Welwitschia mirabilis: Observations on general habit, seed, seedling, and leaf characteristics

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INTRODUCTION

Welwitschia mirabilis, of the order Gnetales, class Gymnospermae, is a rare and strikingly bizarre plant. It is geographically restricted along the south-west coast of Africa to a narrow margin of the Namib, one of the world's most extreme deserts. The only species in the genus, *Welwitschia* survives in very severe localities where the annual rainfall is often less than 25 mm and where, in terms of precipitation, the coastal fog is equivalent to about a further 50 mm. Kers (1967) has recently described in detail the distribution of *Welwitschia*, and Schulze (1969) has given an account of the climatic conditions prevailing at Gobabeb, the southern-most limit of this species.

Welwitschia, of which the oldest living specimens are estimated at 1 500 to 2 000 years, has invoked much botanical speculation. It is an evolutionary offshoot of the plant kingdom and is capable of tolerating severe conditions of stress. Much has been written about this plant and often erroneous concepts have been perpetuated from text to text, but except for Rodin (1953, 1958), Martens (1959, 1961, 1963), and Martens and Waterskeyn (1963), little basic work has been carried out on this species.

Our research group in the Department of Botany, University of Natal, is interested particularly in those characteristics which afford this species its remarkable resistance to desiccation. Many aspects of its anatomy, physiology and biochemistry are at present under investigation. This paper reports on some preliminary observations recorded in respect of certain striking and probably anomalous features.

MATERIALS AND METHODS

Observations were made during six different visits at various seasons from 1967 to 1969 on plants growing in various parts of the Namib, from the Kuiseb River to the Petrified Forest, west of the village of Welwitschia. The greatest amount of time was spent on the Welwitschia Fläche, a desert plain about 50 km east of Swakopmund and east of the confluence of the Khan and Swakop Rivers where extensive morhpological and physiological observations were made.

Seedlings were raised in the laboratory from seed collected from plants growing on the Fläche. Embryos were cultured on agar containing White's (1954) nutrient medium. Conventional histological methods were used to prepare plant tissue for light microscopy. For electron microscopy *Welwitschia* tissue pieces were fixed in buffered 3,0% glutaraldehyde, post-fixed in 2,0% osmium tetroxide, embedded in epoxy resin, sectioned, and stained according to Reynolds (1963). Sections were viewed in a Hitachi HU 11E electron microscope. Scanning electron micrographs were made from discs of leaf tissue These discs were first dehydrated through an acetone series, after which their surfaces were coated in a vacuum evaporator with a layer of aluminium approximately 250-500°A thick. This tissue was viewed in a Hitachi SEM 2.

OBSERVATIONS AND DISCUSSION

General growth habit.

Figure 1 is a longitudinal section through a five to ten-year-old plant and shows the general morphology of *Welwitschia*. The plant body, which has been adequately described by Verdoorn (1966), resembles a woody carrot. The stem is exceedingly fibrous and has a prominent, thick corrugated periderm. Some of the most magnificent specimens are found on the Welwitschia Fläche and one of the largest plants, growing in a wash, measured 1,5 m from the soil surface to the highest part of the stem. Another giant, the Pforte Welwitschia (Fig. 2), is 1,2 m tall and the circumference at the base of its leaves is 8,7 m. In one huge, dead specimen the terminal groove in the rim of the stem curved and invaginat-

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ed for a circumference of 10,8 m. This plant could well have lived to an age of 2 500 years or more.

Unequal growth causes the stems of these plants to become weirdly distorted and the two strap-shaped leaves, growing from a terminal groove in the photosynthetic tissue of the stem, follow this pattern of irregular growth. The leaves bulge and split lengthwise and may become so contorted that an impression of a multi-leaved plant is created (Fig. 3).

Welwitschia is a dioecious plant, bearing either micro-or megastrobili. Its inflorescences arise from the meristematic tissue of the stem on the adaxial but occasionally also on the abaxial side of the leaf. The megastrobilus (Fig. 4) consists of an axis bearing, on the average, 90 to 100 megasporophylls or bracts arranged in an opposite, decussate manner. Figure 5, represents the mean bract counts of 100 randomly selected megastrobili or cones and shows that only 50 to 60 per cent of the bracts normally are fertile. The sterile bracts are situated at the apex and base of the cones. The seeds which develop from the fertile bracts are frequently infected with a fungus, *Aspergillus niger*. Of 10 000 seeds collected from plants growing in an area of 2,6 km^2, 80 per cent were infected by this fungus.

The fungal infection appears to be closely related to the activities of a sucking insect, *Probergrothius sexpunctatis*, found in the Namib. It has been claimed that these insects are the chief pollinating agents of *Welwitschia*. However, they cannot fly, and since the plants are usually scattered they would have to traverse an extremely hot gravel surface. Temperatures as high as 65°C were recorded on the desert floor. Furthemore, relatively few of these insects and their red nymphs are found on male plants. *Probergrothius* frequents the female plants which bear large, succulent cones, in preference to the microsporangiate plants. These insects do not feed on the exudate which collects at the tips of the bracts (Fig. 4) but probably probe the phloem of the younger cone stalks with their long probosci, in which process fungal spores probably could be introduced through the resulting apertures. Alternatively, these insects might feed on the developing embryo, which would account for the observation that most of the infected seeds correspond to the fertile or mid-region of the megastrobilus, namely that region where the bracts are morphologically mature. Clearly, much work waits to be done in this respect.

Seed and seedling characteristics.

Seed units of the *Welwitschia* consist of a seed and a papery husk of winged perianth segments. The mean weight of 1 000 seed units was found to be 1,20±0,13 g per seed unit, and that of the seed itself 0,41±0,04 g. If the fertile seed is dispersed by wind, it is suggested that very strong gusts would be required to effect the successful distribution of what is a rather substantial reproductive unit. An investigation of the effect of wind velocity on seed movement is currently in progress in an attempt to establish its role in dispersal.

The capacity of the seed unit to imbibe water, as for example under conditions of cloudbursts, is shown in Figure 6. Through imbibition the seed more than doubles its initial weight within seven hours, after which the rate of uptake decreases. The husk appears to have a greater capacity for imbibition than the seed over a longer period of time. Now, since conditions of fog seldom last for longer than a few hours — by 10:30 hours the fog on the Fläche has generally disappeared — it would appear that the major source of imbibitional water derives from precipitation. *Welwitschia* communities are frequently found in groups of similar ages (sizes) and it is suggested that this grouping may be related directly to freak single precipitations of approximately 25 mm, or to several downfalls, each yielding less than 25 mm, in the same localized area. If they were available, meteorological data might in fact confirm this.

Under greenhouse conditions *Welwitschia* seeds germinate well within 11 to 21 days if soaked with the equivalent of 25 mm of rain (Fig. 7). Seeds did not germinate with an equivalent of 6,25 mm of rainfall; however, if a further 6,25 mm of rain was applied within 24 hours, then up to 35 per cent germinated. This clearly points to the presence of an inhibitor, which must be first leached from the seed or seed-coat before germination will proceed. This is simply a physiological mechanism which ensures the germination of a seed only under conditions suitable for growth, and a phenomenon not uncommon to the seeds of desert species.

We have evidence for the presence of this inhibitor but as yet are uncertain as to whether it is present in the seed or in the husk. Characteristically, seeds which are moistened excessively do not germinate but develop an extremely unpleasant acetamide-like odour.

Observations under desert conditions therefore lead us to conclude that seeds will germinate only under conditions of sudden and sufficient rainfall. The presumed inhibitor must be leached out of the seed as well as out of reach of the developing rootlet. The sand below the leaves of the *Welwitschia* is usually cool and moist since much of the condensate from the fog runs down the leaf and onto the sand, but no seedlings have ever been observed near the parent plant. In fact, in three years only one very young plant, itself about three years old, has been found in the Namib. The inference is that either the parent plant exudes, or has leached from it, substances toxic or inhibitory to the germination of seeds and the establishment of seedlings, or that moisture in the form of condensate is available only to leach out a limited quantity of inhibitor from the seed itself, just sufficient to prevent subsequent root growth and development.

Most of the seeds which are shed from the mature megastrobili fall within a radius of about 2 m of the plant. A female plant of average size may bear from 70 to 100 or more cones, so that eventually up to 10 000 or more seeds may be dispersed around the plant. Assuming that 50 per cent of these seeds are fertile and that 80 per cent of the fertile seeds are infected with *Aspergillus niger,* at least 1 000 or 10 per cent of the total seed-crop theoretically is germinable. However, it is doubted that one-hundreth of one per cent of all the seed produced ultimately germinates and develops into mature plants.

Under laboratory conditions (30°C) seeds germinate within 48 hours and root growth proceeds at rates of up to 1,5 mm per hour. Figure 8 shows two seedlings whose cotyledons are at different stages of development. The cotyledons are photosynthetic organs and remain so, even after they are surpassed in growth by the two true leaves which develop much later. Seedlings are difficult to raise from embryo cultures (Fig. 9) which indicates that there might be growth factors other than those contained in conventional tissue culture media which are specific for optimum growth. Nevertheless, embryo cultures are provinding useful material for the study of respiratory activity in the various plant parts.

The root cap is extensive and in a developing root has a telescopically-layered appearance. The extent of the root cap and its relationship to the cortex is shown in Figure 10, a transverse section through the root tip about 1,0 mm from the apex.

At the ultrastructural level the cells of the root and particularly those of the root cap give evidence of great physiological and metabolic activity. These cells (Fig. 11) have numerous starch-storing plastids (A) in various stages of apparent breakdown, and dictyosomes (D) from the membranous plates of which vesicles (V) in different stages of development appear to be budding off. The root tip and rootcap cells are highly osmiophilic and fats and oil droplets (F, G) seem to form important fractions of the total cellular constituents. The relationships between cellular structure, organelle activity and respiratory activity of the root are presently under study.

Leaf characteristics.

Rodin (1958) has reported comprehensively on the anatomy of the developing leaf of *Welwitschia.* There are, however, further aspects that warrant closer scrutiny. The leaves are generally broad, flat and coriaceous, and they are probably the longest-lived in the plant kingdom. The broadest unbroken leaf found on a plant on the Fläche, measured 179 cm. At one point the stem of this plant had become invaginated and the leaf had split, leaving a remnant 17,7 cm wide, thus giving a total leaf width of 193 cm. This particular leaf was 6 m long of which 3,15 m were living tissue. Dimensions of leaves such as these and others, which although split and twisted are equally immense, give an indication of the extensive surface areas of these desert plants. Calculations of the leaf surface area on one plant showed that up to 22,7 x 10^3 cm^2 of tissue were exposed to the wide range of conditions of temperature and moisture on the Fläche. Leaf growth rates of 50 plants recorded over a two-year period averaged 13,8 cm per year. It can be estimated that one *Welwitschia* plant could therefore produce up to 150 m of leaf tissue over a growth period of 1 000 years.

Figure 12 shows some of the cell types of which the leaf is composed. The adult leaves have bilateral symmetry and on average are 1,4 mm thick. The bottle-shaped epidermal cells (A, B) are surfaced by a three-layered cuticle about 20 μ thick. The epidermis itself is composed of a single layer of polygonal cells, each cell approximately 45 x 24 μm. Stomata, surprisingly, are very numerous. On the adaxial surface there are approximately 14 stomata per 100 epidermal cells as compared with 20 per 100 abaxially. Careful counts have shown that there are about 24 000 stomata per cm^2. The stomata are sunken but only to a depth corresponding to less than the length of one epidermal cell, namely approximately 37 μm.

A characteristic feature of the leaf is the number of massive sclereids (C); these are distinctively ramified, crystalliferous cells. Their function is mechanical and since they are frequently situated below the stomata, their presence is probably responsible for an increased internal volume in the immediate vicinity of the pore. This would be an important factor in gas exchange between the plant and the atmosphere. The palisade cells (D) are up to 75 μm long and make up three to four layers of irregularly arranged columnar cells. Sclerenchymatous fibres (E) occur in large bundles and are probably the single most important structural cell type of this leaf. Transfusion tracheids (F), with reticulate or scalariform secondary thickening, surround the vascular bundles with their prominent vessels (G), the presence of which distinguishes *Welwitschia* from other members of the Gymnospermae which lack vessels.

Figure 13 is a phase contrast photomicrograph of a transverse section of the adaxial surface of a *Welwitschia* leaf. Note the massive sclereid with crystals embedded in its walls lying amongst the long, tapering palisade parenchyma, and the substomatal cavity. Two bundles of thick-walled fibres, of which the lumina are virtually obliterated, are seen in transverse section.

Figure 14 is a scanning electron micrograph showing the topography of the adaxial surface of a *Welwitschia* leaf. The difference in structure (or composition) between the cuticles overlying the epidermal cells and the guard cells is apparent. The cuticle of the epidermal cells is loosely granular, whereas that of the guard cells appears compact, probably as a result of suberization. By comparison, the leaf of *Nerium oleander* is strikingly more xeromorphic in appearance than that of *Welwitschia.*

It seems evident that the architectural anatomy of the leaf is such that optimal properties of both rigidity and flexibility result. The leaf is sufficiently rigid to grow out in a curve of considerable length before touching and eventually lying on the sand surface. The protoplasts of the cells of that part of the leaf in contact with the ground are denatured by the high surface temperatures which prevail and the leaf tips consequently wither and are frayed from being scoured on the gravel by winds. However, even under gale force conditions, the living part of the leaf, particularly a broad leaf, remains remarkably rigid and immobile. It is suggested that the splitting and tearing of these leaves is the result not so much of wind action than of differential pressures caused by unequal growth of the meristematic terminal groove of the stem which gives rise to the leaf.

Absorption of water through the stomata must be regarded as probable, until evidence to the contrary is produced. The stomata remain open until the fog has lifted and, although much of the condensate runs off, the direct uptake of a proportion of this water cannot be discounted.

Finally, one is tempted to conclude that *Welwitschia* has more outstandingly mesomorphic than xeromorphic characteristics, and that its adaption to this narrow fog fringe has ensured this species' survival. Further north *Welwitschia* does grow beyond the fogbelt but under conditions which normally support a savannah-like vegetation.

Figures 15 and 16 are of paintings of various plant parts at different stages of development and are to a large extent self explantory. Details are enlarged on in the appropriate legends.

SUMMARY

Certain aspects of the growth habit and other characteristics of *Welwitschia* have been reported on. These have been based largely on observations and measurements in the field as well as on laboratory work with seeds and seedlings. This species has a capacity for producing vast numbers of seeds, of which only about 10 per cent are germinable. Germination and seedling establishment on the Welwitschia Fläche call for special conditions of rainfall, sufficient to remove an inhibitor (presumbaly endogenous) and, once the seed has germinated, to provide adequately for seedling establishment. The successful establishment of *Welwitschia* communities would appear to be related to chance rain showers occurring in close sequence in localized areas.

The Namib fog appears to be a very important source of moisture and the leaf anatomy suggests that the uptake of water by the leaf is probably an important survival factor.

Serious doubts have been expressed as to whether *Welwitschia* is not perhaps facing extinction. Considered against this plant's longevity and remarkable adaption to its environment there should be no reason for concern. It is proper, though, that this plant be afforded the National protection it deserves, and in this respect it is extremely gratifying to know that the Welwitschia Fläche, where the oldest and largest plants occur, has now been incorporated into the Namib Desert Park.

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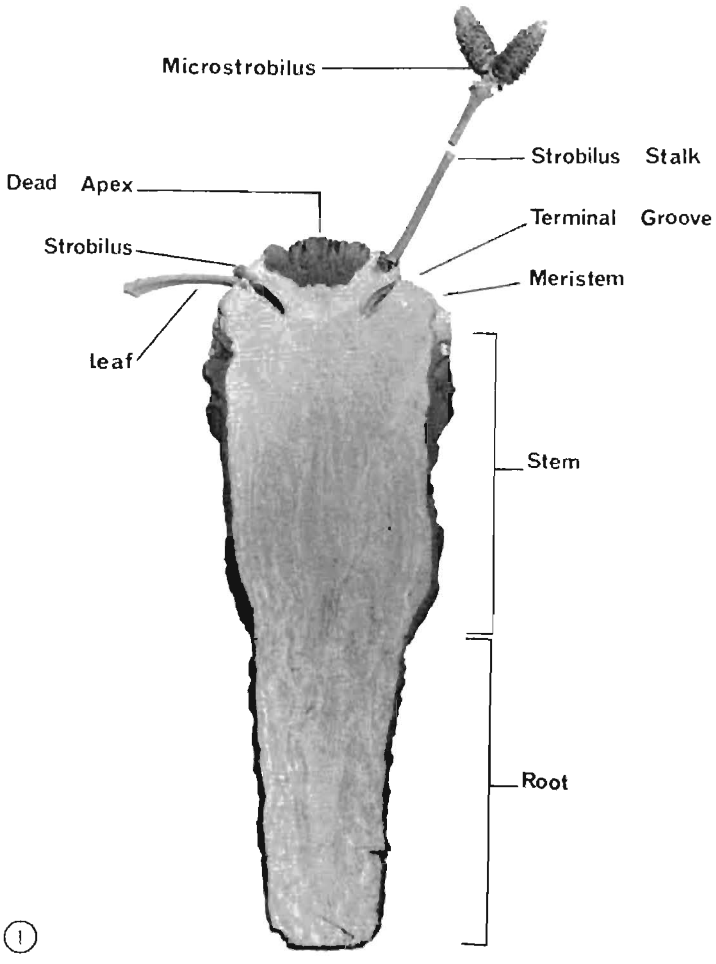


Figure 1. Longitudinal section through a young plant showing insertion of leaf and strobilus into stem, and the relation of stem to root. Part of the root has been removed. Note the dead apex, and terminal groove from the base of which the meristem of the leaf base perpetuates growth as well as photosynthetic tissue.

Figure 2. Pforte Giant. Megasporangiate *Welwitschia*, growing near the road to Jakkalswater on the Welwitschia Fläche. The circumference at the base of the leaves of this 1,2 m tall plant is 8,7 m. It is one of the largest living specimens. Note the Marmor Pforte in the background.

Figure 3. A very large microsporangiate plant growing on the gravel Fläche. The immense leaf surface area can be clearly appreciated from this photograph.

Figure 4. Megastrobili with droplets exuding from the tips of the megasporophylls. The rose-tinged megastrobili are at the stage where the megagametophytes are filling out. This is a particularly sensitive stage in development because a sucking insect, *Probergrothius sexpunctatis,* punctures the ovules as its proboscis probes the phloem of the megastrobilus stalk, and in the process introduces an aspergillus fungus which infects the seed.

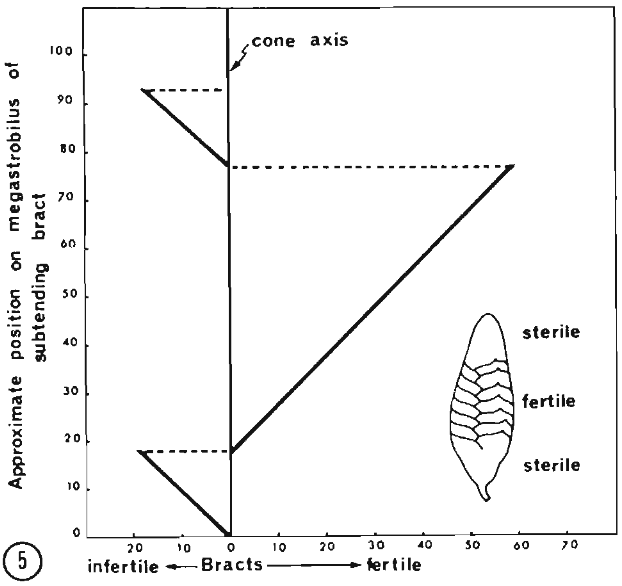


Figure 5. A graph which depicts the distribution of fertile and sterile megasporophylls (bracts or cone scales) on the cone or megastrobilus. The largest proportion of fertile bracts are found from about position 20 to 80 on the cone axis; in other words, approximately 60% are fertile. The figures are the means of counts made of 100 randomly selected cones.

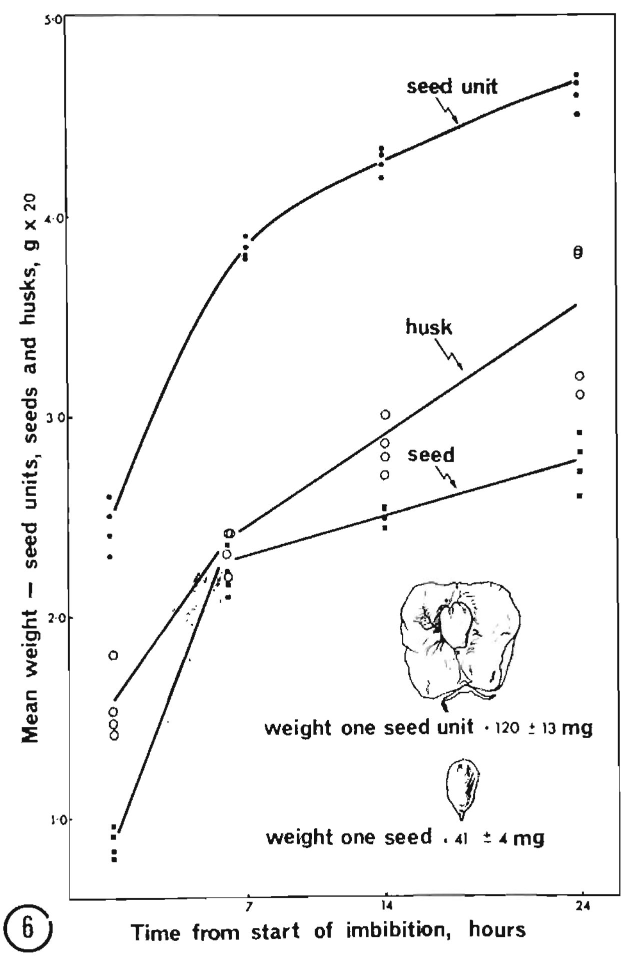


Figure 6. Curves to show the relative amounts of water imbibed over a 24-hour period. The greatest amount of water is taken up by the seed within 7 hours. Note that the seed weighs approximately one third as much as the seed unit, and that the husk has a greater capacity for water uptake over a longer period of time.

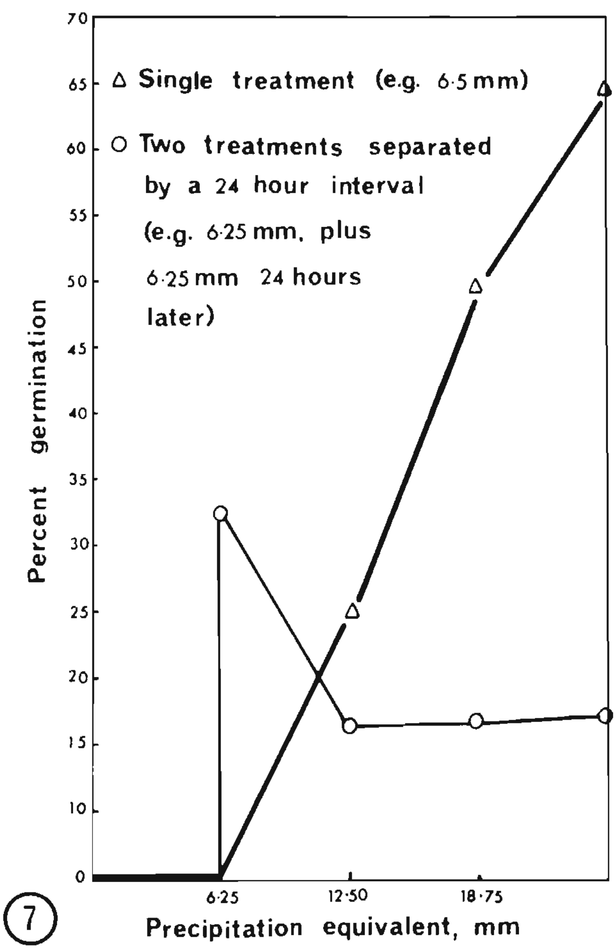


Figure 7. Germination response to precipitation from 6,25—25 mm is virtually linear. In excess of 25 mm the seeds tended to rot. Two 6,25 mm treatments separated by 24 hours, produced a better germination response than 12,50 mm at one time.

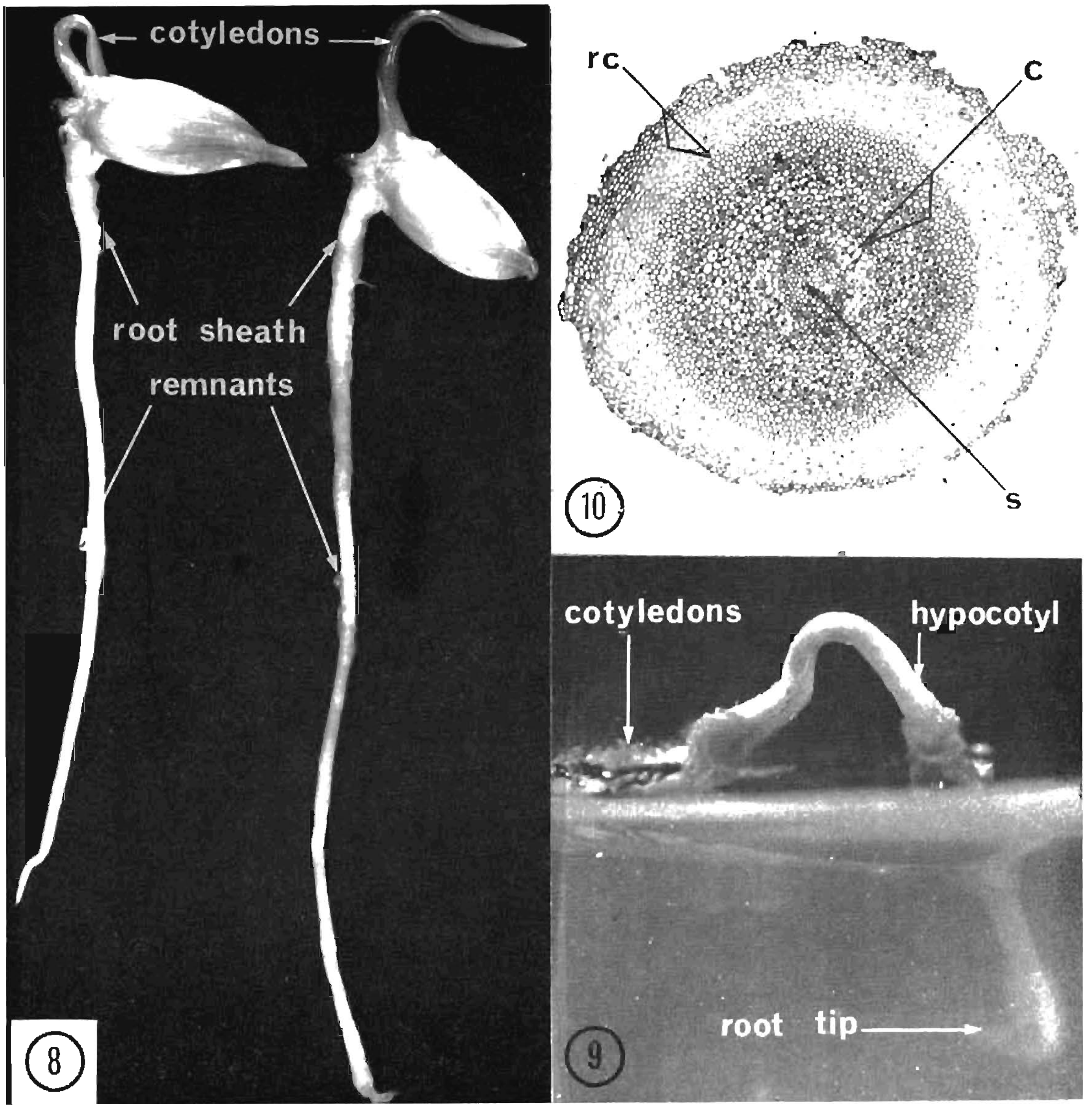


Figure 8—10. Seedling development. Fig. 8. Young seedlings, life size, 6 and 7 days after germination at 30°C. Cotyledons are seen gradually unfolding. Rate of root growth is extremely rapid. Note the root apex well-protected by the rootcap or sheath.

Figure 9. *Welwitschia* embryo cultured on agar containing White's medium, 7 days after transfer. Under these conditions there is extensive development of the hypocotyl.

Figure 10. Transverse section through the root tip showing an extensive root cap (rc), cortex (c), and stele (s). Note the solubilized cell walls in the root cap (x75).

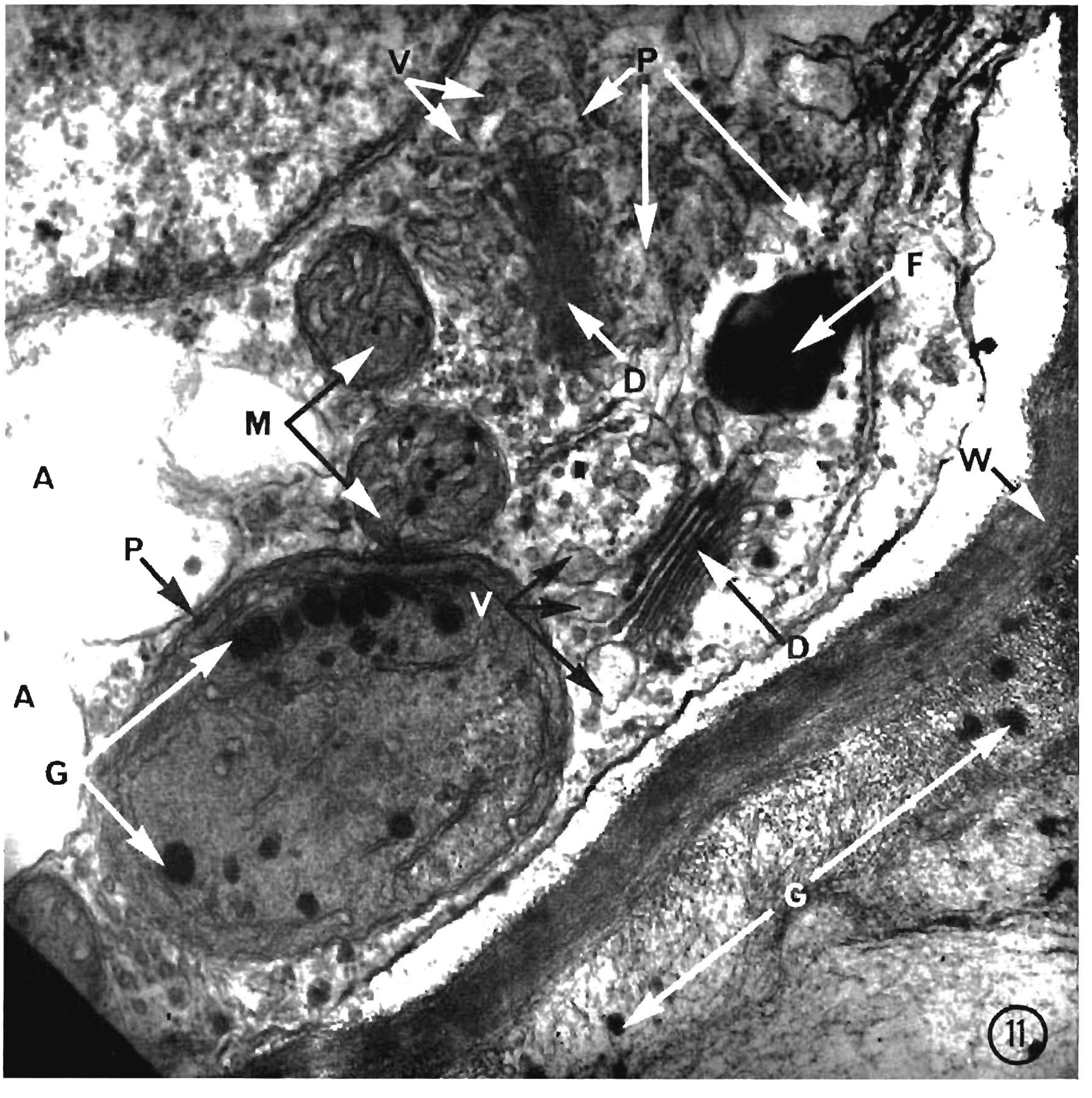


Figure 11. Electron micrograph of rootcap cell. Dictyosomes (D) are numerous with many vesicles (V) in various stages of dispersal. Osmiophilic globules (G) probably indicate fat-rich droplets. Plastids (P), amyloplasts (A) and mitochondria (M) also are numerous. Fat droplets (F) and the cell wall (W) are also indicated (x45 900).

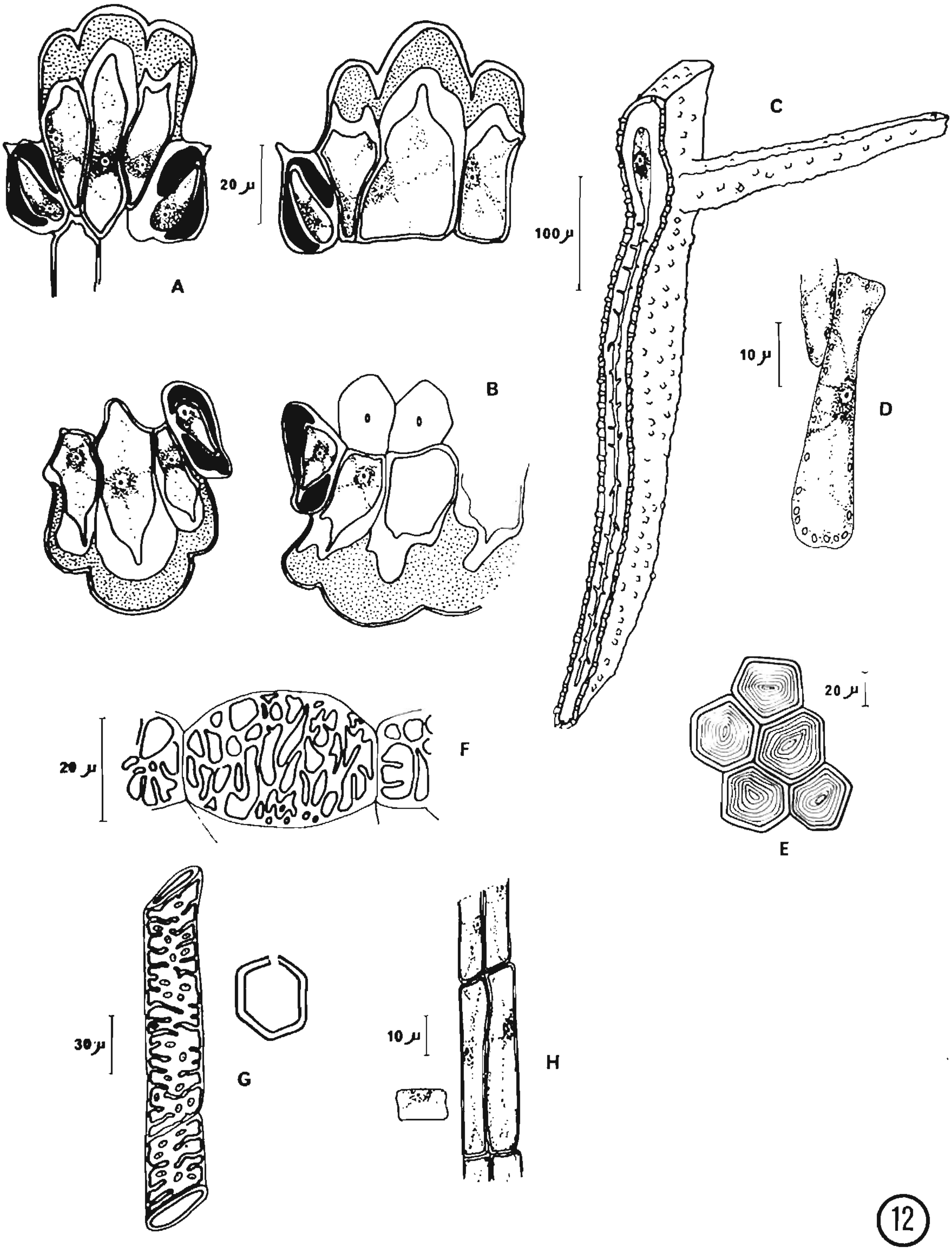
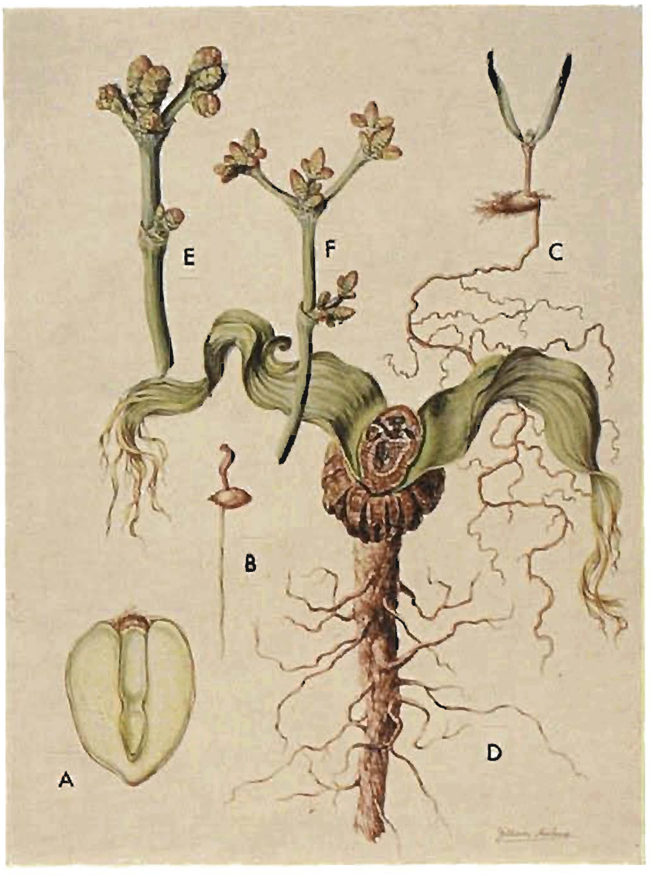


Figure 12. Cells of the leaf. A, B. Bottle-shaped adaxial and abaxial epidermal cells, respectively, showing stomata and guard cells. Note the triple-layered cuticle, the centre layer of which is crystalline. C. A massive sclereid: a cell type which is very common and most frequently found immediately below the epidermis, embedded between palisade parenchyma and often protruding into the sub-stomatal cavities. D. Palisade parenchyma: long cells containing 20—30 chloroplasts. E. Transverse section of sclerenchyma fibres. F. A transfusion tracheid: these cells surround the vascular bundles and probably play a rôle in water transport. G. Vessel element: a type of water-conducting xylem cell common in the angiosperms but not found in other gymnosperms. H. Phloem or sieve cells.

Figure 13. Phase-contrast photomicrograph showing a transverse section of part of the adaxial side of a leaf. Note the massive sclereid situated in a substomatal cavity. The stoma is closed and the heavily cuticularized subsidiary cells nearly meet, thus reducing the movement of water vapour through stomatal evaporation. Nuclei are prominent in the palisade parenchyma. Sclerenchyma fibres are also seen.

Figure 14. Scanning electron micrograph of part of the adaxial leaf surface showing a depressed stoma with its pore and thickly cuticularized guard cells. The ridges on the adjoining cells correspond to bulges of the cuticle over the necks of the bottle-shaped epidermal cells.



Figures 15—16. Paintings showing various parts of the *Welwitschia* plant. Fig. 15. A. Seed with embryo consisting of cotyledons and hypocotyl-root axis, embedded in nutritive tissue. B. Five-day-old seedling. C. Sixty-day-old seedling. Cotyledons are now the photosynthetic organs, the young leaves just emerging and the remnants of the seed still attached. D. A five-year-old plant with two strap-shaped leaves arising from a terminal groove at the apex of the stem. A scar of a previous micro- or megastrobilus stalk is visible. Note the taproot with its many lateral roots. The stem is protected by a well developed periderm. E, F. Young mega- and microstrobili, respectively.

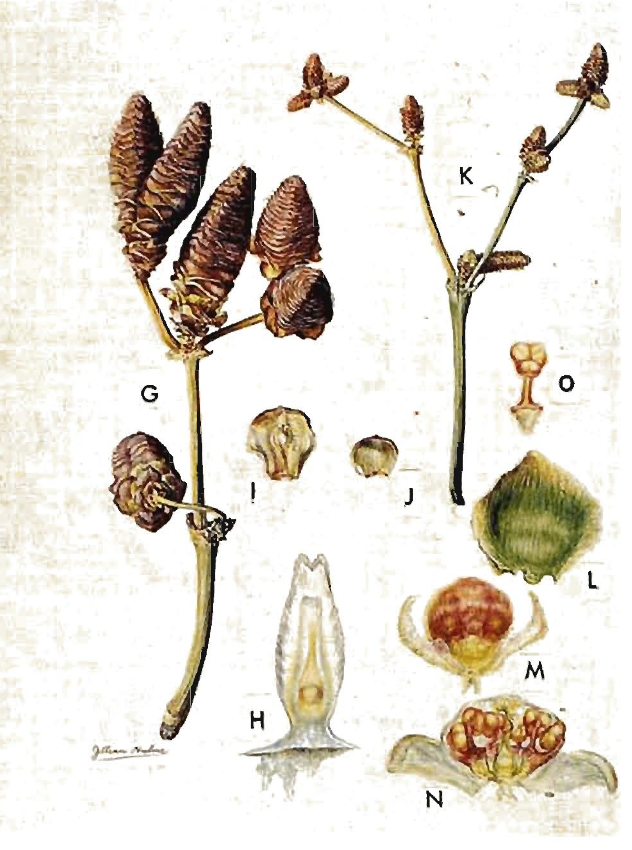


Figure 16. G. Mature megastrobili. Note that the megasporophylls are arranged in opposite, decussate pairs. H. A female flower with nucellus, outer and inner integuments. I. Subtending bract or megasporophyll, each one bearing a single ovule or flower on its upper surface. The outer integument is expanded to form a broad wing. The seed is mature. J. A small sterile megasporophyll or bract from the base of the megastrobilus. K. Mature microstrobili. L. The microsporophyll or bract which protects the male flower. M. The male flower is enclosed within a perianth. Note the lateral bracts. N. The perianth, formed from two bract-like structures, is opened to show two of the six anthers and an aborted pistil of which the ovary contains a single, sterile ovule; also a spirally curved style and a broad, flaring stigma. O. Sporangium, or anther and filament.