Welwitschia mirabilis: paradox of the Namib Desert

Chris H. Bornman

Welwitschia mirabilis, endemic to the Namib Desert of South West Africa, exhibits very few of the characteristics normally associated with xerophytic or drought-tolerating species. Recent research suggests that water is absorbed by stomata on the upper surface of its enormous leaves during early morning fogs and that the ultrastructure of the food-conducting tissue provides evidence against the hypothesis of mass-flow of dissolved organic substances by hydrostatic pressure.

South West Africa has been called the ageless land, the disputed land, and the last frontier land. It is probably any one or all of these; certainly, from the wet, tropical Okavango in the north-eastern panhandle of the Caprivi to the parched, diamond-studded Oranjemund in the southwest, it is a land of paradox. And nowhere are the paradoxes so strikingly displayed as in the Namib Desert.

The Namib is one of the smallest and oldest of the world's deserts, stretching 1500 km along the west coast, 80 to 130 km wide and comprising 15 per cent of the total land area of SWA. Conveniently, the Namib may be subdivided into three parts: the northern Namib, from the Kunene to the Huab River; the pebble or gravel plain or central Namib, from the Huab to the Kuiseb River; and the sand sea or dune or southern Namib, from the Kuiseb to the Orange River.

The pebble Namib (figure 1) is an area of accumulation, the irregularities in the topography having been filled in with windblown rock debris and sand. The sand sea Namib is derived from the seashore by winds blowing from a southwestern direction. R. F. Logan [1] refers to the coastal area of the Namib as a region of paradoxes in that the hottest days come in winter, rain seldom falls yet the air is more humid than almost any other place on earth; fog blankets a parched land, and despite the fact that there is almost no vegetation, there is evidence of a rich and varied fauna. Except for episodic downpours the Namib is in fact practically devoid of rainfall, and moisture is almost entirely derived from heavy fogs which enshroud the coast for about 300 days a year. Westerly winds often drive the fog up to 80 km inland.

Fauna and flora of the Namib

Numerous species of larger animals, birds and reptiles make the Namib their home but relatively few are endemic to it. Small cryptic mammals, especially rodents, are more typical of the Namib and new species, such as the Golden Mole *Eremitalpa* sp., are still being discovered. The arthropod fauna is confined almost entirely to the Hexapoda and Arachnida. Large spiders are a feature of the dunes and the only known beetles with white elytra in the world occur in the northern Namib. The spider-like Namib Sand Runner *Stenocara phalangium* has the reputation of being the beetle with the longest legs in the world (up to 6 cm long), allowing it to carry its body high above the heated ground surface. The Saucer-beetle *Lepidochora* sp. which lives in the depths of the sand and emerges only at night, in contrast, is a peculiar disc-shaped insect covered with a dense layer of moisture-absorbing scales.

On an expedition in the autumn of 1969 following a season of exceptionally good episodic showers, I recorded 53 species of plants, excluding the Gramineae, in flower. Two of the most unusual plants in the world occur only in the Namib. Both are long-lived perennials. One of these the Namib Nara *Aconthosicyos horrida* (figure 2), is a much-branched, dense shrub with photosynthetic spines and leaves that are reduced to minute scales. It is a dioecious member of the cucurbit family which grows on small dunes in the sand sea Namib and bears pale orange fruits about six inches in diameter. The Topnaar Hottentots, a tribe of Kuiseb River nomads, extract about 30 tons of seed from the fruits annually and export them to Cape Town where they are used in the baking industry as a substitute for almond flavouring. This plant was first described by Dr Friedrich Welwitsch who, in 1861, also first described the other endemic species which now bears his name, *Welwitschia mirabilis*, the main subject of this article.

The paradox of *Welwitschia*

Imagine a plant that flourishes in a desert as extreme as the Namib yet appears to have few morphological characteristics normally associated with xerophytic or drought-tolerating species; with leaves of immense surface areas that persist for the life-time of the plant; with an unbranched stem, a relatively shallow root system, a water-conducting system or xylem typical of the angiosperms or ovary-covered seed plants, and a food-conducting system or phloem like that of the gymnosperms or naked-seeded plants; with a male reproductive organ that closely resembles the angiosperm flower and a female reproductive structure that appears more closely analogous to the ovuliferous scales of the conifers; with a shoot apex that dies shortly after germination resulting in this plant's closed system of growth; and a plant which takes up to two years to shed its seed leaves or cotyledons and grows to an estimated age of 2000 years and probably more. Such a morphologically striking plant is *Welwitschia mirabilis* which appears to be a very isolated member of an ancient developmental series, probably representing a parallel line of evolution in the plant kingdom and ending in a blind alley [2].

For a century now *Welwitschia* has aroused great interest and even greater conjecture. Surprisingly little has been written about it and, probably as a result of the inaccessibility of material, investigations and observations have not always been as complete as a plant of such a bizarre nature warrants. Unfortunately, too,

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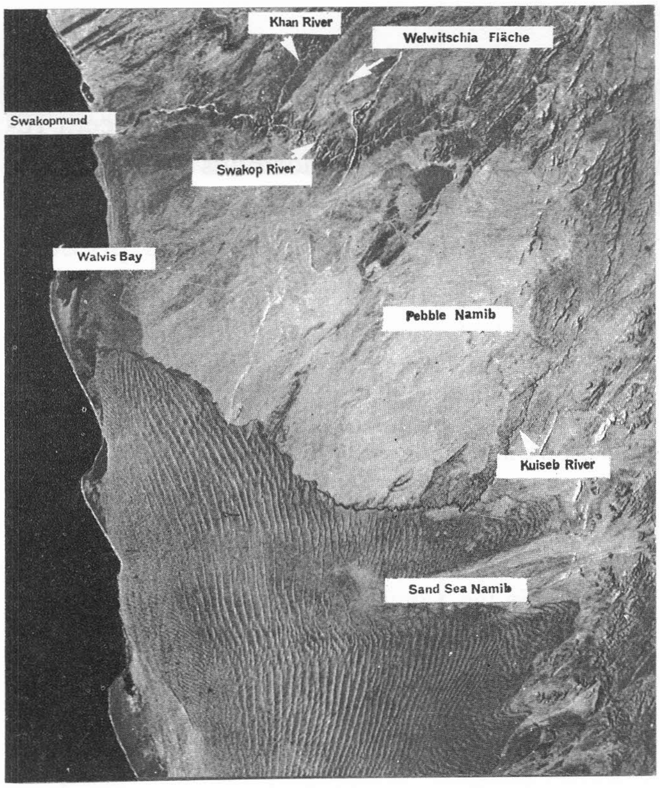

Figure 1 Bird's eye view of part of the Pebble and Sand Sea Namib showing the Welwitschia Fläche where most of the author's work has been carried out over the past 5 years. This photograph was taken by the crew of Gemini IV at a distance of 215 km. (Reproduced by kind permission of the U.S. Embassy, Pretoria.)

Figure 2 The Namib Nara, *Aconthosicyos horrida,* endemic to the Namib Desert, growing on a sand dune. This densely-tangled shrub has long spines which are the photosynthetically functional organs.

erroneous concepts have been perpetuated from textbook to textbook.

The plant body

Welwitschia is a monotypic species grouped with the genera *Ephedra* and *Gnetum* under the plant order Gnetales in the class Gymnospermae. In many respects these three genera are strange bedfellows. *Ephedra,* with about 35 species, is shrubby and broom-like with minute leaves and the whole aspect of this plant is xeromorphic. *Gnetum* is a jungle genus comprising about 34 species of which most are climbers with net-veined angiospermic leaves. The genus *Welwitschia* comprises a single species and in distribution is confined to the narrow coastal belt of the Namib from the Kuiseb River northwards to Cabo Negro in Angola. The oldest colony of plants including the two largest (figures 3, 4) and some of the most magnificent specimens known, are found on the Welwitschia Fläche or Flats, an area of the pebble Namib about 50 km east of Swakopmund at the confluence of the Khan and Swakop Rivers (figure 1).

The plant itself consists of a woody, unbranched stem shaped like a top or a turnip (figure 5), with a crater-like depression surrounded by a rim of green, photosynthetic, and meristematic tissue. The rim is grooved and in the grooves are inserted a single pair of leaves, parallel-veined and persistent. If the leaves die the remainder of the plant also perishes. The taproot is elongated but is relatively shallow. The plant is dioecious and the inflorescences arise from the meristematic tissue of the stem just above, but sometimes below, the insertion of

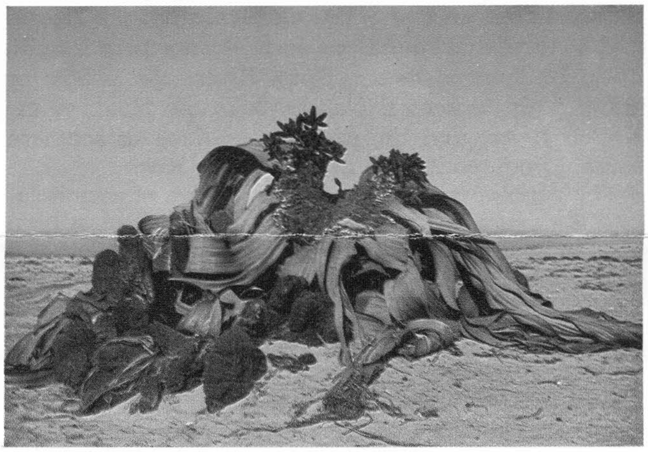

Figure 3 The Husab *Welwitschia,* the largest specimen known. This female plant is about 1500 years old. Note the fog closing in from the west (9.45 hrs) and the twisted stem with the two original leaves split into multiple fragments. Chunks of dead stem consisting of dense and compact secondary wood are lying in the foreground.

Figure 4 The Pforte *Welwitschia,* the second largest of its kind, is also a female plant. Plants such as these produce a microclimate in which various species of insects, rodents, reptiles, birds, and small animals find an ecological niche.

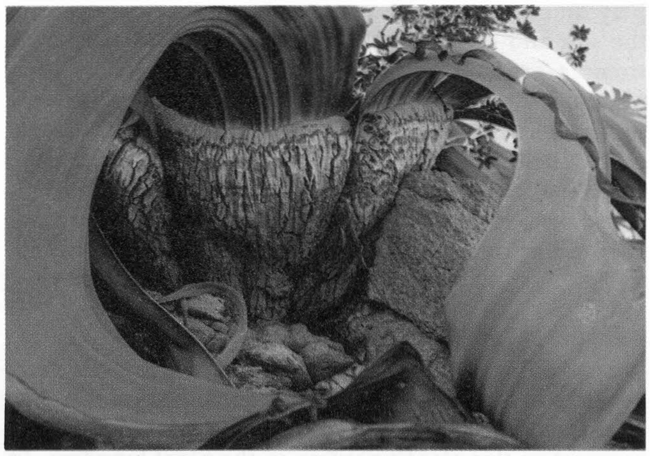

Figure 5 A male *Welwitschia* growing in a rock cleft and showing clearly the turnip-shaped stem with its green, meristematic tissue from which the two giant leaves arise. Note that the leaf is parallel-ribbed.

the leaf. The male flower is pseudo-hermaphroditic and is borne on small salmon-coloured cones. The female flower consists of an envelope of two united scales and a single terminal ovule borne on large green to yellowish cones resembling those of the pines. Contrary to a popularly held view, pollination is effected by wind and not by a large sucking hemipteran, *Probergrothius sexpunctatis*, which feeds on the young ovules and phloem of the female cones. Although winged, this insect cannot fly. The pollen grains have the aerodynamic shape of a rugby ball and during a Föhn or fall wind abound in the air.

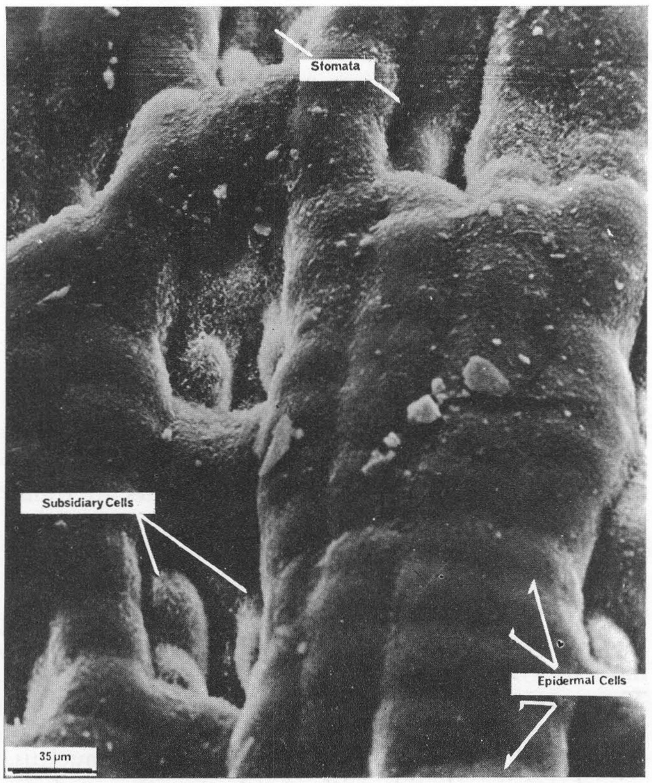

Figure 7 A scanning electron micrograph of part of the upper surface of a *Welwitschia* leaf. Note the sunken stomata with closed pores. The ridge at the middle to the right-hand side indicates a bundle of fibres below the epidermis. The broader bands of fibres are interconnected by smaller, anastomosing bundles as shown at the upper left.

Figure 6 Photomicrograph of transection of upper portion of leaf shows bottle-shaped epidermal cells overlain by a reddish cuticle. In the centre is a tightly closed stoma and below it a substomatal chamber in which water, water vapour and gases are collected momentarily before being dispersed. The long, sausage-shaped cells are palisade parenchyma, and the thick-walled cells with occluded lumina are fibres of great tensile strength and shown in figure 7 as a muscular ridge below the epidermis.

The leaf

The leaves are the most conspicuous, striking and anomalous of the plant's organs. Commonly, they sprawl in a torn and tangled mass over the desert gravel lending the plant a weird, grotesque appearance. The leaves are the longest-lived in the plant kingdom and are exceedingly tough and strap-shaped, and are continually

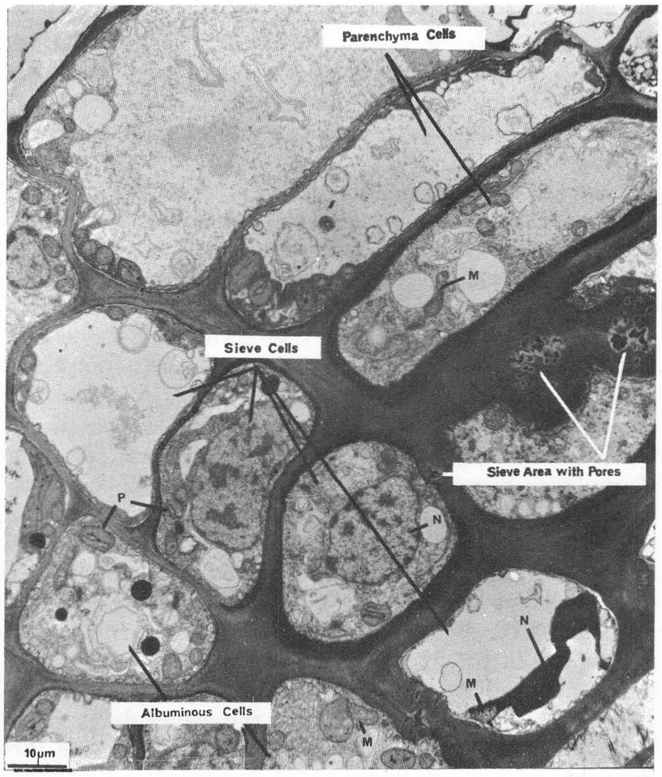

Figure 8 A transmission electron micrograph of part of a vascular bundle in the leaf of *Welwitschia* showing sieve, albuminous and parenchyma cells. The two central sieve cells are still immature. The mature element at the lower right has retained its nucleus (N) which partly engulfs a mitochondrion (M). The sieve area with pores indicates a common juncture of the walls of two sieve cells. Note plastids (P).

perpetuated at the rate of 8–15 cm a year from a basal intercalary meristem (this type of meristem together with the parallel venation of the leaf are characteristic also of monocotyledonous flowering plants). In younger plants the two opposite leaves grow up and curve outwards away from the stem, touching the sand about 0·3 to 1·2 m away. The protoplasmic contents of the cells at the terminal portion of the leaf that lies on the desert floor are simply roasted to death as a result of surface temperatures that, again paradoxically, are highest during the winter months on days of Föhn winds from the east. These winds, which originate over the interior upland and warm up as a result of compression, also fray the leaves by scouring the terminal parts back and forth across the gravel with the result that the leaf tips split and die back progressively as growth occurs.

The leaves can assume enormous proportions. A leaf of one of the giants was found to have an unbroken width of 1·8 m and a length of 6·2 m of which 3·7 m were living tissue. It was calculated that this plant, considering both leaves together with their multiple remnants, had a total leaf surface area of approximately 21 m^2 of living tissue, a desert food factory by any standards! The mean leaf width of a group of 25 young plants, about 20 years old, was 22 cm and the mean length 1·2 m of which 0·7 m were living. The longest leaf I have found measured 8·8 m, 7·3 m of which was photosynthetic tissue.

What, it may be asked, is the significance of such large exposed leaf surfaces to, of all plants, a desert species, when alongside a *Welwitschia* grows a tiny 5 cm tall *Albuca* sp., a member of the lily family with tightly-spiralled, tomentose leaves: the one plant's very survival dependent upon its ability to reduce the surface area of its leaves in order to counter water loss by evaporation and transpiration and the other's apparently not? The answer quite clearly must be sought in the coastal fog which moves inland before dawn and disappears at about 10.00 a.m. (see figure 3).

The condensate of the fog, which in terms of precipitation is equivalent to an annual rainfall of 50 mm, collects on the leaves of the *Welwitschia* and is absorbed through the stomata and conducted to various parts of the plant via an extensive system of xylem vessels and transfusion tracheids. It is not surprising therefore, to find that the leaf possesses millions of stomata or minute epidermal pores on both the upper and lower surfaces. Careful counts have shown that there are approximately as many stomata adaxially as abaxially, namely 22 200 per cm^2. Xerophytes normally have no stomata on their upper leaf surfaces and those on the abaxial surface are few and deeply sunken. Using tritiated or deuterated water we have found that water is absorbed during a period that coincides very closely with the appearance and disappearance of the fog. In fact the stomata close shortly after the fog has lifted. In 1967, an extremely dry year, when fog was recorded on the Fläche on only 100 days, the plants exhibited severe chlorosis, the leaves dying back from the tips. Some plants in fact did not survive the drought.

The epidermis of the leaf is covered by a waxy cuticle consisting of three layers, only 1/40 the total thickness of the leaf (figure 6). This, also, is rather surprising since cuticles of desert species usually are extremely thick. However, the central layer of cuticle is the thickest and contains crystals of calcium oxalate which probably play an important role in reflecting radiant energy from the sun and consequently in keeping the leaf cool. The stomata are sunken, but not as deeply as in most xerophytes. However, they can shut tightly and are invariably supported below by huge, exceedingly strong mechanical cells. The leaf is furthermore constructed of very long, tapered fibres analogous to flexed steel rods (figure 7). These leaf characteristics suggest a remarkable overall adaptation to the desert conditions with the prevailing fog.

Food-conducting tissue

Our work on *Welwitschia* [3, 4, 5] has a twofold purpose: to relate anatomical structure and physiological function to desiccation resistance, and to attempt to place in perspective this plant's position in the plant kingdom. In this regard the work carried out recently in our laboratory by R. F. Evert of the University of Wisconsin, a leading authority on the anatomy of the phloem, is quite significant.

We succeeded in getting finer fixation and more stages of development of the phloem than has been achieved for any gymnosperm previously. The phloem of *Welwitschia*, in contrast to the xylem, is definitely gymnospermous and consists of sieve cells—the food-conducting cells proper, parenchyma, and albuminous cells, the latter now shown for the first time (figure 8). Our most striking finding was that the nucleus is retained in the mature sieve cell with its envelope intact. This is the first time that this has been demonstrated in either the gymnosperms or the angiosperms. The classical view holds that the nucleus becomes necrotic and gradually disappears during development of sieve elements. Evert had shown previously that in some gymnosperms the nucleus is retained in the mature sieve cell albeit without its nuclear membrane. Furthermore, it was not uncommon in *Welwitschia* to find the nucleus, located in the middle of the sieve cell, filling the intra-cellular space from one tangential wall to the other, and often completely engulfing mitochondria. Fine strands of endoplasmic reticulum (ER) traverse and criss-cross the mature cell from the parietal cytoplasm on one wall to that of the other. Two types of ER prevail: coarse and fine. The finer ER is associated with pores in the sieve areas, forming massive aggregations on either side with the pores themselves being virtually occluded. No phloem protein or slime seem to be present in the sieve cells of *Welwitschia*. The significance of these observations must be considered in relation to the controversy existing between botanists in regard to the mechanisms by which foods and solutes are transported in the phloem. Currently, two major hypotheses are propounded: that of mass flow or movement of assimilates along concentration gradients, and that of diffusional or molecular movement in which it assumed that the sieve element plays an active role with sugar molecules moving independently of those of water. There are other hypotheses, too, such as electro-osmotic movement and cytoplasmic streaming. However, the anatomy of the mature sieve cell, replete with nucleus, mitochondria, plastids with starch granules, and an intricate three-dimensional network of ER, militates against the movement of solutes by mass-flow, at least as far as hydrostatic pressure is concerned. This work may have a profound effect on the concepts of food transport in plant tissues in general.

The stem and root system

Except where the plants grow on rocky ledges, on steep inclines, or in rock clefts (figure 5), the stem is often completely buried in the sand. In older specimens it is often thrust upward and as a result probably of damage to the rim-like meristem and differential growth pressures, it becomes much invaginated and twisted. The concave apex can have a diameter of up to 1 m; one huge plant in the Mesom Wash measured 1·8 m across. The two tallest plants known, the Husab *Welwitschia* (figure 3) and the Pforte *Welwitschia* (figure 4) are 1·5 m and 1·2 m from the base to crown, respectively. The latter plant occupies an area 9·1 m in circumference and its stem, measured along the terminal groove, has a circumference of 5·7 m.

Contrary to reputed depths of from 30 to 45 m, the root system is rather shallow and simple, consisting of a tapering tap root with a few non-tapering extensions, lateral roots, and a network of delicate spongy roots. A transect adjacent to a young plant 1·7 m from leaf tip to leaf tip and with a leaf surface area of 0·8 m^2 revealed a taproot with taproot extension 1·6 m deep, a region of about 25 cm from the surface downwards of dry sand and gravel, followed by about 50 cm of moist sand in which the spongy root network was distributed. The total length of the root system of this plant, excluding the spongy roots, was 26·5 m. Measurements of the root systems of plants removed during bulldozing operations near the Brandberg suggest that *Welwitschias* do not have taproot extensions deeper than 3 m. One may conclude that the primary function of the root is one of anchorage and not uptake and transport either of water or mineral elements.

Conclusion

Welwitschia, although growing in the Namib Desert, is in aspect nonxeromorphic and depends for its survival on the coastal fog. It is interesting to speculate that this plant probably originated under tropical conditions and that during its evolutionary development it gradually adapted to the changing climatic conditions culminating in those as severe as on the South West African coast.

Acknowledgement

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References

[1] Logan, R. F. 'The strangest climate'. *SWA Ann.*, **129**, 1970.

[2] McClean, R. C. and Ivimey-Cook, W. R. 'Textbook of Theoretical Botany'. Vol. 1. Longmans, Green, London. 1960.

[3] Bornman, C. H., Elsworthy, J. A., Butler, V., and Botha, C. E. J. '*Welwitschia mirabilis:* Observations on general habit, seed, seedling, and leaf characteristics.' *Madoqua Ser.* II, **1**, 53, 1972.

[4] Butler, V. 'The morphology and vascular anatomy of *Welwitschia mirabilis* seedlings'. M.Sc. thesis. Univ. of Natal. 1971.

[5] Button, J., Bornman, C. H., and Carter, M. *J. exp. Bot.*, **22**, 992, 1971.

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