Chapter 16
The Namib Desert Biome

Key Concepts and Questions: This Chapter Will Explain

- *What defines a desert.*
- *When and how the Namib Desert landscape was formed.*
- *How the South Atlantic Anticyclone, the Benguela Current, and associated wind systems determine the nature of the climate and ecological processes along the Angolan coast.*

Context: What defines a desert?

Geographers apply the term **desert** to areas where the mean annual precipitation is below 250 mm. In this volume the term is used in a narrower sense, for the extremely arid Namib Desert of Angola and Namibia, where annual rainfall averages less than 150 mm per annum and where animals and plants exhibit remarkable adaptations to survive, grow and reproduce under unusually harsh environmental conditions. A **harsh environment**, such as a desert or an arctic tundra, is defined as one in which specialised morphological, physiological or behavioural adaptations, that are not found in related species, have evolved to survive such conditions.

The Namib Desert extends as a narrow belt, less than 200 km wide, across 2100 km of the southwest African coastline, from the Carunjamba River in Namibe province of Angola to just south of the Orange River near Namibia's border with South Africa. The environmental conditions across this long narrow belt of hyper-arid climate are not uniform, and range from summer rainfall in the north to winter rainfall in the south. The rainfall within the belt decreases 6- to tenfold from the Escarpment to the Atlantic Ocean. Linear oases follow some of the ephemeral rivers that cross the desert, with associated large mammals such as Savanna Elephant, Black Rhinoceros and Giraffe penetrating deep into the desertic landscapes.

In Angola, the Namib Desert occupies a narrow belt 20–80 km wide along the coastal plain, as a wedge between the Atlantic Ocean and the first foothills of the Angolan Escarpment, where it transitions into the Namib Savanna Woodlands ecoregion. The Angolan Namib Desert ecoregion includes vegetation types 28 and 29 of

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Barbosa (1970) merging with the western half of Type 27. This defines the ecoregion as a narrow tongue, northwards from the Cunene, past Moçâmedes to the Carunjamba River near Lucira (Fig. 2.37).

Angola's Namib Desert (Ecoregion 15)

16.1 The Age and Evolution of the Namib Desert

The Namib Desert of Angola and Namibia, and the Atacama Desert of Chile, are reputed to be the oldest deserts in the world. Exactly how old they are is still uncertain, and the history of the Namib is still the subject of much debate. John Ward, a South African geologist with extended experience in Angola and Namibia, reviewed hypotheses on the age of the Namib in two important papers (Ward et al., 1983, Ward and Corbett, 1990). Based on an understanding of the stratigraphy (layering of geological sediments) of southwestern Africa, Ward described five phases to illustrate the long history of Namib aridification.

Post-Gondwana Erosion Phase (*Cretaceous*: 130–80 Ma)

Following the breakup of Gondwana (130 Ma), much of the Great Escarpment was formed between 120 and 100 Ma by the uplift of the Earth's crust, with some features of the escarpment dating back to much earlier times, relicts from 300 million years ago. The evolving Namib landscape was eroded by both marine and terrestrial forces. As much as 2 km depth of soil and rock was stripped off the landscape. In Angola, some of the products of this erosion are known as the Giraul conglomerates, exposed along the Giraul River in Namibe. Offshore deposits are several km thick, the result of many millions of years of erosion of the terrestrial landscape. Marine erosion resulted in a beveled platform named the **Namib Unconformity Surface**. This landscape feature, which cuts across schists, gneisses and granites, dates from 85 Ma. Numerous inselbergs rise above the coastal plains. By 80 Ma, the separation of Africa from South America and the establishment of the South Atlantic Ocean was concluded. At the end of the Cretaceous (66 Ma), the physical boundaries of the Namib (Great Escarpment, Atlantic Ocean, and the Namib Unconformity Surface) were in place.

Proto-Namib Desert Phase (*Paleogene*: 55–23 Ma)

The earliest unequivocal evidence of desert conditions in the Namib (from 55 Ma—the Eocene Epoch) is provided by extensive fossil dunes known as the **Tsondab Sandstone Formation**. Southerly winds, driven by **the South Atlantic Anticyclone** which had established by this time, and the position of the Namib in the southwestern rain-shadow of the southern African subcontinent, were the key drivers of aridity and the formation of the extensive sand dunes of the Proto-Namib (also known as the Palaeo-Namib).

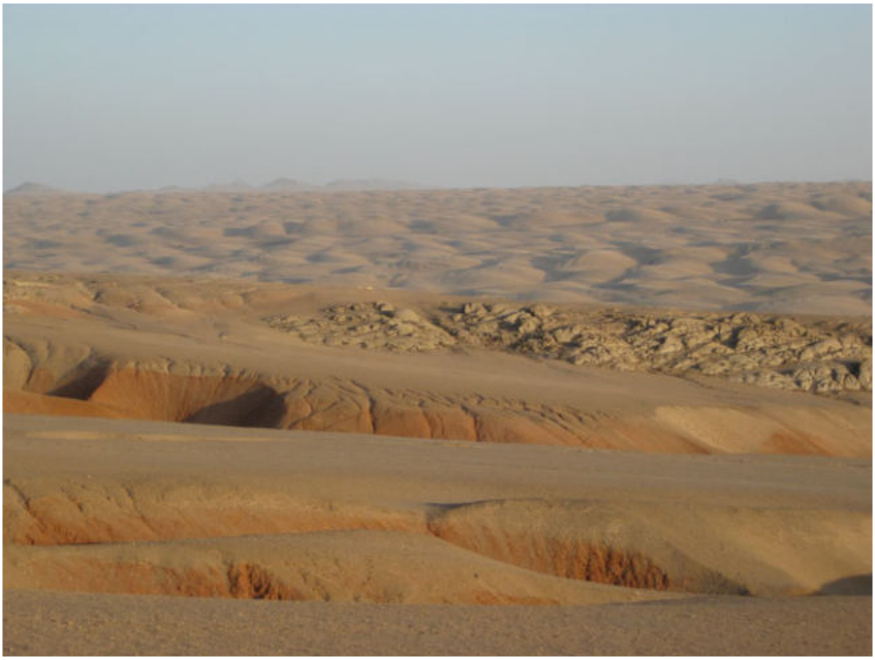

Fig. 16.1 Ancient and modern dune systems of the Namib Desert. In the foreground, the eroding face of a deep red fossil dune of Tsondab Sandstone underlies the paler sands of the modern Namib. In the background, behind the granite exposure, and south of the Cunene (hidden from view), lie the dunes of the Cunene Sand Sea

The reddish-brown Tsondab sandstones, of up to 220 m depth, were deposited over a period of 20–30 million years. They extend from central Namibia to the Curoca River in Angola. Remnants of these ancient dunes are mostly preserved under later gravel, calcrete and sand deposits, but an example can be seen in Iona National Park, at the southern end of the Vale dos Rinos (Fig. 16.1).

The environmental conditions through this long period were not uniformly stable. Fossil evidence from 47 to 42 Ma, for example, reveals humid summer-rainfall conditions with wooded vegetation in the area that is now Namib Desert. But by 34 Ma the Antarctic Ice Sheet had formed, with consequent aridification in the period known a 'Ice-house Earth'. Semi-arid climates with woodlands and early African mammals (Afrotheria) such as elephant shrews, golden moles and hyraxes are revealed in the fossil record. Even primate fossils were found in these fossil beds. But as Ward et al. (1983) caution, the presence of primates (and other mammals associated with wooded vegetation, such as elephant, giraffe and rhino) does not imply widespread mesic conditions. These mammals today penetrate deep into the Namib Desert along the linear oases of wooded river beds, which provide narrow fingers of suitable habitat within an otherwise hostile environment.

Pluvial (Humid) Phase (*Early-Middle Miocene*: 23–14 Ma)

A period of more humid conditions during the Early to Mid-Miocene is indicated by widespread deposits of gravels that overlie the Tsondab Sandstone Formation. The erosion and deposition of these gravels would have required a wet period reflecting higher rainfall on the interior plateau, escarpment and desert tract. This period was not necessarily uniformly moist. Eggshells of three genera and eight species of ostrich, including Giant Ostrich—*Diamantornis wardi*—associated with arid environments—have been found in the Tsondab sandstones of ca. 19 Ma.

Pedogenic (Calcrete) Phase (End Miocene: 14–11 Ma*)*

Following the more humid phase, a semi-arid period of summer rainfall with 350–450 mm per annum, supported the development of calcareous soils, signaling the onset of aridity with the full establishment of the Benguela **up-welling** system from 10 to 7 Ma. These calcretes, of up to 5 m thick, cover the older gravels and sandstones, and predate their erosion by westward flowing rivers (Cunene, Ugab, Kuiseb) that cut across the Namib in response to uplift during the Pliocene (5.3–2.6 Ma).

Namib Desert Phase (Late Miocene—Holocene: 10 Ma*—present)*

The Namib reached its extreme aridity in the Late Miocene (about 10–7 Ma) when the Antarctic Ice Sheet reached full development. The establishment of the cold, upwelling Benguela Current occurred during this period and accentuated desertic conditions. While it is not considered a primary contributor to the formation of the Namib Desert, the Benguela Current has played a key ecological role through the coastal fog that it triggers (Sect. 16.3). Behavioural adaptations such as 'fog-basking' in Tenebrionid beetles would have followed the establishment of the Benguela Current and the high frequency of coastal fogs. The combined forces of the northward-moving Benguela Current, and the easterly trade winds that blow across its surface waters, cause the upwelling of cold water from 300 m depth, which brings rich nutrients to the surface. These waters, when exposed to sunlight, create ideal conditions for marine productivity, based on abundant phytoplankton, and supporting vast populations of fish, seals and seabirds.

The dunes of the Central Namib Sand Sea are considered of Plio-Pleistocene age, (from 5 Ma) with those of the Curoca being more recent, and their development continues to the present day.

Source of the Dune Sands

Besides the age of the Namib, a second question relating to the evolution of the Namib has enjoyed much interest: the source of the sands that characterise the desert dunes. The answer lies in the patterns of landscape evolution over many millions of years. The courses of most rivers draining southern Africa have changed dramatically since the continent's formation. At about 42 Ma, the Orange River (on the border between South Africa and Namibia) cut a deep course through the landscape, eroding the Jurassic sandstones of the South African Drakensberg. About this time, the Orange River breached the Great Escarpment, thereafter depositing vast amounts of sediment sourced from the eroded sandstone into the sea. The geological, oceanographic and climatic history following these events resulted in dune systems being formed on the coasts of Namibia and Angola. These dunes accumulate sand through the combination of river, marine and wind transport of the sediments.

Today, as in the past, the sediments from the interior of southern Africa are carried to the sea by the Orange River and are transported northwards by strong and persistent **longshore swell-driven waves**, which create what is described as a **marine conveyor belt**. Some of these sediments are washed ashore and blown inland by the southerly and southwesterly winds generated by the South Atlantic Anticyclone, as described in Sect. 16.3. The marine conveyor belt system, starting at the mouth of the Orange River, ends 1750 km farther north in the marine canyons at the mouths of the Bero and Giraul rivers. These deep canyons direct the remaining Orange River sediments out to the deep ocean, preventing their further migration up the coast. The submarine sand conveyor provided by the coastal waters off Namibia and southern Angola is the longest 'sand highway' on Earth (Garzanti et al. 2014, 2017). Most of the sand from the Orange River ends up in the Central Namib Sand Sea of Namibia but sufficient quantities reach Angola to provide 74% of the sand of the dunefields of Iona National Park. The balance of sand of the Iona dunes comes from the Cunene River (18%) and the Hoarusib River (8%) in Namibia.

Synopsis

While geologists continue to debate the age of the Namib Desert, they agree on the three key drivers of its origin and ecology. These are the combined influences of the South Atlantic Anticyclone, the subcontinental rain shadow, and the upwelling of the Benguela Current. Collectively, these factors have resulted in hyper-aridity, off-shore and onshore winds, and fog—the forces driving the formation of the Namib Desert over many millions of years, and of the unique adaptations evolved in animal and plant life.

16.2 Landscapes and Soils

Today the Namib Desert comprises a wide diversity of landscapes, the most iconic of which are the Sand Seas of the Central Namib and the Cunene-Curoca dunes south of Moçâmedes. Most of the Namib Desert lies on an extensive peneplain, a gentle seawards-tilted erosional surface. The erosion reveals a complex pattern of geological evolution through 1800 million years, from the oldest intrusive igneous anorthosite rocks of the Kunene Complex to the modern mobile sands of the Namib Sand Sea.

The Namib presents a living text book on Angolan geology. Along the coast, in addition to the Pleistocene sands, the deep marine deposits of the Benguela and Namibe Sedimentary Basins include Lower Cretaceous to Miocene clays, limestones, sandstones and conglomerates. Many of these are rich in fossils of marine vertebrates and invertebrates (Mateus et al., 2019). Further inland, extensive plains stretch to the horizon. The landscape is traversed by geological features such as jointing, onion-skin weathering, dolerite dykes, and quartzitic and marble exposures. Outcrops of metamorphic and igneous intrusions, including granite, limestone, dolorite, schist and amphibolite, interrupt the plains. The surface is a mix of gravel and broken rocks, formed from the breakdown of duricrusts. These planation surfaces have been incised by small gullies, but are also bisected by major rivers, some perennial (Cunene), but mostly ephemeral (Curoca, Bero, Giraul, Bentiaba, Carunjamba). Figures 16.2, 16.3, 16.4 and 16.5 illustrate some Namib Desert landscapes.

Soils are seldom formed in this dry, hot, windswept landscape. What one finds in most areas is a hard crust formed by the cementation of quartz gravel or through evaporation of the little water received from rain and fog. Evaporation concentrates gypsum or calcium to form gypcretes or calcretes respectively. But some raw soils accumulate in breaks in the hard surface, providing enough reserves of nutrients and water to sustain the sparse vegetation that can survive this harsh environment.

Gypsum (calcium sulphate) is formed by the reaction of sulphuric acid with calcium carbonate, with the moisture provided by fog, and the sulphate produced by marine phytoplankton, and carried inland by the southwesterly winds. Over millions of years, the influence of the Benguela Current has produced gypcrete pavements of over four metres in depth. Gypcretes are usually found within 50 km of the sea. These

Fig. 16.2 Landscapes of the Angolan Namib. Contrast between a white marble and black dolerite

Fig. 16.3 A quartz gravel pavement with scattered *Commiphora* and *Acacia trees*

Fig. 16.4 Landscapes of the Angolan Namib. Calcrete pavements broken by a dry stream bed

Fig. 16.5 Sand dune and marble outcrop, central Iona

pavements are the habitat of profuse lichen fields in the Central Namib of Namibia, but lichen communities are less well developed on the Angolan coast.

Calcrete crusts are formed in situ by atmospheric precipitation of calcium carbonate in an arid environment. Calcretes cover much of the Angolan Namib, as extensive plains, bare of anything but sparse dwarf shrubs and hardy grasses for most of the time. However, following episodic rain showers, the gravel plains turn verdant green with annual species of *Aristida, Schmidtia* and *Stipagrostis* grasses. Rain events, in which from 10 to 50 mm may fall over only a few days, are sufficient to trigger the rapid growth of the annual grasses.

Most symbolic of deserts are the mobile sand dunes that have formed the dune system between the Foz do Cunene and the Curoca River. The Angolan Namib dunes take on a variety of forms—linear, star, barchan or longitudinal—depending on wind direction and age of formation. Many dunes preserve evidence of changed wind patterns through drier and wetter phases of the Pleistocene, processes that continue to the present day.

The sand dunes do not develop organic soil as it is normally understood, with recognizable horizons and general stability. But even these moving sands have been colonised by sand-stabilizing grasses such as *Stipagrostis sabulicola* and succulent shrubs such as *Trianthema hereroensis* (in Namibia), and the spiny *Acanthosicyos horridus* (in Angola). Despite their inhospitable appearances, the Namib dunes support a diverse spectrum of vertebrate and endemic invertebrate animals (including the iconic bicolour fog-basker *Onymacris bicolor* (Fig. 11.7).

16.3 Climate: The South Atlantic Anticyclone, the Benguela Current and Wind

Whereas factors such as soils, fire and herbivory shape the mesic and arid savannas of Angola, it is the extreme aridity of the Namib, and subtle aspects of rare moisture sources, that dominate its ecosystem structure and functioning. Here the climatic processes, developed over many millions of years, will be discussed, addressing a central question: why is the Namib so dry? It will also show why wind (the movement of air from areas of high atmospheric pressure to areas of low pressure) is such an important factor in the evolution and dynamics of the Namib.

Three major oceanic/atmospheric processes interacting in diverse ways account for the maintenance of the hyper-aridity of the Namib and its extraordinary biota. These are the quasi-stationary offshore South Atlantic Anticyclone, the Benguela Upwelling Current, and the winds associated with these oceanic and atmospheric phenomena.

As described in Chap. 5.3, the atmosphere over southern Africa is dominated by two pressure systems. These are the low-pressure Intertropical Convergence Zone (ITCZ), which lies over the Equator, and a sub-tropical belt of high pressure (which includes the South Atlantic Anticyclone) which lies over the Tropic of Capricorn. In summer, moist air produced along the ITCZ moves south, sheds its moisture, and sinks, as dry air, in the high-pressure belt. Moisture from the ITCZ, which accounts for the high rainfall of northern Angola, does not reach the Namib.

Paradoxically, despite its position bordering the Atlantic Ocean, the Namib receives its sparse rain not from the Atlantic, but from the Indian Ocean. In summer, the southeast trade winds bring moisture across the continent from the Indian Ocean. With rare exceptions, most of this moisture is lost before it reaches the west coast. But a little moisture reaches the Namib in unpredictable showers that can bring an abundance of life to the desert. These episodic rainfall occurences are especially evident during **La Niña** events, when the easterly trade winds strengthen and carry Indian Ocean moisture further west than normal. In 1976, during such an event, over 100 mm rain fell over the Central Namib, with the grasslands producing 56 times the normal standing crop, attracting Gemsbok and Springbok populations of 50 times the density of surrounding areas (Seely & Louw, 1980). A similar event occurred in January 2021 during the passage of cyclone Eloise across southern Africa.

The South Atlantic Anticyclone, positioned over the ocean, creates a pressure gradient from west to east, between cold sea and warm land, which in turn produces strong **onshore** winds through most of the year. These winds become **southwesterlies** due to the effect of the Coriolis force, and are strongest in early to mid-summer. They are responsible for maintaining the northward movement of sands from the Foz do Cunene—probably the windiest place in Angola—to the Curoca, where the dune head is periodically washed out to sea by once-in-a-century floods.

To residents in Moçâmedes, an all too familiar weather feature is that of the dust-laden but warm **easterly winds** that occur during autumn and winter. These winds are due to the periodic weakening of the South Atlantic Anticyclone. At these times the air pressure over the subcontinent is higher than that over the Atlantic. A pressure gradient from east to west brings the east winds across the warm land surface, with the air being heated further by **adiabatic** heating due to the increased pressure on the air mass as it descends down the escarpment. These winter **katabatic 'berg'** winds pick up dust and plant debris as they move across the landscape and down the escarpment, bringing nutrients to the animals of the dune sea, and depositing the fine organic matter that they carry from the interior.

The prevalence of **fog** (***cacimbo*****),** for up to 120 days per year, is a unique and critically important feature of the Namib. The narrow coastal belt from Tômbua to Lucira, in particular, experiences drenching over-night fog as a result of a **temperature inversion** created by the cold Benguela Upwelling Current. Normally, air temperatures decrease with altitude by between 0.6 and 0.9 °C per 100 m rise in elevation (Chap. 5.4). However, over the cold Benguela Current, the air temperature increases with height. The warm air above acts as a 'cap' to normal convection, inhibiting the rise of the cool, moist air which would normally form rain clouds. Instead, this humid air moves inland as a shallow layer of fog, bringing very limited, but important moisture to a narrow belt along the Namib coast. Figure 16.6 illustrates the atmospheric processes along a latitudinal cross-section above the Angolan coast, from the Congo to the Cunene.

Two types of fog occur over the Namib. First, a shallow bank of very moist air, usually up to 200 m high, is borne on southwesterly winds and carried up to 15 km into the desert. The fog is deposited as a fine drizzle or film of moisture on soil, plants or animals, such as *Onymacris* beetles, behaviourally adapted to intercept fog on the crests of desert dunes. Second, a high fog (more correctly a low **stratus or strato-cumulus** cloud) forms at 100–600 m height in the atmosphere as a wedge of

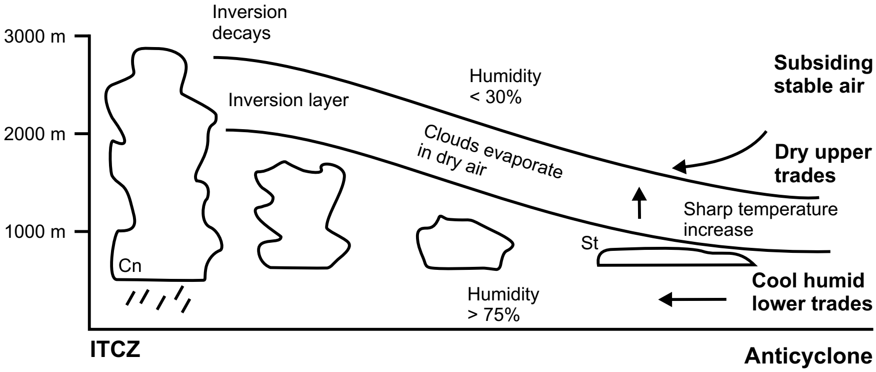

Fig. 16.6 A simplified cross-section of the atmosphere above the Angolan coast from the Congo River (left), to the Cunene River (right). Note the influence of the inversion layer over the cool southern coast, rising and breaking down before the Inter-tropical Convergence Zone in the north. St = fog-bearing stratus clouds; Cn = rain-bearing cumulo-nimbus clouds. Redrawn with permission after Leal (2004) *The African rain forest during the Last Glacial Maximum.* Ph.D. thesis, Wageningen University, Wageningen

Table 16.1 Climatic data for Stations in the Angolan Namib Desert Ecoregion

Station	Province	Altitude (m)	MAP (mm)	MAT (°C)	Hottest month(°)	Coldest month (°C)
Lucira	Namibe	5	104	21.2	26.2	18.0
Moçâmedes	Namibe	44	37	20.0	24.2	15.5
Tômbua	Namibe	4	12	20.1	24.2	14.5

Mean Annual Precipitation (MAP), Mean Annual Temperature (MAT) and Mean monthly temperatures for the hottest and coldest months

moist air trapped below an inversion layer of warmer air. This fog penetrates up to 100 km inland from the coast, especially up valleys and into depressions. Beyond the Namib, it is particularly important along the Angolan Escarpment, where it supports a rich diversity of vegetation, including the 'coffee forests' of Uíge and Cuanza-Sul.

Research in the Namib has shown that fog deposits up to five times more moisture than rain in the narrow belt of the 'hyper-arid' coast. Fog supports a rich lichen flora on the coast northwards of Moçâmedes, where crustose lichens cover the rocky desert surface, and foliose lichens hang as tassels from the shrubs and short trees of an otherwise desolate landscape.

In the creation and maintenance of the Namib Desert, **wind** has been a key contributor to processes at macro to micro levels. From the earliest events that triggered the aridification of the Namib, through the development of the marine conveyor belt of sand transportation and deposition, the processes of dune formation and dynamics, the transfer of infrequent and sparse rainfall from the Indian Ocean to the Namib, and of fog from the Atlantic to the Namib coast, wind driven by atmospheric forces has shaped the desert. At the micro-scale, organic detritus carried into the dune fields by 'berg' winds supports the abundant life of a harsh environment, sustained by the fog carried by cool breezes from the ocean. Few ecological systems demonstrate the interactions between ocean, atmosphere and land more clearly than the Namib.

There are very few weather stations in the Angolan Namib Desert, but the few that exist give an indication of the extreme aridity of the ecoregion (Table 16.1). The importance of fog as a source of moisture is not captured in the rainfall statistics, nor is the cooling influence of the 'wind chill' factor of cold northerly winds that are a characteristic of the coastal margin.

16.4 Floristic Composition and Physiognomy of the Angolan Namib Desert Ecoregion

The phytogeography of Angola was briefly described in Chap. 1. Most of Angola is covered by the mesic and arid savannas of the Zambezian regional centre of endemism. The far north of Angola falls within the Guineo-Congolian regional centre of endemism. Small outliers of the Afromontane centre of endemism occur as relict forests along the high mountains of Huíla and Huambo. The southwest of Angola has representatives of the Karoo-Namib regional centre of endemism, a floristic division that includes much of Namibia and South Africa, characterised by an arid climate with less than 500 mm rainfall per annum.

Within the Karoo-Namib regional centre of endemism, several local Centres of Endemism have been recognised by botanists. The Angolan Namib Desert ecoregion, as defined here, forms the extremely arid western component of the floristic 'Kaokoveld Centre of Endemism' (KCE) as described by Craven (2009). The KCE, defined on purely floristic composition, includes two further ecoregions in Angola, the Namib Savanna Woodlands and the Angolan Mopane Woodlands, both of which are defined according to their ecological characteristics. As Craven (2009) suggests, the flora of the Angolan Namib is much more closely related to that of Namibia than it is to the rest of Angola.

The KCE embraces the full geographic range of *Welwitschia mirabilis*, which is the floral icon of the Namib. In addition to this charismatic species, over 1600 plant species are found in the KCE, with 20% being endemic. The history of the flora and fauna of the KCE is complex. The KCE has many species, of both animals and plants, that have close relatives in the **Horn of Africa**, some 5000 km distant. These include species of mammals (Dik-dik, Gemsbok, Bat-eared Fox); amphibians, scorpions of the genus *Parabuthus* and plant genera such as *Kissenia, Pterodiscus, Thamnosma, Tribulocarpus,* and *Turnera.* These **disjunct distributions** are explained through the existence of an **arid corridor** running across Africa during dry phases of the Pleistocene, along the hot dry valleys and lowlands of the Rift Valley and of the Luangwa, Zambezi and Limpopo rivers (Juergens et al. 1991). The arid corridor would have expanded and closed during successive cold/dry and warm/moist periods of the Pleistocene Ice Ages, affecting not only arid ecosystems but also rain forests, as decribed in Chap. 12.1. The link between *Welwitschia* and its relatives in South America go back much further, perhaps to the Cretaceous.

In her detailed study of the flora of the KCE, Namibian botanist Patricia Craven (2009) defined three groups that form clear patterns in Angola.

The Welwitschia Group

The *Welwitschia* Group is characterised by *Arthraerua leubnitziae, Adenia pechuelii Welwitschia mirabilis*, *Zygophyllum stapffii, Z. orbiculatum* and *Z. simplex.* It is confined to the coastal strip, on coastal sands, gravel plains, hills and rocky outcrops. The climate is characterised by frequent fog reaching up to 60 km inland from the ocean. Mean annual precipitation is less than 200 mm, usually received in summer. The area occupied by this Group is subjected to strong, hot, dry east winds alternating with cold, moist southwesterly winds. It has a recorded flora of more than 200 species, of which 55 are endemic to Angola. Genera with endemic species include *Aloe, Commiphora, Euphorbia, Indigofera, Lotononis, Merremia* and *Petalidium.* Of particular interest is the very high diversity of succulent tree genera. These includes 12 species of *Euphorbia*, of which five occur only in Angola, and 11 species of

Commiphora. Life forms include short-lived non-woody dwarf shrubs with deciduous, succulent leaves (*Zygophyllum orbiculatum*) or rod-like stems (*Euphorbia damarana*).

The Kaoko Group

The Kaoko Group of the KCE is characterised by *Sesamothamnus guerichii.* It lies inland of the *Welwitschia* Group, reaching the Escarpment, up to the 1500 m contour, across rocky slopes, water courses, rugged mountains and hills. Annual rainfall is received mostly in summer, of up to 200 mm in the west and up to 350 mm in the east. It experiences no frost nor does it receive any moisture from fog. The flora has been poorly studied in Angola, but a high level of endemicity has been recorded with about 60 species known to be endemic to the Group. Endemic species include those in the genera *Bayensia, Hibiscus, Petalidium*, *Salsola, Sesamothamnus* and *Stipagrostis.* This group includes five species of *Commiphora*, and seven species of *Euphorbia.*

The Northern Succulent Group

In addition to these two groups, Craven (2009) describes a Northern Succulent Namib Desert Group, found in the coastal rocky hills and sandy valleys from Moçâmedes to Carunjamba River near Lucira. This includes a remarkable diversity of succulents, many of which are **pachycauls** (thick stemmed succulent trees, stout with few branches) such as species of *Adenium*, *Cyphostemma, Moringa, Sesamothamnus* and *Sterculia.* Other succulents here include species of *Euphorbia, Hoodia, Huernia, Kalanchoe, Kleinia, Talinum* and *Tavaresia.*

Physiognomy of the Vegetation

The physiognomy of the sparse vegetation of these three groups is dominated by dwarf shrubs and short trees, with short grasses, both annuals and perennials. These may be lush green and dense immediately after rain but are soon grazed by antelope or become moribund and gradually decompose as termites, ants and winds reduce them to a grey stubble. Trees and shrubs are often spinescent or succulent. The shrublands often have *Welwitschia mirabilis* as a conspicuous feature, but this amazing plant (Box 16.1) is most robust in the deep coarse sands of dry riverbeds (***chanas***). It is also found on rocky outcrops, together with succulent species of *Cissus, Commiphora, Euphorbia, Hoodia, Sterculia*, and hardy forbs and shrubs such as *Blepharis, Dicoma, Galenia, Helichrysum* and *Pterodiscus.* Close to the coast, succulent-leaved dwarf shrubs of *Mesembryanthemum, Salsola* and *Zygophyllum* become conspicuous.

As one progresses inland, the vegetation physiognomy and floristic composition gradually transition to that of the Namib Savanna Woodlands. Trees of such genera as *Acacia, Boscia, Colophospermum, Combretum, Commiphora, Sterculia* and *Terminalia* become more abundant, forming small savanna woodland communities on rocky outcrops, with grasses and shrubs on the deeper sands. A striking feature in Iona National Park are the broad inter-montane plains. These are covered with a rich carpet of *Stipagrostis* and *Schmidtia* annual grasses after infrequent rains (Fig. 16.7).

Fig. 16.7 Annual and perennial grasslands (*Stipagrostis, Schmidtia*) on the intermontane plains of Iona National Park

Conspicuous on these plains are the ’fairy circles’ (Fig. 11.16; Box 11.1), the origin and dynamics of which continue to puzzle scientists (Fig. 16.8).

16.5 Faunal Composition of the Namib Desert

The extreme aridity of the Namib Desert places severe limits on the survival of most vertebrates, especially amphibians. However, many reptiles and birds have developed successful adaptations to life in the desert (Chap. 11). The largest bird on Earth, the African Ostrich, was once common on the margins of the Namib, while two large bustards (Ruppell’s Korhaan and Ludwig’s Korhaan) are still to be found on the gravel plains and intermontane grasslands of Iona. Mammal species include nomadic herds of Springbok, Gemsbok, Plains and Hartmann’s Zebras, and sedentary carnivora such as Meerkat and Aardwolf. Brown Hyaena and Cheetah range widely over the desert margins. Table 16.2 lists vertebrate species typical of the Namib Desert Biome.

Box 16.1 Welwitschia Mirabilis: The Miracle Plant of the Namib

The botanical icon of the Namib, *Welwitschia mirabilis* has a long and illustrious history and a remarkable biology which should be studied by every

Fig. 16.8 The inland margin of the Angolan Namib Desert interfaces with Namib Savanna Woodlands

Table 16.2 Vertebrate Species Typical of the Namib Desert of Angola

- **Reptiles**: Feathered-Tailed Gecko, Namib Web-Footed Gecko, Common Namib Day Gecko, Anchieta's Dune Lizard, Kaokoveld Girdled Lizard, Desert Plated Lizard, Speckled Sand Skink, Dotted Blind Dart Skink, Namaqua Chameleon, Namib Rock Agama, Anchieta's Dwarf Python, Peringuey's Adder, Western Sand Snake
- **Birds**: Lappet-faced Vulture, Ludwig's Bustard, Ruppell's Korhaan, Burchell's Courser, Gray's Lark, Herero Chat, Tractrac Chat
- **Mammals**: Bat-eared Fox, Meercat, Brown Hyaena, Aardwolf, Springbok, Kirk's Dik-dik, Gemsbok, Hartmann's Mountain Zebra

Angolan ecologist. This unique, monotypic genus and family represents an early Gymnosperm order (Gnetales) that was present in Brazil and Angola long before South America and Africa split apart in the late Cretaceous (100 Ma). Its only known relatives are preserved as fossils from the early Cretaceous (112 Ma), including *Priscowelwitschia austroamericana* from Crato, northeast Brazil.

This extraordinary plant was discovered for science by the Austrian botanist and physician Friedrich Martin Joséph Welwitsch on 3 September 1859, while collecting botanical specimens just south of Moçâmedes. Welwitsch was truly the father of Angolan botany. In his relatively short time in the country from

1853 to 1861, he collected over 8000 herbarium specimens, representing 5000 species (over 80% of the country's flora), of which 1000 were new to science. He is honoured not only in order (Welwitschiales), family (Welwitschiaceae) and genus names of *Welwitschia*, but also in the names of over 300 other species of plants. He collected from the Congo basin to the Namib, and from the coast to the central highlands. His correspondence with the leading botanists of the day placed the then scientifically unknown Portuguese colony of Angola on the global botanical map.

Fig. 16.9 Probably the largest and oldest specimen of *Welwitschia mirabilis*

Welwitsch was immediately aware of the scientific importance of the peculiar plant he found scattered about on the desert landscape, possessing features of widely different plant families: proteas, casuarinas and conifers. He recorded the sensations he felt: "I could do nothing but kneel down on the burning soil and gaze at it, half in fear lest a touch should prove it a figment of the imagination." He sent material to Sir Joseph Hooker, Director at the famous Royal Botanic Gardens, Kew, London. Hooker's response was equally enthusiastic: "A discovery that I do not hesitate to consider the most wonderful, in a botanical point of view, that has been brought to light in the present century." Hooker named the plant as a new genus *Welwitschia*, in the Class Gnetales in honour of Welwitsch.

Interestingly, it was Joachim John Monteiro, the British-trained mining engineer and naturalist who sent additional material to Hooker, on which his monograph on *Welwitschia* was based (Hooker, 1863). Monteiro collected plants, birds and butterflies while on his extensive geological explorations of the country from 1858 to 1876. A final historical fact worthy of mention was that the founder of the famous Kirstenbosch Botanical Garden in Cape Town, Harold Pearson, who visited Angola in 1909 to study the species, was the first botanist to observe that *Welwitschia* is pollinated by insects, and to observe that *Welwitschia* has the ability, when two or more plants grow closely together, to form natural grafts. This early observation explains the enormous specimens one finds in Angola, that are possibly several plants growing back-to-back, pushing up vertically rather than spreading laterally (Figs. 16.9 and 16.10).

Fig. 16.10 Female cones of *Welwitschia*, with two permanent leaves emerging from the meristematic apical rim of the corky tree trunk

Welwitschia mirabilis occurs in numerous, often disjunct populations from just north of Bentiaba in Angola to the Kuiseb River in Namibia, over a distance of 1096 km. It has been found within 5 km of the coast to nearly 150 km inland. Its main distribution falls in the summer rainfall, northern Namib, mostly to the west of the 100 mm isohyet, although extending across an annual rainfall gradient from 20 mm to over 200 mm. At the moister, eastern limit, competition for resources with angiosperm trees, shrubs and grasses may limit the successful establishment of *Welwitschia*. In Angola, two main populations are found. One lies from 10 km inland of the coast near the species's type locality at Cabo Negro and stretches inland towards Virei. The other major population, also from about 10 km from the coast, is centred on Espinheira and extends inland towards Iona Posto. The species occurs across an extremely wide range of rocky substrates—granite, limestone, basalt, sandstone, mica schist, calcrete, gypcrete and gravel—but is most robust on the sandy alluvial soils of dry riverbeds. In a detailed study of the phylogeography of *Welwitschia*, Juergens et al. (2021) confirmed the existence of two distinct gene pools, representing two subspecies. The two subspecies (*Welwitschia mirabilis ssp. mirabilis* and *W. mirabilis ssp. namibiana*) are separated not by a clear physical barrier such as the Cunene River, but by a more subtle change in environmental factors some 200 km south of the river.

So what makes *Welwitschia* deserve the name *mirabilis* (the miracle plant)? What is it that so fascinates scientists? There are two lines of interest.

The gymnosperms reached their peak during the Triassic and Jurassic geological periods—250–145 million years ago—during the age of the dinosaurs. This makes *Welwitschia mirabilis* a 'living fossil'—a faint shadow from the distant past. But while having the typical gymnosperm characteristics of 'naked seeds' and nutrient conducting sieve cells, it has angiosperm-like water conducting vessels (xylem) and angiosperm-like male flower characters. It also has parallel-veined leaves like the monocotyledons (grasses) and many more intriguing and contradictory anatomical features. *Welwitschia* therefore follows none of the carefully designed rules of evolutionary biologists. It also provides some surprises for the ecologist, as described below. It ignores all the rules for survival in the oldest desert in the world. *Welwitschia* grows very slowly and lives to a very great age, unlike the fast-growing and short-lived desert annuals that pop up in their millions after rare rain events to flower, set seed, and go dormant for many years before reappearing after the next shower of rain.

On germinating, *Welwitschia* seeds produce two short-lived seed leaves (cotyledons) and immediately thereafter, another two, opposite, foliage leaves—which it keeps for life. No other plant shares this unique character. Nothing more—no flushes of bright new leaves every spring, no spreading branches to carry flowers and fruit—just a stumpy, short, headless trunk. Basically, the plant has a modest taproot, a stunted stem, and two long strap-like leaves. The two leaves are extruded, conveyor-belt fashion, at a rate of about 13 cm per annum from the meristematic tissue that forms the margins of the truncated head of the plant. The leaves are finely grooved and sinuous. Continuous growth means that the ends of the leaves are repeatedly beaten by the desert winds, drying out into tattered, grey or brown tassels. Some leaves have been recorded as long as 11 m, and the breadth of leaf bases can be as much as a metre.

Welwitschia, in common with many gymnosperms, is dioecious, with separate male and female plants carrying their reproductive organs on short branches. These produce secretions that are visited by a diversity of insect pollinators. The leathery leaves have none of the characteristics expected in desert plants—such as small size, deciduousness and succulence. However, recent research by Gert Kruger and colleagues from North-West University in South Africa found novel anatomical and physiological features in *Welwitschia* that can account for its success. The broad leaves have abundant, deeply sunken stomata (Fig. 16.11) on both upper and lower surfaces, which are further protected from dehydration by a thick cuticle. Despite the exposure of the broad, lengthy leaves to solar radiation throughout the day, strong structural features prevent wilting and the collapse of the mesophyll cells which contain the photosynthetically active chloroplasts. The leaves have vertically aligned 'walls' of stiff hypodermal fibres, which act like reinforcing structures, supporting the mesophyll cells against collapse should turgor pressure be lost during prolonged drought. (Fig. 16.12). Kruger et al. (2017) found that the combination of anatomical structure and photosynthetic response to moisture availability has enabled an opportunistic survival strategy through rapid and reversible switch-over from water conservation to CO_2 assimilation as required. It is these specialised features that have ensured the survival of *Welwitschia* in the Namib Desert for perhaps 100 million years.

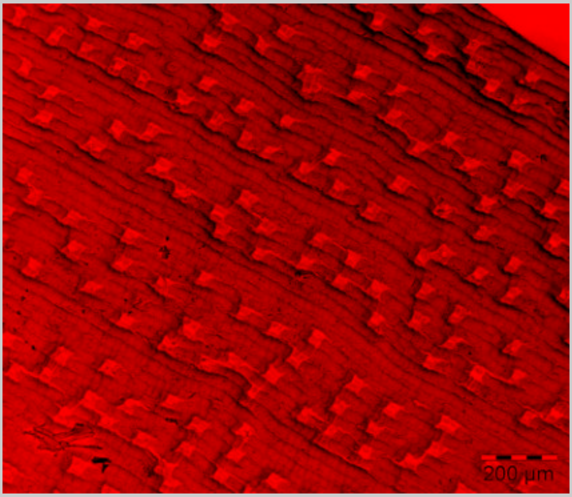

Fig. 16.11 Anatomical adaptations to aridity in *Welwitschia mirabilis* leaf. Leaf epidermis with stomata and deeply sunken subsidiary and guard cells. *Photo* Gert Kruger

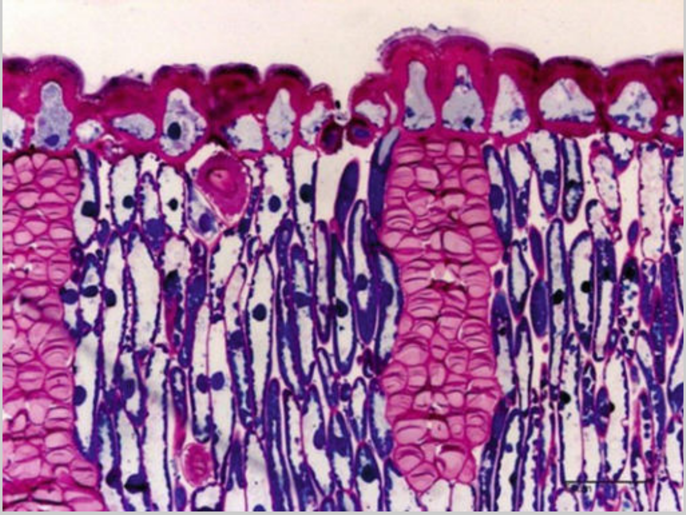

Fig. 16.12 Light micrograph of the supportive ‘beams’ of hypodermal fibers (pink) which prevent the collapse of substomatal space and mesophyll during high levels of drought stress. *Photo* Gert Kruger

Much has been speculated about the adaptation of *Welwitschia*’*s* leaves to harvest water from the fog that prevails over part of its range. This suggested dependency on fog cannot explain for the many *Welwitschia* that grow on the hot rocky outcrops and valleys in the eastern hills of Iona, seldom reached by the cool winds and fog off the Benguela Current. Long-term studies in Namibia (Henschel & Seely, 2000) found no direct correlation between fog deposition on leaves and their growth, nor was it recorded in the study by Kruger et al. (2017).

The stem of *Welwitschia* is woody, covered in a corky bark, and is hollowed into a basin-shaped crown. Most of the stem lies below ground, seldom rising more than half a metre above the surface. The carrot-like taproot does not, contrary to early speculation, appear to penetrate deep into the desert sands. Henschel et al. (2019) excavated seven mature plants and found them to lack taproots greater than 2 m depth. Henschel measured lateral roots extending up to 9 m, while lateral roots of up to 15 m have been mentioned in earlier studies. The rooting strategy is opportunistic, with a dense network foraging for water from the shallow surface layers of the soil. A remarkable finding by Henschel et al. (2019) was that the study plants sourced moisture from perched water within the gypsum substrate. **Perched water** is that which is held in upper soil layers by an impenetrable substrate (gypcrete or calcrete) below them. They concluded that the surface soil water would be supplemented overnight from fog, or by upwards diffusion from within the gypsum horizon. What is clear is that successful germination and seedling establishment requires a good rain event to provide the water needed to sustain root growth within the surface soil. Recruitment is episodic, reflected in the age distribution profiles of *Welwitschia* populations in different areas of Iona. In January 2009, following good rains in 2008, there was an abundance of small, 20-cm-tall seedlings around Espinheira. Most of these had died by December 2011. For establishment success, *Welwitschia* seedlings need successive episodes of above average rainfall.

As might be expected with slow growth, *Welwitschia* plants, once established, live to a great age. Accurate measurements have not been achieved, but a combination of evidence from growth rates of known-age plants, counts of growth rings, and carbon dating, suggests that large plants might be 500 years old, and the rare, exceptionally large plants, as much as 1800 years old. A peculiarity of *Welwitschia* is that in contrast to most trees, which have their growth rings in the inside of the stem, *Welwitschia* has its growth lines on the outside—along the growing tissue on the rim of its basin-shaped head.

The apparent poor fit of *Welwitschia*'*s* growth form, morphology and natural history to its harsh environment is difficult to explain. Yet it has succeeded, indeed prospered for many millions of years, in the world's oldest desert. It has also puzzled, perplexed, intrigued and entertained the intellect of scientists for 150 years, and will surely continue to do so for many more.

As a recent review of the evolution of seed plants suggests: "The placement of the Gnetales and ramifications for angiosperm evolution remains one of the most controversial issues in seed plant phylogeny" (Ran et al. 2018).

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