

Welwitschia mirabilis: structural and functional anomalies

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ABSTRACT

Welwitschia mirabilis displays certain morphological and physiological features that may be regarded as either gymnospermous or angiospermous. It appears to be a C3/CAM plant, the CAM pathway of photosynthetic CO₂ fixation probably having evolved in order to adapt to the extremes of the Namib Desert habitat. The apparent ability to switch from C3 to CAM suggests that *Welwitschia* originated during a time when more favourable climatic conditions prevailed. And this raises a question: is the Namib Desert not a comparatively young desert? Seen *in toto*, the many anomalies (eg. gymnospermlike sieve cells, megastrobili, naked-seededness; angiospermlike vessel elements, microstrobili, CAM, mode of chlorophyll formation) confirm the viewpoint that *Welwitschia* represents an extremely specialized endpoint in plant evolution and that it is not closely related to any extant gymnosperm or angiosperm.

1. INTRODUCTION

Welwitschia mirabilis, monogeneric, monospecific Namib Desert endemic, is considered to be a gymnosperm (Foster and Gifford, 1959) although the patristic relationship with other taxa in this classis is not clear. Even the degree — if any — of cladistic relationship with *Ephedra* and *Gnetum* with which it is grouped in the Gnetales, is obscure. There is a lack of fossil evidence to clarify the latter relationship. The position of *Welwitschia* in the hierarchy of the plant kingdom therefore remains tenuous (Benson, 1971) and recent morphological, anatomical, physiological and biochemical investigations (Bornman *et al.*, 1972, 1973, 1974, 1976; Dittrich and Huber, 1974; Evert *et al.*, 1973; Schulze *et al.*, 1976; Senger and Bornman, 1976; Whatley, 1975) have revealed further anomalous features without really contributing to a clarification of its taxonomic status.

In a part of the central Namib, *Welwitschia* can be found growing over at least an 150 km west-east transect ranging from coastal lichen desert through full desert and grassland scrub-desert to grassland-savanna. A community comprising numerous, large, presumably old and visually vigorous specimens, occurs in the full desert of the *Welwitschia* Flats at the confluence of the Khan and Swakop rivers, within the ambit of the coastal fog. This remarkable long-lived, large-leaved plant lacks many of the xeromorphic features that characterize most of the species with which it shares its biome. The range of *Welwitschia's* phenotypic plasticity must be regarded as narrow; the geographically-confined desert habitat probably limits the effects that environmental factors otherwise might be expected to have.

This brief review notes and considers those features,

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primitive, advanced and unusual, that accord this aberrant member of Africa's flora its degree of anomalouslyness.

2 MATERIALS AND METHODS

Leaf and cotyledonary material were collected from field- and greenhouse-grown plants and prepared for light and electron microscopy as reported earlier (Evert *et al.*, 1973).

3 OBSERVATIONS AND DISCUSSION

3.1 Morphological anomalies

Welwitschia mirabilis is an acephalous plant, its shoot apex becoming overgrown and obliterated by tissue of the developing stem shortly after germination, resulting in the closed system of its growth.

The leaf is the longest-lived in the plant kingdom. It possesses a basal or intercalary meristem and is parallelveined, features common also to the Monocotyledoneae; it is isolateral and amphistomatic. The origin of the stomata is syndetochelic (the subsidiary cells deriving from the same protodermal cell as the guard-cell mother cell), whereas commonly in the gymnosperms the stomatal type is haplochelic (the subsidiary cells are not related to the guard cells). For a desert — or any — species, the number of stomata, which occur in about equal numbers ab- and adaxially, is exceedingly great (Bornman *et al.*, 1972). The cotyledons live and remain photosynthetic for approximately one to two years.

Transfusion tracheids abound in the leaf, ensheathing each vascular bundle and, joined end to end, running the length of it. This specialized conducting tissue also occurs in the stem and root.

Like other Gymnospermae the phloem tissue comprises sieve cells, albuminous cells and parenchyma (Evert *et al.*, 1973). However, unlike other Gymnospermae, *Welwitschia* (as well as *Ephedra* and *Gnetum*) has xylem tissue typical of the Angiospermae.

3.2 Reproductive anomalies

The seeds are borne naked on scales, deriving from a single terminal ovule on a megastrobilus or cone, in other words they are gymnosperm-like. The embryo is embedded in a nutritive gametophytic tissue (Bornman *et al.*, 1976). The male reproductive structure is a pseudo-hermaphroditic flower consisting of six stamens each with a trilobular anther and an aborted pistil, in other words angio-

sperm-like. Unlike any other known plant, fertilization occurs in the pollen tube rather than in the embryo sac or archegonium. The embryo, upon germination, develops a non-vascularized foot-like protuberance reminiscent of that of the pteridophyte *Selaginella*. This protuberance has been shown to have an haustorial function (Butler, 1976). A similar structure, but vascularized, also occurs in *Gnetum*.

3.3 Physiological and biochemical anomalies

3.3.1 Photosynthetic pathways

There probably are a number of pathways by which photosynthetic carbon dioxide (CO₂) fixation is accomplished but three of them are becoming better understood. Firstly, in most plants the first stable product of CO₂-fixation is 3-phosphoglycerate (3-PGA); and since it is a 3C-compound, the plants in which this form of fixation occurs, are known as C3-plants. In many tropical species, especially in the panicoid grasses, the primary fixation product is the 4C-organic acid oxalacetate (OAA). Plants with this type of fixation are termed C4-plants. In the third case, many succulent species, particularly those belonging to the Crassulaceae, Cactaceae and Euphorbiaceae, and plants that occupy an arid biome, open their stomata during the night, take in CO₂ and fix it into OAA which is subsequently converted to malate, isocitrate and other organic acids. During the day when these plants close their stomata, CO₂ is released from the oxidation of these acids and used immediately for photosynthetic carbon reduction. Such plants are said to have a Crassulacean acid metabolism and are referred to simply as CAM-plants.

3.3.2 Ecological adaptations

The CAM type of photosynthetic carbon metabolism is an adaptation that allows efficient utilization of water. Cool night conditions, as often occur in the Namib, are not conducive to transpiration; and during hot day conditions the stomata of CAM-plants remain closed. As a consequence, the ratio of transpiration to photosynthesis is low and such plants can photosynthesize and conserve over long periods the water they store in their fleshy leaves and stems (Ray, 1972). This would appear to be the kind of adaptation that would suit perennial, drought-tolerant desert species (possibly *Hoodia* and *Sarcocaulon* — Schulze and Schulze, 1976) very well. However, neither in aspect nor in internal structure does *Welwitschia* even remotely resemble the typical succulent. Also, *Welwitschia* may open its stomata during the day, but only during the early and mid-morning periods when this coincides with the incident fog (Bornman *et al.*, 1972).

The leaves of C4-plants usually have the so-called Kranz anatomy, that is, a distinct bundle sheath

parenchyma surrounding the vascular tissue, the chloroplasts of which differ in size and structure from those of the adjoining mesophyll parenchyma. C4-plants furthermore have a very low CO₂ compensation point, which means a larger potential for CO₂ uptake. Under conditions of stress a C4-plant uses water more efficiently relative to its photosynthetic capacity than does a C3-plant with its high CO₂ compensation point. Also, in contrast to C3-plants, C4-plants lack (or have a greatly diminished) photorespiration, which means that photosynthetically-fixed CO₂ is not released and wasted. The latter are much more efficient in production of photosynthate than C3-plants at high light intensities and high temperatures or at low CO₂ concentrations. In fact, their photosynthetic temperature optimum is above 30°C, a temperature at which C3-plants are completely inactive photosynthetically. A C4-type of photosynthetic metabolism would thus appear to be an advantage in a desert environment with its high temperatures and light intensities, especially to annual, rapidly-growing, drought-escaping grasses such as for example *Stipagrostis namibensis*.

The vascular bundles in the leaf of *Welwitschia* are not surrounded by a bundle sheath of parenchyma as is the case for example in the C4-grass *Setaria* (Figure 1), but instead by well-developed transfusion tracheids (Figure 2). The cotyledonary leaves — which have a short life expectancy — also do not possess a distinct bundle sheath (Figure 3). Whatley (1975) recently reported the occurrence of a peripheral reticulum in chloroplasts of *Welwitschia*, a feature once thought to be confined to C4-plants but which, it appears, also occurs in certain CAM-plants as well as in C3-plants. A peripheral reticulum therefore does not seem to be the sole prerogative of a C4-plants' plastid. Whatley makes the interesting suggestion that the peripheral reticulum in *Welwitschia*'s chloroplasts presupposes that this feature was available to chloroplasts prior to angiosperm evolution (and by implication prior to C4 and CAM evolution). It is a pity that because of a lack of material, Whatley's observations were based only on the cotyledon which, in relation to this plant's life-span, hardly has any relevance at all as a photosynthetic organ.

Figures 4 and 5 are electron micrographs showing details of mesophyll parenchyma cells approximately midway between two vascular bundles and adjacent to a vascular bundle, respectively. In the latter case, the mesophyll cell adjoins a differentiating transfusion tracheid. Obviously, a much more detailed study is required to ascertain with certainty whether qualitative and quantitative differences exist between the cellular inclusions of the mesophyll cells relative to the position of the latter in the leaf. However, Figures 4 and 5 would suggest that the chloroplasts (Ch) possess morphological similarity. Even chloroplasts in *Welwitschia* callus cultures appear similar in size and shape to those shown here.

C3-plants that are found in the Namib Desert habitat (see Schulze *et al.*, 1976) are either ephemeral or have developed drought-evading

morphological and anatomical features. The latter include the ability to reduce surface area either by the folding or abscising of leaves. In addition, such plants usually have thick cuticles and few, deeply-sunken, abaxially-occurring stomata. Some species are aphyllous or possess greatly reduced leaves.

3.3.3 ¹³C: ¹²C Ratios

It is to be expected that C3-, C4- and CAM-plants would reflect in their biochemical activities the diversity that is characteristic of their form, structure and other functions. For example C3-plants should have a preponderance of RuDP-carboxylase, the enzyme that fixes CO₂ to ribulose-diphosphate in the Calvin (C3) cycle. Likewise, PEP-carboxylase, Malic enzyme, NADP-malate dehydrogenase and NAD-Malate dehydrogenase could be expected to occur in C4- and CAM-plants in various amounts and proportions.

Dittrich and Huber (1974), ruling out the possibility of C4 metabolism because of the lack of Kranz anatomy, investigated CO₂-fixation in the three genera of the Gnetales and found that *Welwitschia mirabilis* contained substantial activities of PEP-carboxylase, malic enzyme and NADP-malate dehydrogenase. In contrast *Ephedra gerardiana* and *Gnetum gnemon* apparently do not possess the necessary set of enzymes for CAM. They concluded that *Welwitschia* "clearly exhibited" Crassulacean acid metabolism and is therefore the most primitive CAM-plant known.

The CO₂ fixed in photosynthesis can incorporate in photosynthates either the radioactive isotope ¹⁴C (used experimentally) or the stable isotopes ¹²C and ¹³C, the latter which occur in atmospheric CO₂ in the ratio of 98,89%¹²C: 1,11%¹³C, respectively. As explained simply and elegantly by Osmund and Ziegler (1975), some plants incorporate a slightly higher proportion of ¹³C than ¹²C into sugars during photosynthesis. These are so-called *heavy* plants; others that incorporate a lower proportion are *light* plants. A value, the δ¹³C value⁸, has been established to measure the amount of ¹³C taken up relative to ¹²C during photosynthesis. Smith and Epstein (1971) determined δ¹³C values for plant tissue from 104 species (60 families) and *inter alia* grouped them into two categories: those with low δ¹³C values (−24 to −34‰) and those with high δ¹³C values (−6 to 19‰). *Welwitschia* was the only gymnosperm with a high δ¹³C value, namely −14,4‰ (see Table I).

Carbon isotopic ratio determinations have an important predictive significance. It appears, as a general rule, that plants with enriched δ¹³C values are C4-plants and those with low values are C3-plants. CAM-plants occupy a more or less intermediate range. The value for *Welwitschia* quoted above (−14,4‰) would immediately suggest that this plant's photosynthetic metabolism is that of a C4-plant. However, Schulze *et al.* (1976) recorded in the Namib a range of values for *Welwitschia* from −17,39 to −23,31‰ (Table 1). Interestingly, they found no variation in δ¹³C values over the

length of the leaf, but a considerable variation in the leaves of plants depending upon their habitat.

$$\delta^{13}\text{C}^0_{\text{‰}} = \frac{^{13}\text{C}}{^{12}\text{C}} \frac{^{12}\text{C}}{^{13}\text{C}} \frac{\text{Sample}}{\text{Reference}} - 1 \times 1000$$

(See Smith and Epstein, 1971, for explanation.)

Plants on the coastal gravel plain yielded higher values than those growing in the grassland-savanna. Schulze *et al.* concluded that *Welwitschia* with a less negative $\delta^{13}\text{C}$ value than C3-species and a more negative $\delta^{13}\text{C}$ value than C4-species, assimilates CO_2 partially via the CAM pathway. At least, *Welwitschia* appears to have the ability to alternate between CAM- and C3-metabolism depending upon environmental conditions.

3.3.4 Chlorophyll formation and distribution

Senger and Bornman (1976) recently ascertained that the mode of light-dependent chlorophyll formation in *Welwitschia* is typical of that in the Angiospermae and not of that in the Gymnospermae which, except for *Cycas* and *Ginkgo*, form chlorophyll in the dark. Ratios of chlorophylls a:b are much lower in desert-growing plants than in greenhouse-grown seedlings and plants. However, no significant differences in the *in vivo* spectra of chlorophylls between *Welwitschia* and other plants were detected and on this basis no taxonomic inferences could be drawn.

3.3.5 Uptake and movement of tritiated water

Bornman *et al.* (1973) reported that *Welwitschia* could absorb and transport the water which condensed on its leaves during the fog. They compared rates of uptake of tritiated water under conditions of fog and föhn and suggested that the stomata might be the path of entry. It appeared, too, that water taken up by the leaf was transported preferentially in a proximal direction (away from the point of application in this case) towards the basal meristem. The mode of entry of at least some of the condensed fog is by no means clear. Dr W. Barthlott (Heidelberg, Germany) in a personal communication (1976) produced scanning electron microscopical evidence of adaxial cuticular depressions containing numerous micropores in the leaf of *Welwitschia*. Might water be absorbed through the cuticle? However, if water is able to enter the leaf via these cuticular interruptions there seems to be no reason why it should not also be lost similarly.

4 CONCLUSION

It has come to be assumed that C3— or Calvin cycle photosynthesis is the ancestral condition and therefore associated with primitive plants. Such plants typically lack the Kranz syndrome. Likewise, the C4— or Hatch-Slack type of photosynthetic carbon dioxide fixation appears to be an evolved condition, associated in particular with members of the grass

family. Such plants typically possess the Kranz syndrome and respond well to environmental conditions of high temperatures and light intensities. CAM photosynthesis appears to be the prerogative of succulent plants, many of which inhabit arid areas. It is regarded as a derived or advanced condition, although it has not been found in the grasses.

Welwitschia mirabilis, a non-Kranz plant, with both primitive and advanced morphological, anatomical and reproductive features, seems to reflect an equal physiological diversity: chlorophyll formation is light-dependent as is the case in the angiosperms; of all the gymnosperms it appears to have the least negative $\delta^{13}\text{C}$ value; and to date it is the most primitive plant in which CAM has been detected. Furthermore, it is not a typical succulent.

Further studies (CO_2 compensation point, post-illumination burst, oxygen effect on photosynthesis, etc.) are required to establish with certainty this plant's ability to switch from C3 to CAM, but it seems that *Welwitschia* evolved the CAM syndrome as a secondary physiological phenomenon in order to adapt to the climatic upheaval of progressively developing conditions of aridity. In this connection two questions can be raised: firstly, did *Welwitschia* not originate under more moderate temperate or tropical conditions; and, if this indeed was the case, is the Namib Desert, in contrast to the popularly held view, not a comparatively young desert?

The degree of anomalousness (summarized in Fig. 6) which is emerging in respect of *Welwitschia mirabilis* appears to underscore its defiance of being categorized as either gymnosperm or angiosperm, and places new emphasis on Foster's and Gifford's (1959) view that it be regarded rather as an extremely specialized endpoint in evolution which is not closely related to any extant gymnosperm or angiosperm.

5 ACKNOWLEDGEMENT

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Table 1. Isotope discrimination of some selected species.

Family	Plant	Photosynthesis	$\text{T}^{13}\text{C}^0/\text{‰}$	Reference
Gymnospermae	<i>Welwitschia mirabilis</i>	CAM/C3	–14,4	Smith, Epstein (1971)
Gymnospermae	<i>W. mirabilis</i> (coastal desert)	CAM/C3	–18,3 to –21,2	Schulze <i>et al</i> (1976)
Gymnospermae	<i>W. mirabilis</i> (grassland desert)	CAM/C3	–20,3 to –23,2	Schulze <i>et al</i> (1976)
Gymnospermae	<i>W. mirabilis</i> (grassland-savanna)	CAM/C3	–20,7 to –22,9	Schulze <i>et al</i> (1976)
Gymnospermae	<i>Ginkgo biloba</i>	C3	–25,6	Smith, Epstein (1971)
Gymnospermae	<i>Podocarpus elata</i>	C3	–26,6	Smith, Epstein (1971)
Gymnospermae	<i>Cycas revoluta</i>	C3	–27,0	Smith, Epstein (1971)
Gymnospermae	<i>Gnetum africanum</i>	C3	–30,2	Smith, Epstein (1971)
Gymnospermae	<i>Pinus halepensis</i>	C3	–30,8	Smith, Epstein (1971)
Gramineae	<i>Eragrostis nindensis</i>	C4	–12,6	Schulze <i>et al</i> (1976)
Gramineae	<i>Stipagrostis namibensis</i>	C4	–13,9	Schulze <i>et al</i> (1976)
Gramineae	<i>Saccharum sp.</i>	C4	–13,9	Smith, Epstein (1971)
Gramineae	<i>Zea mays</i>	C4	–14,0	Smith, Epstein (1971)
Asclepiadaceae	<i>Hoodia currori</i>	Succulent*	–11,7	Schulze <i>et al</i> (1976)
Zygophyllaceae	<i>Zygophyllum simplex</i>	Succulent*	–14,0	Schulze <i>et al</i> (1976)
Euphorbiaceae	<i>Euphorbia transvaalensis</i>	Succulent*	–15,4	Schulze <i>et al</i> (1976)
Amaranthaceae	<i>Arthraerua leubnitziae</i>	Aphyllous	–22,0	Schulze <i>et al</i> (1976)
Euphorbiaceae	<i>Euphorbia phylloclada</i>	Succulent*	–22,1	Schulze <i>et al</i> (1976)
Amaranthaceae	<i>Celosia spathulifolia</i>	C3	–22,3	Schulze <i>et al</i> (1976)
Zygophyllaceae	<i>Zygophyllum stapfii</i>	Succulent*	–22,3	Schulze <i>et al</i> (1976)

*CAM?

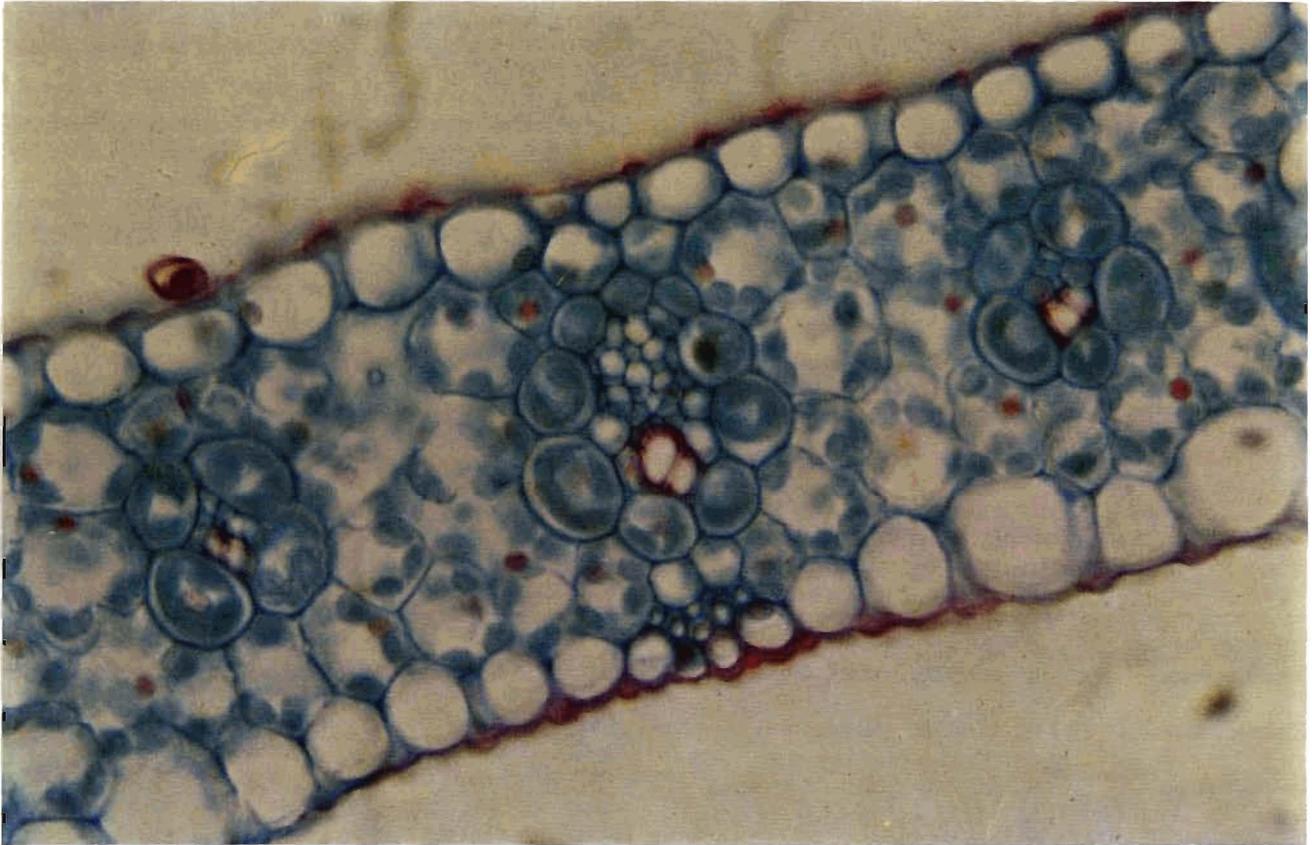


Plate 1. Transverse section of leaf of *Setaria* sp. showing three vascular bundles each surrounded by a distinct bundle sheath of large parenchyma cells, displaying the so-called Kranz syndrome. *Setaria* is a C4-plant. X200.

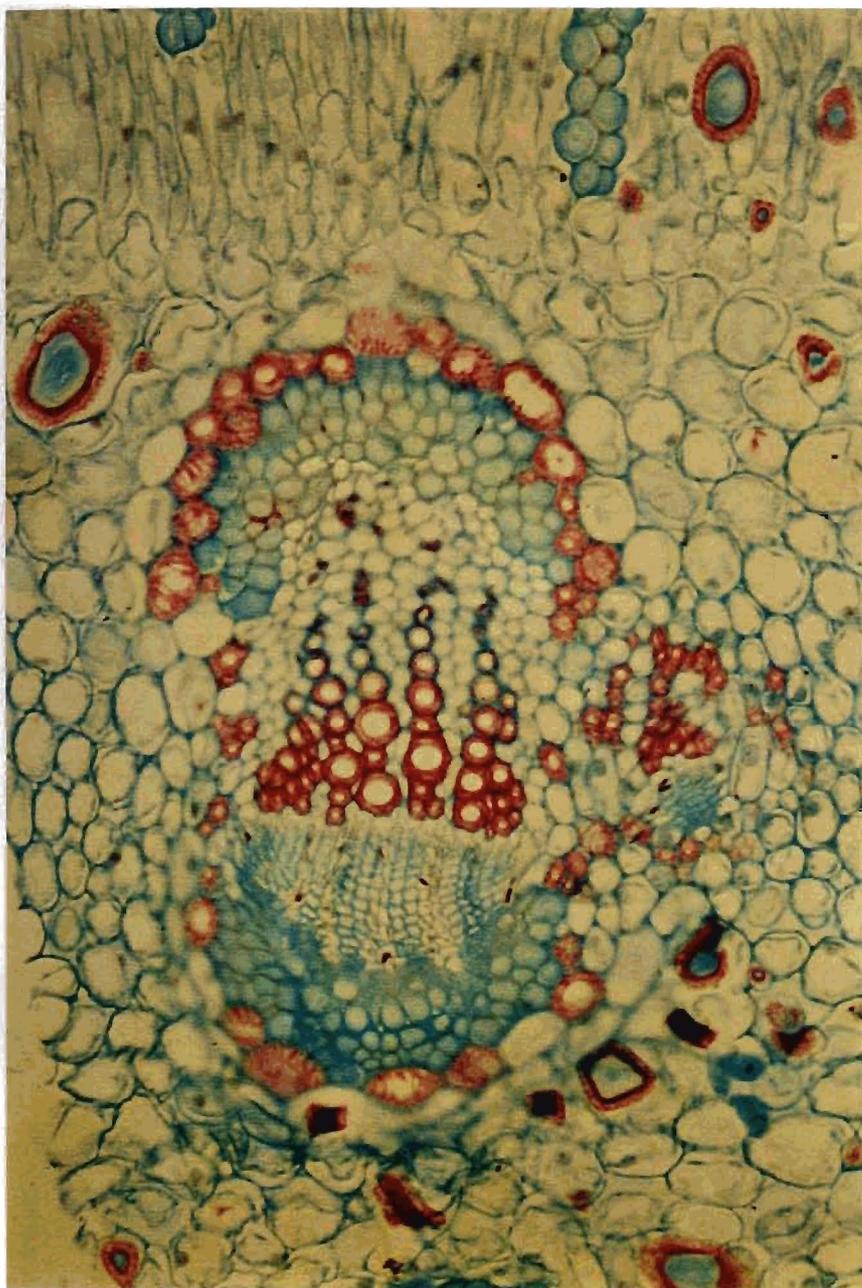


Plate 2. Vascular bundle of a 3-year-old leaf of a desert-growing *Welwitschia* plant. Note nearly complete ring of transfusion tracheids (red-staining, perforated cells) surrounding bundle that is capped ad- and abaxially with fibres. There is no bundle sheath.
X 50



Plate 3. Vascular bundle of a 1-year-old cotyledon of a desert-growing *Welwitschia* seedling. Note that the cotyledon is isobilateral and that spherical mesophyll cells vary in size, contrasting with elongated palisade parenchyma. There is no distinct bundle sheath. Differentiation of transfusion tracheids is already occurring.
X 50

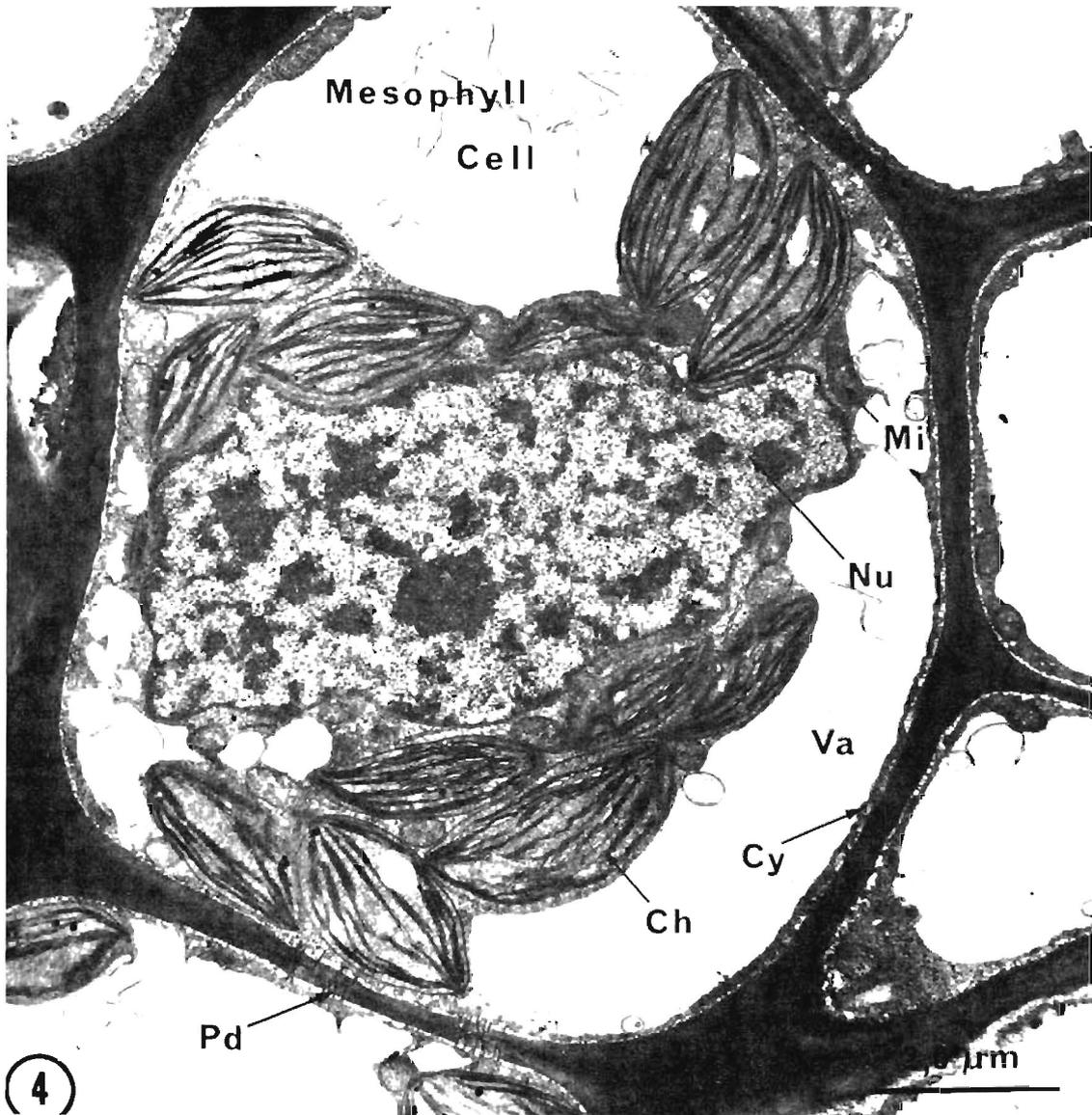


Plate 4. Mesophyll cell, approximately midway between two vascular bundles, in a three-year-old leaf of a desert-growing *Welwitschia* plant. Ch, chloroplast; Cy, cytoplasm; Mi, mitochondrion; Nu, nucleus; Pd, plasmodesmata; Va, vacuole.

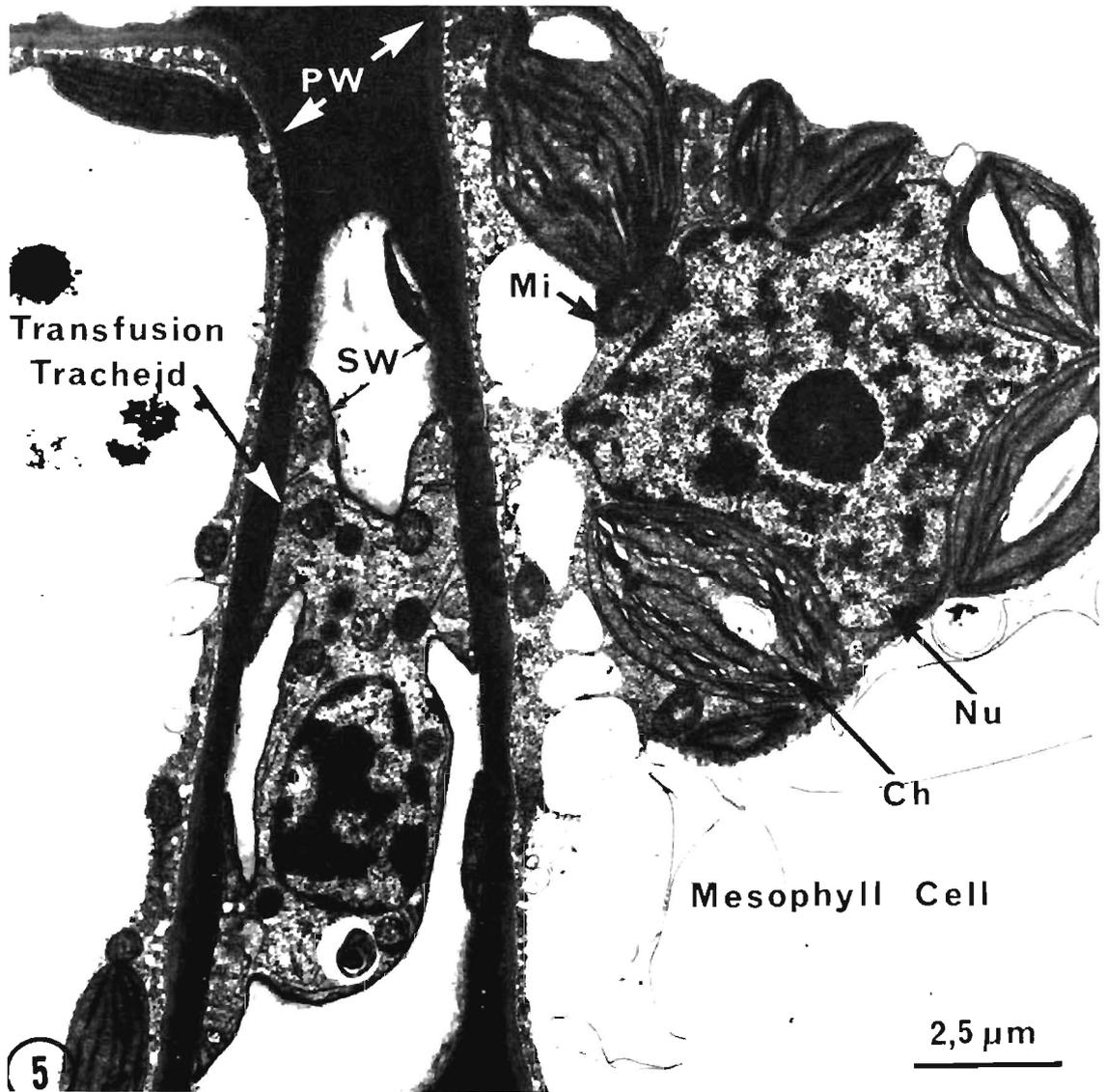


Plate 5. Detail same as in Figure 4, except that the mesophyll cell adjoins a differentiating transfusion tracheid to the inside of which (left) is a xylem parenchyma cell. Ch, chloroplast; Mi, mitochondrion; Nu, nucleus; PW, primary wall; SW, secondary wall.

WELWITSCHIA MIRABILIS

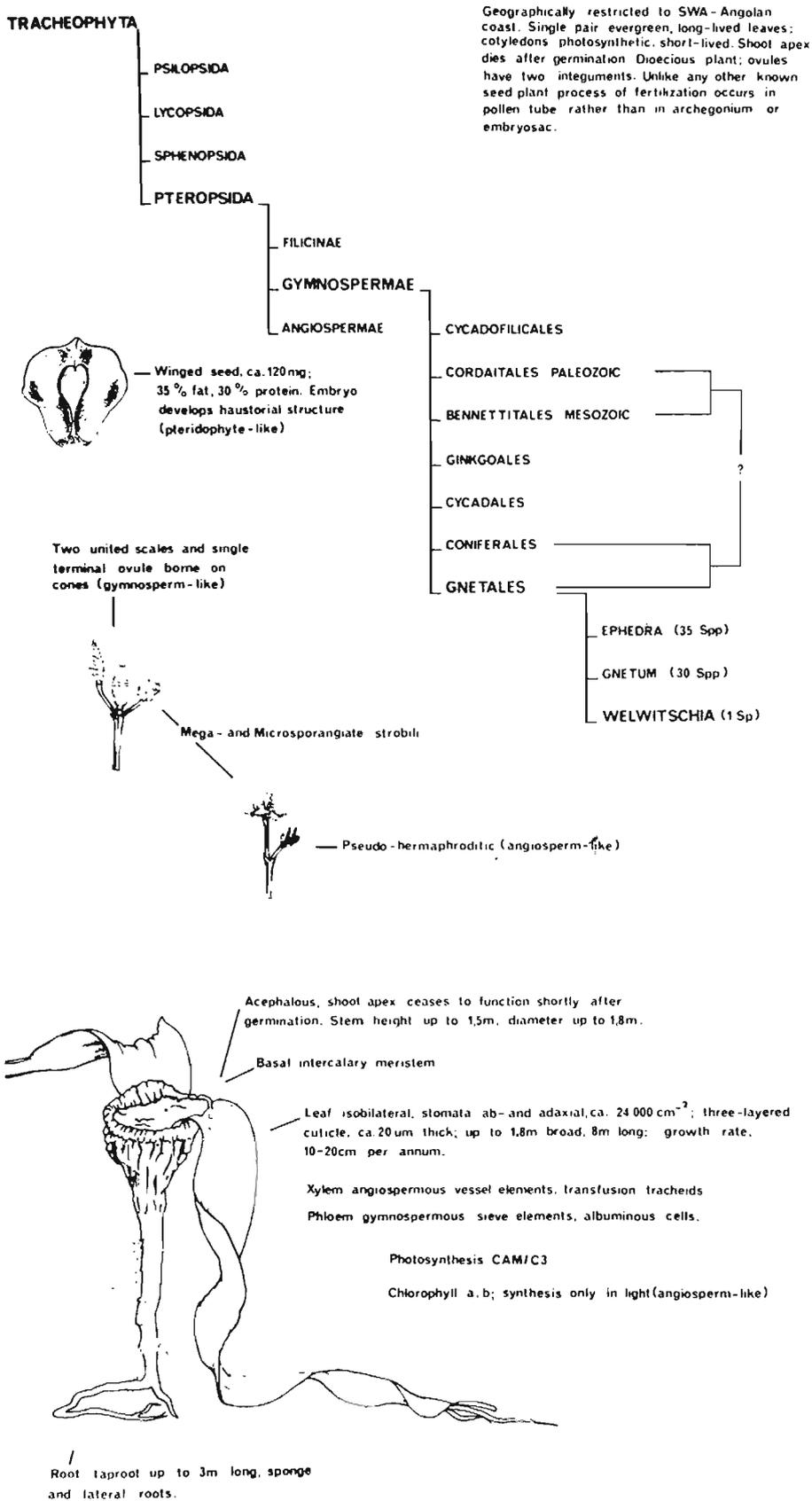


Figure 1. Diagram summarising some of the salient features of *Welwitschia mirabilis*.