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OF THE SEEDLING

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WELWITSCHIA MIRABILIS: MORPHOLOGY OF THE SEEDLING¹

VALERIE BUTLER, CHRIS H. BORNMAN, AND RAY F. EVERT

Department of Botany, University of Natal, Pietermaritzburg, South Africa, and
Department of Botany, University of Wisconsin, Madison, Wisconsin 53706

ABSTRACT

Seedlings of *Welwitschia mirabilis* Hooker were grown from seeds collected on the Welwitschia Fläche at the confluence of the Khan and Swakop Rivers in South-West Africa. Germination is epigeous. Two lanceolate cotyledons constitute the first photosynthetic organs. They reach maximum size in about 9½ weeks, but apparently remain photosynthetically functional for approximately 1½ years. The only pair of foliage leaves are opposite and decussately arranged with respect to the cotyledons. The strap-shaped foliage leaves grow indefinitely from a basal meristem and increase in width by intercalary growth. Another pair of foliar structures is produced by the shoot apex before it becomes meristematically inactive, but they do not develop into foliage leaves. At first narrow and triangular in shape, these primordial leaves gradually thicken and extend laterally, burying the shoot tip. The bases of the foliage leaves become ensheathed in deep grooves which are formed during the development of meristematically active ridges on both sides of the leaves. Strobili of adult plants are usually borne on the inner ridge. The seedling root system is not extensive and appears to serve mainly for anchorage. As *Welwitschia* tends to be confined to a narrow fog belt, it seems feasible that fog condensate, absorbed through the stomata, constitutes its main water supply.

Introduction

Welwitschia mirabilis Hooker is a monotypic species, generally grouped with the genera *Ephedra*

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and *Gnetum* under the order Gnetales (FOSTER and GIFFORD 1959). Its distribution is confined to a narrow coastal belt stretching along the west coast of South-West Africa and Angola. This belt traverses the Namib, an arid extreme desert. *Welwitschia* appears to have few of the adaptive features usually associated with desert plants. Certainly it is not as xerophytic as its habitat would suggest.

Welwitschia's true taxonomic status has not yet been satisfactorily settled. Much has been written on *Welwitschia*, but probably because of inaccessibility of material, investigations have not always been as complete as a plant of this bizarre nature warrants.

The present article, which deals with the morphology of the developing seedling of *Welwitschia*, represents the first of a series of anatomical and morphological investigations of this important species and is followed by articles on the vascular anatomy of the seedling. In applying the term "seedling," we have arbitrarily decided to use the longevity of the cotyledons as a guideline. In our experiments the cotyledons appeared to remain functional for about 18 months.

Material and methods

Plant material examined ranged from embryos to 17-month-old seedlings. Seeds were collected from plants growing on the *Welwitschia* Fläche, about 50 km east of Swakopmund, near the confluence of the Khan and Swakop Rivers. Some seeds were germinated on moist filter paper in an incubator (30 C) while others were germinated in a greenhouse in either vermiculite or sandy soil.

Observations and discussion

The fertile seed of *Welwitschia* consists of an embryo surrounded by gametophytic tissue enclosed by two envelopes. The thin inner envelope or integument forms a long tubular micropyle, the thick outer envelope a strong seed coat, which is expanded laterally into a thin papery wing (fig. 1). The opaque wing is fibrous and very hygroscopic.

The time required for germination ranged from 48 hr for incubated seeds to 8 days for seeds sown in sandy soil in the greenhouse. Most vermiculite-sown seeds required about 5 days for germination. Prior to germination, the white gametophytic tissue and embryo are hard and dry and are separated from one another by a relatively narrow space. The seed has a great capacity for imbibition and, when supplied with water, more than doubles its initial weight within 7 hr (BORNMAN et al. 1972). With imbibition, the gametophyte becomes soft and spongy. Concomitantly, the embryo swells and presses against the gametophyte. In addition, the wing becomes transparent at the edges. When the seed begins to germinate, an unpleasant amide-like odor emanates. At the same time, yellow patches appear on the outer seed coat, including the wing. The tubular micropyle and the inner surface of the outer seed coat turn purple.

Figure 2 shows an excised embryo of a seed in-

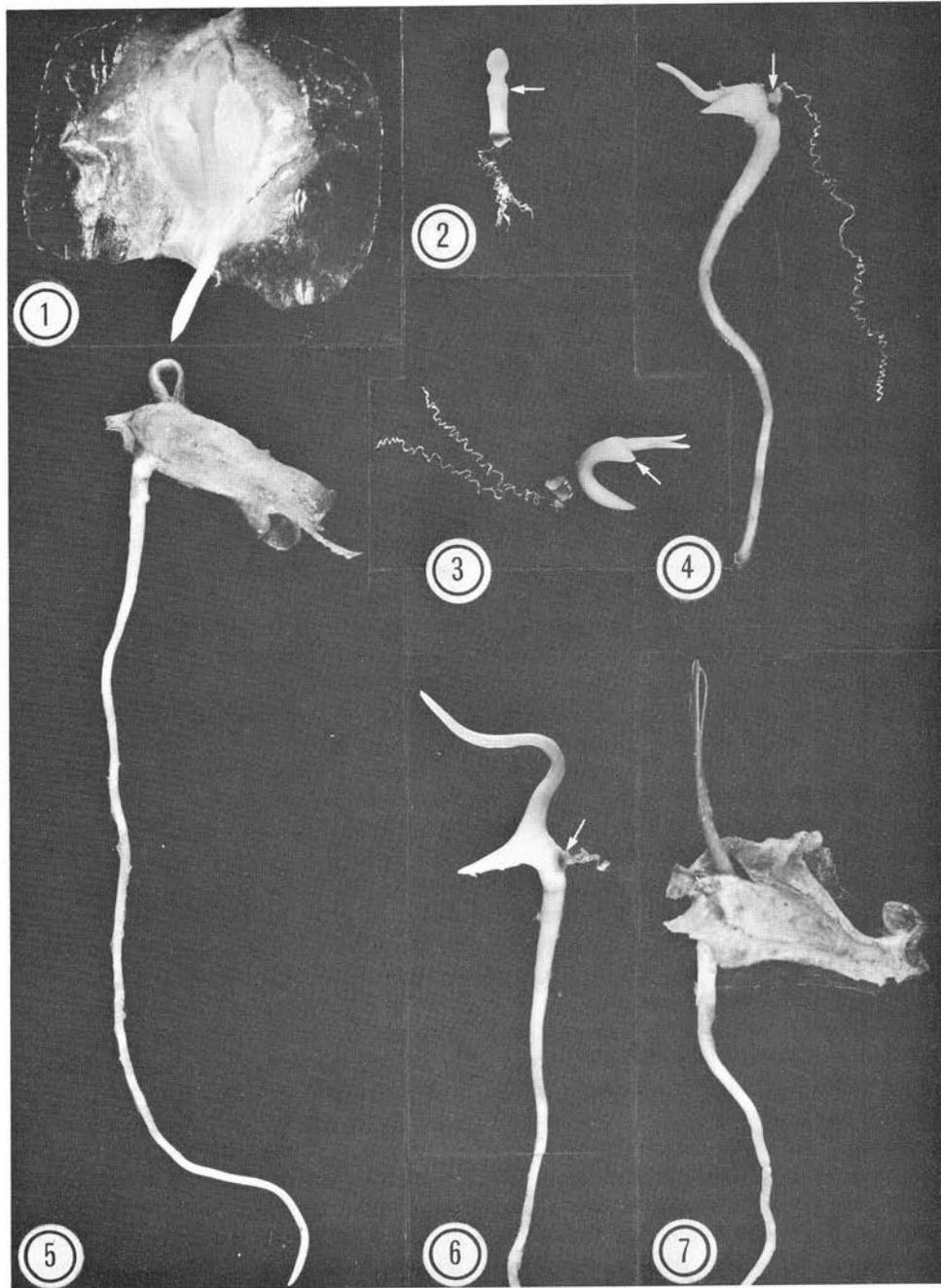
culated for 7 hr. The embryo consists of a long radicle (half or more than the total length of the embryo), a short hypocotyl, and a shoot tip situated between two laterally compressed cotyledons. A uniform bulge or swelling (arrow), called a "collar" by BOWER (1881a), occurs between the radicle and hypocotyl. The tip of the radicle is enclosed within a loose-fitting cap of dead cells, reminiscent of a coleorhiza, to which is attached a much coiled suspensor. The single suspensor is sometimes branched (figs. 2, 3).

Once germination is initiated, the radicle elongates rapidly and is the first part of the embryo to emerge from the seed. The seed, which is laterally compressed, tends to be flattened on one surface and convex on the other. Irrespective of the side on which the seed is placed, the radicle always curves downward, splitting the outer envelope on the lower surface beneath the wing (fig. 1). The radicle does not emerge through the micropyle. As the radicle elongates, it forces the coleorhiza-like structure and suspensor aside, but these structures may remain attached to the germinating seedling at the point of origin of the root (figs. 4, 6, arrows).

As the root elongates and curves downward, the bulge or collar between radicle and hypocotyl forms a protuberance on the lower surface of the embryo. By the time the root has reached about 10 mm in length (after 2 days of germination), the protuberance is very conspicuous (fig. 3, arrow). Continued growth of the protuberance is rapid, and within another 2 days it triples its length (fig. 4). At maturity (7 days after germination), the protuberance is about 6 mm long (fig. 6) and has a flat to slightly concave upper surface, a convex lower surface, and a curved edge. This structure has been variously described as wedge-shaped (BOWER 1881a), footlike, and spadellike (COULTER and CHAMBERLAIN 1910).

Figure 4 shows the relative sizes of the root, hypocotyl, and cotyledons 4 days after germination. Under normal circumstances, at this stage the entire shoot is enclosed within the gametophyte. The cotyledons have changed from a white to a bright orange color and the hypocotyl has acquired a yellowish tinge. As the plumule continues to elongate, it arches upward and eventually splits the outer envelope. Now the hypocotyl appears as an orange loop on the upper surface of the seed, directly above the point of emergence of the root. Concomitantly with increase in length of the hypocotyl, the loop straightens out and brings about withdrawal of the cotyledons from the gametophyte.

The seedling in figures 5 and 6 is 3 days older than that in figure 4. In figure 5 the gametophyte



FIGS. 1-7.—Figs. 1, 5, 7, Seed coat and gametophyte attached. Figs. 2-4, 6, Seed coat and gametophyte removed. Fig. 1, Ventral view of germinating seed showing emergence of radicle. The seed is swollen and the wing is transparent at the edges. Fig. 2, Embryo excised from seed incubated for 7 hr. The cylindrical radicle and hypocotyl are separated by a uniform swelling or collar (arrow). The two cotyledons (only one shown in surface view here) are laterally compressed. A coiled suspensor is attached to the coleorhiza-like cap of dead cells enclosing the radicle tip. Fig. 3, Embryo after 2 days of germination. The radicle has elongated and curved downward. A protuberance (arrow) has begun forming laterally from the collar. The suspensor is branched. Fig. 4, Embryo 4 days after germination. At this stage the cotyledons are orange and the hypocotyl is yellow. Fig. 5, Seedling 7 days after germination. The hypocotyl, which is now arched, has begun to emerge from the seed coat. Fig. 6, Seedling of fig. 5 after removal of the gametophyte and seed coat. Fig. 7, 8-day-old seedling. The plumule is now erect and green. Arrows in figs. 4 and 6 indicate remains of coleorhiza-like structure and suspensor at point of origin of roots. Figs. 1-7, actual size.

and seed coat are still attached and the looped hypocotyl can be seen above the seed coat. The seedling in figure 6 is the same as that in figure 5 but with the gametophyte and seed coat removed to reveal the fully developed protuberance. The cotyledons of the seedling in figure 7 have been completely withdrawn from the gametophyte and they are straightened out. However, the protuberance of this 8-day-old seedling remains embedded within the gametophyte. Once exposed to light, the cotyledon gradually changes in color from orange to bright green, as chlorophyll is increasingly synthesized in the plastids. The seedling is now capable of photosynthesizing and should soon be independent of any remaining nutrient material in the gametophyte.

The embryos and young seedlings in figures 1–7 were grown either in an incubator or in vermiculite in the greenhouse. Figures 8–11 illustrate the emergence of the plumule of a seedling grown under more natural conditions, that is, sandy soil. Note that the shoot tip is protected from abrasive contact with the soil by the looped emergence of the plumule and by the closely appressed cotyledons. As the cotyledons separate, they lengthen and expand (figs. 12–14). The originally cylindrical hypocotyl is now broader in the plane of the cotyledons (figs. 12, 13), that is, it is ovoid in cross section.

The cotyledons of the 15-day-old seedling in figure 14 were folded back in order to reveal the first foliage leaves (hereafter referred to as either “foliage leaves” or simply “leaves”). The two closely appressed leaves are opposite and decussately arranged with respect to the cotyledons. The bases of the cotyledons form a slight sheath around the shoot tip and leaves. The bulge or swelling at the base of the cotyledons in figures 11 and 12 (arrow) is caused by the presence of the newly developing leaves.

Figures 15–22 illustrate further stages in the development of the seedling of figures 8–14. Figure 15 shows the young foliage leaves emerging from the cotyledonary sheath of a 3-week-old seedling. In the 5-week-old seedling of figure 16 the leaves are larger and are beginning to separate. The cotyledonary sheath has begun to split as a result of the increase in width of the leaves. The formation of a bright green swelling or ridge has commenced beneath each leaf at the point of union of the two cotyledons. One such ridge can be seen in figure 16 (arrow).

When the leaves of a 7-week-old seedling are separated, two tiny triangular-shaped outgrowths can be found projecting upward (fig. 17) from either side of the shoot tip. These structures have

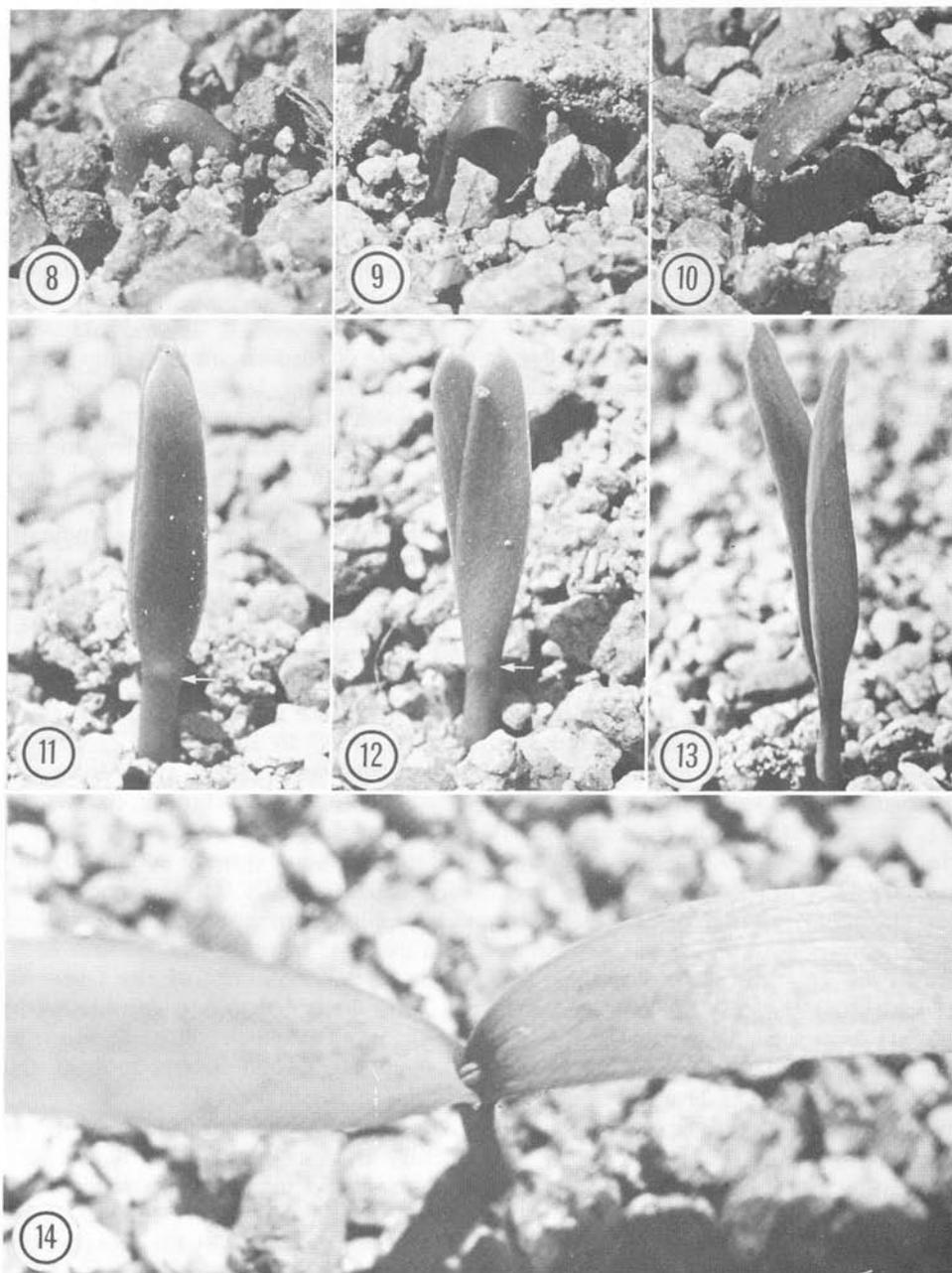
been referred to as “scaley bodies” by MONTEIRO (1882) and as “lateral cones” by BOWER (1881*b*). It has been suggested by SYKES (1910) and PEARSON (1929) that they represent arrested cotyledonary buds. However, they clearly do not develop in the axils of the cotyledons, but at a slightly higher level than the foliage leaves, in relation to which they are decussate. We agree with MARTENS and WATERKEYN (1963), who considered them to be primordial leaves.

Figure 18 shows a 9½-week-old seedling. The lanceolate cotyledons are now fully formed. At this stage the foliage leaves are linear in shape and much longer than the cotyledons. The foliage leaves are basiplastic, that is, they grow in length indefinitely through activity of a basal meristem and widen by intercalary growth. The leaves of adult plants may eventually split longitudinally, parallel with the main veins, which imparts a tattered, ribbon-like appearance to the leaves. By 9½ weeks the primordial or reduced leaves have thickened and widened and have almost completely enclosed the shoot tip. Apical growth has ceased and no more leaves are initiated. At about the same time (i.e., in the 9- to 10-week-old seedling), cork formation becomes apparent at the base of the hypocotyl, where vertical brown cracks arise in the epidermis.

Cork formation spreads acropetally in the hypocotyl and basipetally into the root. In the 5-month-old seedling of figure 19, cork formation has also been initiated in the ridges beneath each leaf. The much stouter hypocotyl of the 1-year-old seedling of figure 20 is completely surrounded by a thick, brown, watertight layer of cork, which is traversed by many cracks and fissures brought about by expansion of the hypocotyl.

The bases of the cotyledons are no longer contiguous in the 1-year-old seedling (fig. 20). This is the result of increased meristematic activity and growth of the ridges beneath the leaves. SYKES (1910) and PEARSON (1929) reported that the tops of the ridges (one is just visible in fig. 20, arrow) are white in appearance. All examined during the present study were green.

After the first year, the cotyledons are still fleshy and smooth and have a thick cuticle. The less smooth foliage leaves are more highly veined than the cotyledons and are more fibrous and tough. With the intercalation of bundles at the base of the foliage leaves slight convolutions begin to appear in the leaf. Both cotyledons and leaves are green. Small bluish freckles occur on the cotyledons while bluish longitudinally oriented streaks occur on the leaves (fig. 21). Except for the tips which are dead,

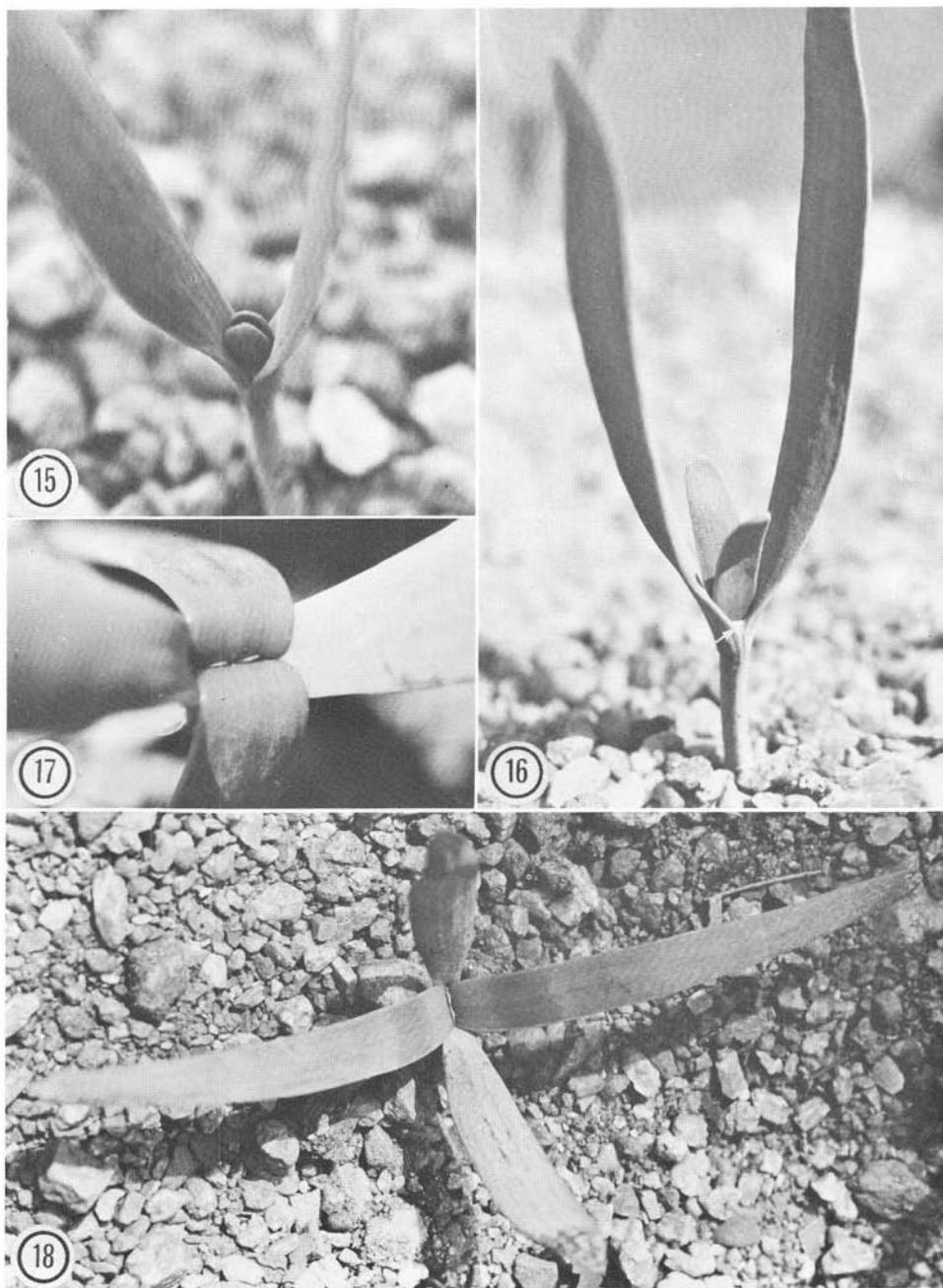


FIGS. 8-14.—Fig. 8, The arched hypocotyl of a germinating seed emerging above the soil. Fig. 9, As the hypocotyl straightens out, it effects withdrawal of the cotyledons from the seed. Fig. 10, The cotyledons are now free of seed and soil. Fig. 11, The closely appressed cotyledons are erect and green. Fig. 12, The cotyledons begin moving apart. Fig. 13, Seedling 2 days older than that in fig. 12. The cotyledons are longer, wider, and farther apart than in fig. 12. Fig. 14, 15-day-old seedling. The foliage leaves are now apparent within the cotyledonary sheath. Arrows in figs. 11 and 12 indicate bulges caused by presence of developing leaves. Figs. 8-13, $\times 1.25$; fig. 14, $\times 4$.

the cotyledons are still living and apparently photosynthetically active.

Eventually, the cotyledons split at the base (fig. 22, arrow). This is apparently a direct result of stresses related to the increase in girth of the hypo-

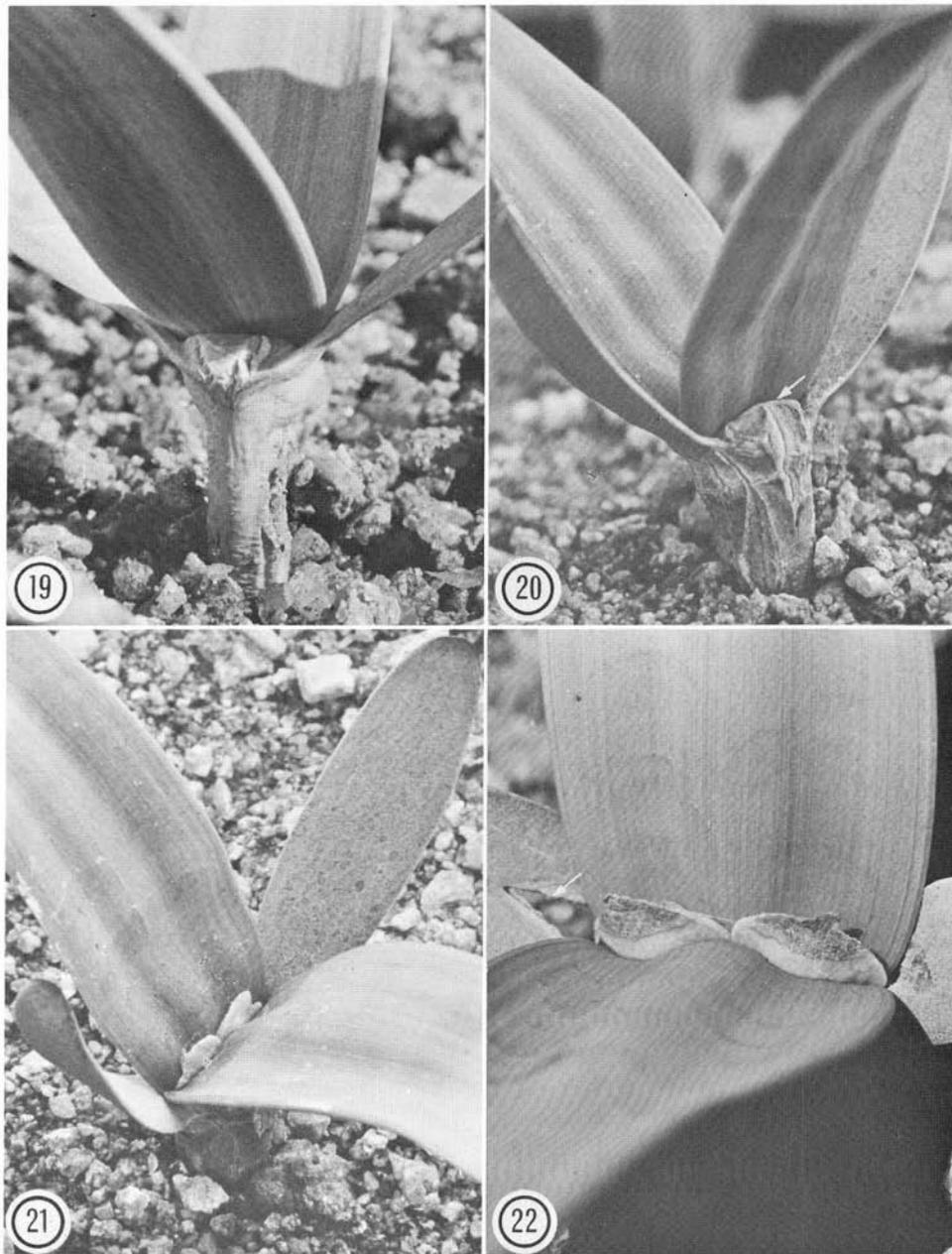
cotyl and in the width of the bases of the leaves. The cotyledons then wither and die but may remain attached to the plant for a number of years. Although the cotyledons eventually fall off, they are not abscised.



FIGS. 15-18.—Fig. 15, 3-week-old seedling. The foliage leaves are emerging from the cotyledonary sheath. Fig. 16, 5-week-old seedling. The foliage leaves have begun to separate. A ridge (arrow) has begun to form beneath each leaf at the point of union of the cotyledons. Fig. 17, 7-week-old seedling. Two triangular-shaped primordial leaves project upward from either side of the hidden shoot tip. Fig. 18, 9½-week-old seedling. The cotyledons have reached maximum size. Figs. 15-18, actual size.

At about the time that the cotyledons begin to split at their bases, the tips of the two reduced leaves begin to die (fig. 22). Eventually, the reduced leaves fuse to form a continuous corky structure under which the shoot tip is thoroughly buried. A ring of tissue is then formed around the fused,

reduced leaves. This inner, continuous ridge, together with the two previously mentioned outer ridges, more or less sheathe the bases of the two foliage leaves. The strobili of the adult plant are borne mainly on the inner ridge. Occasionally, strobili are formed on the outer ridges.



FIGS. 19-22.—Fig. 19, 5-month-old seedling. Cork formation has been initiated at the base of the hypocotyl and in the ridges. Fig. 20, 1-year-old seedling. The stout hypocotyl is surrounded by a thick, brown, fissured layer of cork. The bases of the cotyledons are no longer contiguous. Note meristematic ridge (arrow). Fig. 21, 1-year-old seedling. The primordial leaves are contiguous, and the cotyledons have begun to die back from the tips. Fig. 22, 17-month-old seedling. The cotyledons are split at the base (arrow) and the tips of the primordial leaves are corky. Figs. 19-21, $\times 1.5$; fig. 22, $\times 2$.

Surprisingly, the root system of a *Welwitschia* seedling is not extensive. The initial, rapid elongation of the taproot is not sustained. After 3 weeks, the taproot is only 30 cm long. The total length of the root system of a 1-year-old plant is 2 m.

It has been suggested that *Welwitschia* has a

very long taproot which extends to the water table and enables the plant to obtain moisture necessary for its survival (CHAMBERLAIN 1935). The taproots of all *Welwitschia* seedlings examined during the present study branched after attaining a length of about 10-30 cm. SYKES (1910) was of the opin-

ion that branching of the taproot was due to the influence of some obstacle or injury to the root. Regardless of what factor(s) is responsible for branching of the taproot, branching seems to be the rule and not the exception. Even if the roots of adult *Welwitschia* plants eventually reach underground sources of water, the problem of how the seedlings and young adult plants survive still remains. As most *Welwitschias* are restricted to a narrow fog belt, it seems plausible that their continued existence in the desert is due to utilization of fog condensate. It has been found that the

stomata of *Welwitschia* remain open during periods of low temperature (i.e., during the night and under fog conditions) and close during the day when the temperature rises (BORNMAN 1971). This suggests that absorption of water takes place through the stomata, which are very numerous on both the upper and lower surfaces of the leaves. Not all *Welwitschia* plants are confined to the fog belt. Some *Welwitschias* are to be found in the Kaokoveld. However, this area receives a moderate amount of rain annually.

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