thick, corky and prevents excessive water loss. The branches are deciduous and die down in the dry season.

Reproductive adaptation

Pollination is by insects. Seeds are winged and wind dispersed.

Defence

Mechanical: The old dry persistent annual branches of *D. elephantipes* protect the young soft branches. The thick corky bark is an ideal protection against fire and animal predation. Porcupines are very fond of this species and apart from man are perhaps today their greatest enemies.

Camouflage: The succulent caudex resembles the rocky surroundings and is difficult to detect.

Habitat protection: Most species occur in dense wooded areas and their caudices are in most cases subterraneous.



Dioscorea elephantipes has a cryptic succulent caudex resembling a tortoise shell or rock

8.13 Burseraceae

(1 genus, 10 succulent species in South Africa and Namibia)

This is the well-known Balm family which occurs in the warmer and drier parts of the world. About 10 of the 36 indigenous species are succulent or semi-succulent. It varies from shrubs to small trees and most species are very distinctly aromatic. The succulent species are short, thickset trees or shrubs from the North-western Cape and Namib desert.

Drought adaptation

Some species occur in very dry and remote parts where other plants could hardly survive. The leaves are small, leathery and deciduous during the dry season. Water is stored in the succulent stems.



Commiphora cervifolia have succulent aromatic stems. When touched, highly aromatic sap is sprayed on the intruder



Commiphora gracilifrons from Pofadder is another species with aromatic leaves

Reproductive adaptation

The small yellow flowers suggest insect pollination. The fruit is a fairly large drupe with a colourful pseudaryl and which is possibly dispersed by birds or small mammals.

Defence

The plants are very aromatic and avoided by most grazing animals (Chemical defence). When the stem apices of *Commiphora cervifolia* are touched an aromatic sap under tension is squirted over the disturber. The branches of some species terminate into a sharp point.

8.14 Apocynaceae

(2 genera, 9 succulent species in South Africa and Namibia)

The succulent members of this family are more common in the summer rainfall arid regions of Southern Africa. The plants vary from herbs to large shrubs. Most species are slow growers with sweetly scented flowers.

Drought adaptation

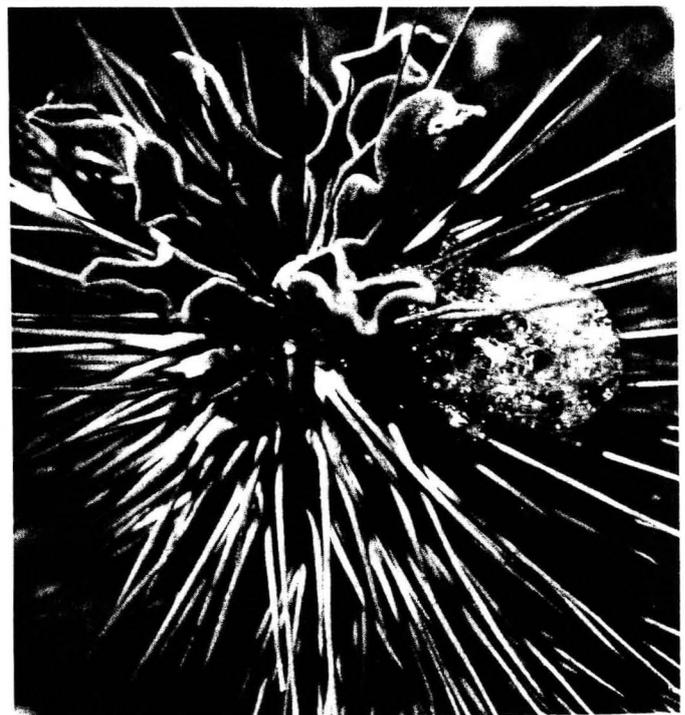
Most succulent members of this family in South Africa are stem succulents and have a subterranean caudex. The leaves are small and leathery. The plants are deciduous during the dry season. *Pachypodium namaquanum* occurs on southern and eastern slopes where it is protected from the hot sun.

Reproductive adaptation

The attractive scented flowers are pollinated by insects. The seeds are produced in paired fusiform follicles which split open longitudinally when ripening, releasing the flat seeds which are attached to a silky parachute (plumed diaspores).

Defence

Mechanical and chemical: The *Pachypodium*s have thorns which are modified stipules. These are very well developed in *Pachypodium namaquanum*. When injured a foamy sap may be excreted around the wound, thus protecting it from predators.



Pachypodium namaquanum. As soon as the stem of this plant is damaged, a poisonous foamy substance rapidly appears at the wound (chemical defence). Note also the thorns (mechanical defence)



Pachypodium namaquanum from Numees. This species is almost always confined to the cooler upper southern and eastern aspects of mountains. The Afrikaans name Halfmens means half human



Pachypodium succulentum has a fleshy caudex. It is widespread in the South-eastern Cape Karoo region

8.15 Cucurbitaceae

(4 genera, about 8 species in South Africa and Namibia)

This family consists mainly of climbers. They are widespread over Southern Africa. It includes *Kedrostis*, *Corallocarpus* and *Gerrardanthus macrorrhizus*.

Drought adaptation

Most taxa have a succulent caudex, which is mostly below soil level. The leaves are often small, leathery and deciduous in the dry season.

Reproductive adaptation

The yellow to white flowers are insect pollinated. The fruits are colourful and dispersed by birds and perhaps also small mammals.

Defence

The succulent caudex is mostly below soil level, and the plants are difficult to see. The caudex of *Gerrardanthus macrorrhizus* resembles a rock. *Kedrostis* is thought to be poisonous (Watt & Breyer-Brandwijk 1962).



Kedrostis africana has a succulent caudex. It occurs in the subtropical eastern parts of South Africa

8.16 Passifloraceae

(1 succulent genus, 7 species in Southern Africa and Namibia)

Most members of this family are climbers of subtropical and tropical origin. They occur in the northern parts of Southern Africa.

Drought adaptation

Almost all *Adenia* species have a succulent caudex which may be submerged or exposed. *Adenia digitata* and *A. hastata* have succulent roots.

Reproductive adaptation

Pollination is by insects. Seeds are mainly dispersed by birds (Ornithochory). The fruits are large, red or yellow in colour.

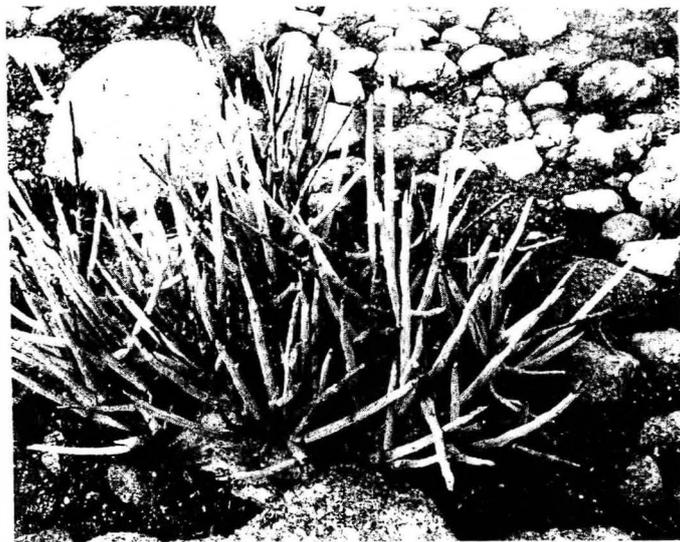
Defence

Mechanical and chemical: Plants often resemble the rocky background. The spines of *A. spinosa* are modified stipules. *A. pechuellii* has sharp spiny modified branches. Most species are poisonous (Watt & Breyer-Brandwijk 1962).

Habitat protection: Plants often occur among dense thorny shrubs, which afford an ideal protection.



Adenia glauca has a succulent caudex. It is a climber from the subtropical summer rainfall eastern parts of South Africa



Adenia pechuellii has spine tipped branches (mechanical defence). Note also the succulent caudex (Summer rainfall Namib region)

8.17 Pedaliaceae

(2 genera, 7 succulent species in South Africa and Namibia)

The family Pedaliaceae are found in the subtropical summer rainfall parts of South Africa. They are mostly stem succulents which vary from dwarf shrubs (*Pterodiscus aurantiacus*) to short thickset trees (*Sesamothamnus lugardii*).

Drought adaptation

Plants are stem succulents. The leaves are small, leathery and deciduous in winter.

Reproductive adaptation

The winged seeds are wind-dispersed.

Defence

Mechanical: *Sesamothamnus* has spines which are modified leaf petioles.

Camouflage: *Pterodiscus* are difficult to detect in its native habitat.



Sesamothamnus lugardii is one of three species of that genus that occur in Southern Africa. It is confined to the arid subtropical regions of South Africa. The leaves are small and leathery

8.18 Chenopodiaceae

(2 genera, 6 succulent species in South Africa and Namibia)

Species in this family are mostly halophytes (occurring in salty soils). They are mostly short shrubby succulents. Some *Arthrocnemum* species resemble *Psilocaulon*, which is an example of convergence.



Arthrocnemum sp. from the Knersvlakte. These succulent species are confined to soils with a high salt content. The leaves also have a high salt content and are avoided by game (chemical defence)

Drought adaptation

The stems are succulent.

Defence

Chemical: The high salt content of the stems make them unattractive to herbivores.

Habitat protection: These plants are adapted to grow in soils with a high salt content and thus receive little competition from other plant species.

8.19 Dracaenaceae

(2 genera, 4 succulent species in South Africa and Namibia)

The family Dracaenaceae occurs in the dry subtropical eastern and northern parts of South Africa. *Dracaena transvaalensis* is a semi-succulent erect shrub. There are three *Sansevieria* species in South Africa.



The leaf apices of *Sansevieria pearsonii* are sharp and dangerous. The dense clusters are a result of vegetative reproduction. It occurs in full sun or light shade and can colonize large parts



This form of *Sansevieria pearsonii* (Tvl) produces stolons usually above the ground. The cryptic transverse bands on the leaves blend with the natural background



The long tubular flowers of *Sansevieria pearsonii* are scented and thought to be pollinated by moths at night

Drought adaptation

The three *Sansevieria* species in South Africa are leaf succulents. The leaves are coriaceous and strong. *Sansevieria hyacinthadei* and *S. aethiopicum* are normally confined to the shade of clumps of bushes.

Reproductive adaptations

Sexual: The flowers of *Sansevieria* species are tubular and scented and are thought to be pollinated by moths. The fleshy berries are yellow and it is not known who the dispersal agents are.

Asexual: *Sansevieria* is stoloniferous and often form large groups. Certain forms of *S. pearsonii* have surface stolons.

Defence

Mechanical: The leaf apices of *Sansevieria pearsonii* are sharp and dangerous. The leaves of the other species are tough, fibrous and leathery.

8.20 Piperaceae

(1 genus, 4 succulent species in South Africa and Namibia)

This genus which is mainly of tropical origin is represented by only 4 species in Southern Africa. They are confined mainly to the subtropical coastal and mountain forests of the eastern and south-eastern parts of South Africa. They occur on local dry sites in high rainfall areas, mostly as petrophytes, chasmophytes or epiphytes. *Peperomia retusa* occurs in the forests of the South-western Cape and is also encountered on the Cape Peninsula.

Drought adaptation

These plants have small succulent leaves and a shallow root system.



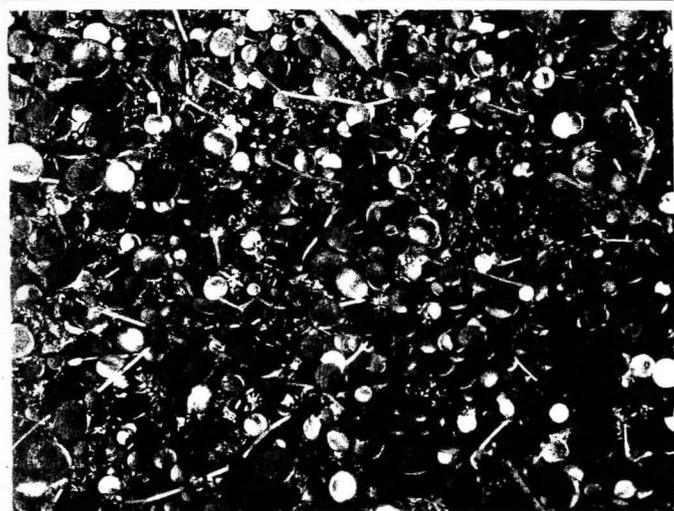
Peperomia blanda is a leaf succulent from the warmer subtropical parts of South Africa (Pongola)

Reproductive adaptation

It is not known who the pollination agents are. The small viscid seeds are thought to be dispersed by small animals.

Defence

Habitat protection: The plants are often small and inconspicuous or occur on steep rock faces or high trees difficult to reach.



Peperomia nana is a procumbent leaf succulent from the dry eastern Cape coastal forests

8.21 Sterculiaceae

(1 genus, 4 semisucculent species in South Africa and Namibia)

There are 4 *Sterculia* species which are semi-succulent, namely *Sterculia rogersii*, *S. alexandrii*, *S. quinqueloba* and *S. africana*. They are small to medium thickset trees which occur in the subtropical northern and north-eastern parts of Southern Africa.

Drought adaptation

The base of the stems are succulent. The leaves are often small, hairy and deciduous during the dry season.

Reproductive adaptation

Flowers are yellow and insect-pollinated. Seeds of *Sterculia murex* are edible and dispersed by humans and baboons.

Defence

The young branches of *S. rogersii* are glutinose and hairy, which makes them unattractive to insects. *Sterculia* fruits are thorny. Some have troublesome acicular hairs on the inside, a protection of the edible seeds.



Sterculia rogersii is a small thickset tree from the subtropical north-eastern parts of South Africa. It has an attractive grey green stem with deciduous peeling bark

8.22 Moraceae

(1 genus, 4 succulent and semi-succulent species in South Africa and Namibia)

The family Moraceae is common in the subtropical semi-arid regions of Southern Africa. Most species are non-succulent. *Ficus tettensis* occurs in the Northern Transvaal. It is a semi-succulent shrub with a yellow stem. Other semi-succulent species include *F. glumosa* and *F. abutilifolia*. All three are petrophytic (growing on rocks).

Drought adaptation

The stems are semi-succulent. The seedling soon develops a succulent caudex. The plants make use of the rock face to obtain extra moisture as well as heat. *F. tettensis* and *F. glumosa* have hairy leaves and are deciduous for a short period.

Reproductive adaptation

Seeds from the small edible fruits are dispersed mainly by birds and bats (Ornithochory and Chiropterochory). The pollinating agents are dwarf wasps.



Ficus abutilifolia has a semi-succulent main branch. It is a Lithophyte that occurs widespread in the subtropical north-eastern parts of Southern Africa. (This plant originates from the confluence of the Jukskei and Crocodile rivers)

8.23 Araliaceae

(1 genus, 3 succulent species in South Africa)

Cussonia occurs mainly in the subtropical eastern parts of South Africa as well as the highveld. *Cussonia thyrsoflora* has a distribution which extends to Cape Town.

Drought adaptation

The succulents or semi-succulent species dispose of a caudex and succulent roots. The leaves, although large, are coriaceous. The leaves of *C. paniculata* and *C. gamtoosensis* are grey, an adaptation to reflect the sun.

Reproductive adaptation

The flowers are yellowish green and insect pollinated. The purple berries are dispersed by birds (Ornithochory).

Defence

Mechanical: *C. paniculata* has a thick corky bark which is an ideal protection against grass fires which frequently occur in the area.

Habitat protection: *C. gamtoosensis* occurs in a dense thorny, almost impenetrable environment — the Eastern Cape Valley Bushveld.

8.24 Menispermaceae

(1 genus, 3 succulent species in South Africa)

Menispermaceae is a family of tropical origin, occurring in Africa and Asia. It consists mainly of climbers of which the genus *Tinospora* is succulent or semi-succulent. It occurs in the dry subtropical summer rainfall parts of South Africa. The genus *Tinospora* is widely distributed in Central and Southern Africa.

Drought adaptation

Tinospora have climbing succulent stems. The plants are deciduous, losing their leaves during the dry winter months. *T. fragosum* has succulent roots.

Reproductive adaptation

Sexual: The small inconspicuous greenish-yellow flowers are insect pollinated. The colourful reddish fleshy berries are dispersed by birds (Ornithochory).



Tinospora fragosum from the arid bushveld regions of Transvaal and northern Namibia. Note the survival root at the base of the stem

Vegetative reproduction: *Tinospora* occurs in wooded dry bushveld regions. The plants are often disturbed by game which also feed on this plant, with the result that the stems are frequently broken off. *Tinospora* has the amazing ability to grow a survival root, often from heights of up to 6 m. The initial root is thin and grows very fast (40–110 mm per day). It appears at about the end of October or the beginning of November, which coincides with the onset of the rainy season. It re-establishes its connection with the soil and the plant continues its vital life processes. The root eventually thickens to a rope-like pseudo-stem. If the root is damaged it will reroot in the same way.

Defence

Habitat protection: The arboreal habitat of the species protects it from grazing game.

8.25 Begoniaceae

(1 genus, 3 succulent species in South Africa)

The begonias are of tropical origin. Five species occur in the eastern parts of South Africa. Two of these are succulents (*Begonia caffra* and *B. sutherlandii*).

Drought adaptation

The South African *Begonia* species have succulent caudices. The leaves are deciduous in winter. They occur in well-drained habitats in the forests of the Eastern Cape and Natal.

Reproductive adaptation

The flowers are insect-pollinated. The fruits are flat, winged and wind-dispersed.



Begonia caffra has a succulent caudex. It occurs in the forest regions of the eastern parts of South Africa

8.26 Hyacinthaceae

(2 succulent species in South Africa)

Mostly geophytes with subterranean bulbs, widespread in Southern Africa. (Formerly placed within the Liliaceae).

Drought adaptation

Bowiea has a semi-exposed or subterranean fleshy bulb. The inflorescence is reduced to a succulent many-branched climbing assimilating organ. The one or two initial lanceolate leaves wither at an early stage.

Reproductive adaptation

Sexual: The flowers are insect-pollinated and the winged seeds are wind dispersed. The seeds of *Bowiea gariensis* are dispersed by the long trailing inflorescence of the plant which withers annually in the summer months (Blastochory).

Vegetative reproduction: The fleshy bulb scales will form bulblets when damaged.

Defence

Chemical: All parts of the plants are poisonous and avoided by predators (Watt & Breyer-Brandwijk 1962).

Habitat protection: It often occurs in dense bush, and is difficult to see.



Bowiea gariensis is a succulent geophyte. Note the branched succulent inflorescence. (Upper S. face of Pellaberg)



Scaevola thunbergii is a leaf succulent. It occurs on white sand along the southern and eastern South African coast. Note the superficial resemblance towards *Cotyledon orbiculata*

8.27 Goodeniaceae

(1 genus, 2 species in South Africa and Namibia)

Mostly an Australian family, *Scaevola plumeri* and *S. sericea* are indigenous to the south and east coast.

Drought adaptation

Scaevola occurs just above the high water mark on sand dunes which become very hot in summer. The leaves are succulent and have the appearance of a *Cotyledon orbiculata*, hence the name 'Seeplakkie'.

Reproductive adaptation

It is thought to be insect-pollinated. According to Batten & Bokelmann (1966) the purple drupes are dispersed by birds, while sea currents also play a role in the dispersal of the seeds.

8.28 Moringaceae

(1 succulent species in Namibia)

Moringa ovalifolia occurs in the northern parts of Namibia. It is small and thickset, and resembles a dwarf baobab tree (Convergence).

Drought adaptation

Moringa ovalifolia has a succulent stem and is deciduous during the dry season.

Reproductive adaptation

The flowers are pollinated by insects. The seeds are winged and dispersed by wind.

8.29 Bombaceae

(1 succulent species in South Africa and Namibia)

Only one member, *Adansonia digitata*, occurs in Southern Africa. It is confined to the northern and north-eastern parts. This is the world's largest succulent plant.

Drought adaptation

Water is stored in the succulent stems. The leaves are deciduous during the dry season.

Reproductive adaptation

Pollination is by bats. The fruit is edible, has a delicious pulp and the seeds are dispersed by man and mammals.

Defence

The massive size is its main protection.

8.30 Cactaceae

(1 species in South Africa)

The Cactaceae are at present the world's second largest succulent plant family. Only one species is indigenous in South Africa namely *Rhipsalis baccifera*. It is a stem succulent of the Eastern subtropical coastal regions of South Africa. It occurs in the shade or semi-shade of subtropical coastal forests.

Drought adaptation

The stems are succulent.

Reproductive adaptation

The small fleshy fruits are dispersed by birds and other small animals.

Defence

Habitat protection: It often occurs as a chasmophyte or epiphyte in sheer rock faces or tree trunks.

8.31 Convolvulaceae

(1 succulent species in South Africa)

A small family which consists mainly of climbing plants. *Ipomoea albivenia* occurs in the eastern parts of Southern Africa. It appears to be the only succulent or semi-succulent plant belonging to this family in South Africa.

Drought adaptation

Ipomoea albivenia has a succulent caudex which is often half exposed. The leaves are hairy and deciduous in winter.

Reproductive adaptation

The flowers are large, attractive and white. Insects are possibly the pollinating agents.

Defence

The plants occur in dry wooded river valleys and the succulent stems are not easily detected.

8.32 Welwitschiaceae

Welwitschia mirabilis is the only species in the genus. It is one of the most remarkable palaeoendemics of the Namib desert, occurring from Southern Angola to Central Namibia.

Drought adaptation

It has a thick semi-succulent woody stem. The single leaf pair is leathery. The large flat leaves are adapted to effectively make use of the coastal fog. Fog condenses on the leaves and drops to the ground and is absorbed by the shallow roots. It is also thought that the leaves are adapted to absorb moisture. *Welwitschia* occurs in the fog belt of the Namib desert.

Reproductive adaptation

The cones are thought to be wind pollinated and the seeds are dispersed by the wind.

Defence

The leathery leaves are unattractive to animals.



Welwitschia mirabilis occurs in the fog belt of the northern Namib

Pie diagram showing the succulent riches of South Africa

31 Families

± 3693 species

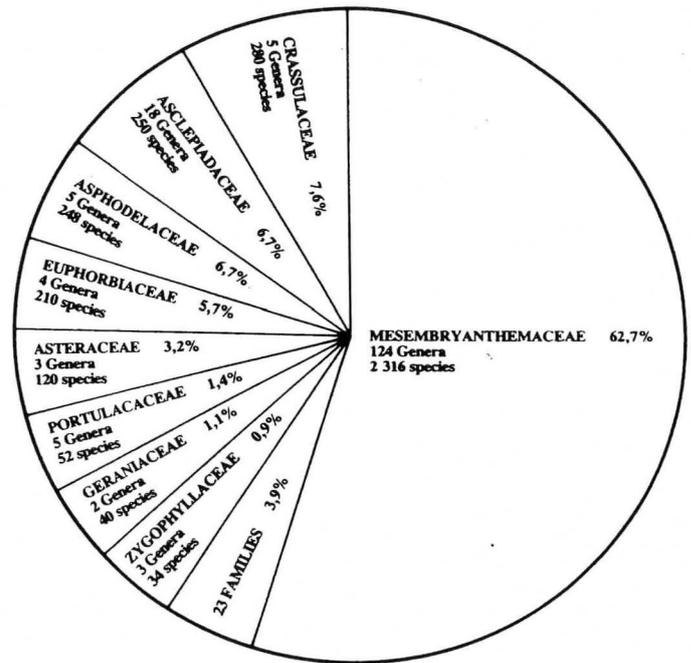


Table IV: The succulent riches of South Africa and Namibia, ranking the families by number of species

Succulent plant family of S.A.	Genera in S.A.	Succulent species	% of total SA succulent flora	Genus with the most species
1 Mesembryanthemaceae	124	2 316	62,7	<i>Ruschia</i>
2 Crassulaceae	5	280	7,6	<i>Crassula</i>
3 Asclepiadaceae	18	250	6,7	<i>Stapelia</i>
4 Asphodelaceae	6	248	6,7	<i>Aloe</i>
5 Euphorbiaceae	4	210	5,7	<i>Euphorbia</i>
6 Asteraceae	3	120	3,2	<i>Othonna</i>
7 Portulacaceae	5	52	1,4	<i>Anacampseros</i>
8 Geraniaceae	2	40	1,1	<i>Pelargonium</i>
9 Zygophyllaceae	3	34	0,9	<i>Zygophyllum</i>
10 Vitaceae	2	30	0,8	<i>Cyphostemma</i>
11 Lamiaceae	3	23	0,6	<i>Plectranthus</i>
12 Dioscoreaceae	1	18	0,5	<i>Dioscorea</i>
13 Burseraceae	1	10	0,3	<i>Commiphora</i>
14 Apocynaceae	2	9	0,2	<i>Pachypodium</i>
15 Cucurbitaceae	4	8	0,2	<i>Kedrostis</i>
16 Passifloraceae	1	7	0,2	<i>Adenia</i>
17 Pedaliaceae	2	7	0,2	<i>Pterodiscus</i>
18 Chenopodiaceae	2	6	0,2	<i>Arthrocnemum</i>
19 Dracaenaceae	2	4	0,1	<i>Sansevieria</i>
20 Piperaceae	1	4	0,1	<i>Peperomia</i>
21 Sterculiaceae	1	4	0,1	<i>Sterculia</i>
22 Moraceae	1	4	0,1	<i>Ficus</i>
23 Araliaceae	1	3	0,08	<i>Cussonia</i>
24 Menispermaceae	1	3	0,08	<i>Tinospora</i>
25 Begoniaceae	1	2	0,05	<i>Begonia</i>
26 Hyacinthaceae	1	2	0,05	<i>Bowiea</i>
27 Goodeniaceae	1	2	0,05	<i>Scaevola</i>
28 Moringaceae	1	1	0,03	<i>Moringa</i>
29 Bombaceae	1	1	0,03	<i>Adansonia</i>
30 Cactaceae	1	1	0,03	<i>Rhipsalis</i>
31 Convolvulaceae	1	1	0,03	<i>Ipomoea</i>
32 Welwitschiaceae	1	1	0,03	<i>Welwitschia</i>

9. Summary of some of the adaptations of Southern African succulent plants to their arid environment

9.1 Drought adaptation

(a) Succulence

Plants have succulent parts above the soil (leaves, stems, caudices) while some species also have succulent roots.

(b) Geophytic succulents

Bulbous or tuberous plants with aerial succulent parts that wither during the dry season (*Bulbine striata*, *B. haworthioides*, *Bowiea* etc.).

(c) Ephemeral succulents (Therophytes)

Succulent annuals (*Dorotheanthus*, *Dinacria* etc.) complete their life cycle within the short rainy season. The plants remain as seeds during the long dry season (Drought evaders).

(d) Deciduousness or leaves that wither

Tylecodon and *Othonna* are deciduous. Leaves of *Monilaria* wither during the dry hot season.

(e) Reduced leaves and compact growth

Leaves are reduced to a small surface to combat superfluous transpiration; oblong terete (*Lampranthus*, *Ruschia*); spherical (*Crassula elegans*); compact and imbricate (*Crassula columnaris*, *C. columella*, *C. barklyi*). (See Mesembryanthemaceae (8.1) and Crassulaceae (8.2)).

(f) Orientation and leaf movements

Leipoldtia grandifolia and some other Mesems have laterally compressed leaves with the flat surface in an erect position. (*Leipoldtia grandifolia* see also 8.1). The orientation of the terete leaves of *Cephalophyllum cersianum* is always towards the sun. (see 8.4)

(g) Wax layers and leaf colour

Some *Kalanchoe* species have a powdery or waxy bloom on the leaves and stems, reflecting the sun and preventing excessive water loss (*Kalanchoe thyrsiflora*, *Cotyledon orbiculata*).

(h) Scales

Anacampteros section *Avonia* have large imbricate scale-like stipules covering the tiny round leaves. The scales protect the leaves and stems from the sun's heat and excessive water loss.

(i) Hairy epidermis

Cotyledon tomentosa, *Senecio scaposus* and *S. haworthii* are examples. The hairy epidermis shades the plant, thus preventing superfluous water loss. The hairs on the leaves of *Conophytum stephanii* are an aid in absorbing moisture from the regular fog in the natural habitat.

(j) Enlarged leaf surface

Tylecodon singularis and *Welwitschia mirabilis* occur in the southern Namib in areas where fog is regularly experienced. The fog condenses on the broad leaf surface and the plants are able to utilise the water.

(k) Leaf skeleton

Conophytum, *Mitrophyllum* and *Sceletium* have leaves that wither during the dry summer months. The old desiccated leaves form a protective sheath over the new season's growth.

(l) Shallow root system

Most succulents have a shallow spreading root system that can effectively make use of light rain showers. *Crassula*, *Gasteria* and most Mesembryanthemaceae are examples.

(m) Seed germination

Seeds of *Cleretum* and other annual Mesembryanthemaceae have an irregular germinating pattern. See Mesembryanthemaceae, section (8.1)

9.2 Reproductive adaptation

Pollination (Technical terms adopted from Real (1983))

Pollination of the Mesembryanthemaceae and Euphorbiaceae is mainly by bees and bee flies (Melittophily, Myophily). The tubular flowers of *Aloe* and *Gasteria* attract birds (Ornithophily). *Pachypodium* and *Adenium* are pollinated by hawk moths (Sphingophily). The white pendulous flowers of *Adansonia digitata* are pollinated by bats during the night (Chiropterophily). The large foul-smelling flowers of the Asclepiadaceae are pollinated by flies (see section 8.3). *Dorotheanthus apetalus* and *Micropterum pappulosum* are self-pollinated. Their flowers are very tiny and inconspicuous.

Seed dispersal

(a) Rain

Rain plays an important role in seed dispersal of the family Mesembryanthemaceae. The hygrochastical capsules open when wet and close when dry and the force of the raindrops on the open capsule disperses the seeds (Rain ballism). See the section on the Mesembryanthemaceae (8.1).

(b) Wind (Anemochory)

Conspicuous and large tall inflorescences and erect dry capsules suggest wind dispersal (Ballistic anemochores). *Portulacaria armiana* has a very tall inflorescence 3 to 6,4 m long (Wind ballist) and the jacitation movement disperses the seeds. The seeds of Crassulaceae are very small and light and dispersed by air movement (Dust diaspores). Apocynaceae and Asclepiadaceae have plumed seeds or seeds attached to tufts of silky hairs. The seeds are dispersed by air currents (Plumed diaspores).

(c) Self-dispersal (Autochory)

Active ballists: *Euphorbia* seeds are borne in capsules that are under tension when drying. The seeds are dispersed explosively (see the section on Euphorbiaceae).

Seeds of *Skiatophytum tripolium* and *Stoerberia carpii* are dispersed by the long spreading branches or inflorescence as found with *Bowiea garipeensis* (Blastochory). *Peperomia* have viscid seeds thought to be dispersed by passing animals (Exozoochory).

(d) Ocean currents

The seeds of *Scaevola thunbergii* are salt tolerant and dispersed by ocean currents (Batten & Bokelmann 1966).

(e) Dispersal by animals

Fleshy fruits suggest animal dispersal. *Carpobrotus*, *Cyphostemma* and *Adenia* are examples (Ornithochory, Mammaliochory). The seeds of *Adansonia digitata* are dispersed by humans and baboons.

9.3 Asexual propagation

Leaves

The leaves of the Crassulaceae are adapted to asexual propagation. The leaves of *Adromischus* in particular, are very brittle falling to the ground where they root and form new plants. See the sections on Crassulaceae (8.3) and Asphodelaceae (8.4).

Stems

Senecio articulatus and *Lampranthus tenuis* have brittle branches that will root when detached. When the succulent twiner *Tinospora* (Menispermaceae) stems become detached from the soil, they have the ability to grow a survival aerial root sometimes from an astonishing distance. See Menispermaceae (8.24). Some succulents repropagate vegetatively from stems, stolons, or proliferation from the base to form dense clusters. See Mesembryanthemaceae (8.1), Asphodelaceae (8.4), Asclepiadaceae (8.3) and Dracaenaceae (8.15).

9.4 Defence

(a) Mechanical

Armoured plants are often conspicuous. They belong to a wide range of families and are armed in various ways to repel predators. These include plants with thorns (see below), scales (*Anacampseros*), thick bark (*Dioscorea*), leaf tubercles (*Haworthia*, *Gasteria*), and hardened phyllopodia (*Tylecodon*, *Othonna*). Thorns are the result of modified leaves (*Hoodia*), petioles (*Sarcocaulon*), thorny outgrowths or bristles on the leaves (*Aloe*, *Trichodiadema*), stipules (*Euphorbia*), modified branches ending in spines (*Adenia spinosa*), inflorescences (*Ruschia pungens*) or spiny remains of fruit capsule (*Ruschia indurata*). The leaf margin of *Gasteria excelsa* is razor sharp.

(b) Chemical

Succulent plants often have a toxic sap (*Euphorbia*, *Tylecodon*, *Adenia*), bitter sap (*Aloe*), or are highly aromatic (*Commiphora*, *Plectranthus*). These plants are usually avoided by animals (see sections 8.2, 8.4, 8.10 and 8.13).

(c) Camouflage

Cryptic plants merge with their background and are difficult to detect by predators; *Lithops*, *Argyroderma*, *Pleiospilos* (abiotic background), *Gasteria obliqua* (biotic background).

(d) Mimicry

The superficial resemblance of one plant to another to deceive predators (*Pelargonium crithmifolium* and *Tylecodon reticulatus*).

(e) Habitat Protection

The dense thorny Eastern Cape scrub (Valley Bushveld) provides protection for many succulent species (*Ceropegia*, *Gasteria*, Crassulaceae).

(f) Dominance over other species

Although *Portulacaria* is a valuable fodder plant its ability to remain dominant seems to play a significant role in its survival strategies.

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