

XV. *The Anatomy of Welwitschia mirabilis, Hook. f., in the Seedling and Adult States. Forming Report No. 2 of the Percy Sladen Memorial Expedition to South-West Africa, 1908–1909. By M. G. SYKES, Girton College, Fellow of Newnham College, Cambridge. (Communicated by Prof. H. H. W. PEARSON, Sc.D., F.L.S.)*

(Plates 34 & 35 and 5 Text-figures.)

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ALTHOUGH the structure of this interesting and isolated genus has already been investigated by various workers *, it seemed advisable that it should be further studied in the light of recent research. A large number of seedlings and young plants (collected and preserved during the recent Percy Sladen Memorial Expedition in South-West Africa) have been most kindly placed at my disposal by Professor Pearson. In addition to these, I have examined two younger seedlings grown in the Cambridge Botanic Garden.

The investigation of this material, while confirming the greater part of the account of the seedling anatomy given by Bower † in 1881, has also brought to light additional points of interest, which appear to be of some importance. In addition to the description of the facts contained in that memoir, this paper includes short discussions of theoretical questions on which evidence is obtained from a study of the mode of growth and the structure in *Welwitschia*, and an attempt has been made to draw attention to such characteristics in the structure of this plant as are of especial interest in connection with recent work.

I am indebted to Professor Pearson for his kind interest in this paper, and to Mr. D. Thoday for valuable assistance in the preparation of the text-figures.

* Hooker, 1863; Bower, 1881; de Bary, 1884, &c.

† Bower, F. O., 1881, I. & II.

Section I.—DEVELOPMENT OF OUTWARD FORM.

The earliest stages in the formation of the seedling from the embryo have been described by Bower* ; and in his later paper he gives a very clear account of the method of growth in older seedlings. I have, however, been fortunate enough to obtain plants of apparently intermediate age which have furnished some further points of considerable interest.

Stage 1.—Pl. 34. fig. 1 shows a seedling about thirteen months old. Its cotyledons are still attached and the feeder inserted in the husk of the seed. The hypocotyl is as yet fairly uniform in thickness, save for a slight swelling at S. The bases of the cotyledons are continuous, and at each of the two points where the margins of the bases join occurs a small swelling (R)†, which, since it appears to have passed unnoticed by earlier observers, is possibly unusually prominent in this seedling. The two plumular leaves are already well developed, and, alternating with the cotyledons, are attached within the ridge formed by the fused cotyledonary bases. The stem apex is as yet only slightly depressed, and is so little differentiated as to be hardly distinguishable: on either side of the apex occurs a small conical process, which, on account of its position, is to be regarded as a bud borne in the axil of the cotyledon‡.

At this stage the cotyledons are green and living, but their bases are mainly composed of corky cells similar to those found on the exterior of the stem. In seedlings representing stages intermediate between those shown in figs. 1 and 2 examined from time to time while growing at the Botanic Garden, it was seen that the steadily broadening plumular leaves pressed against the bases of the cotyledons, and, some time before the latter began to wither, caused a split to appear in the region of pressure, whereby the base of the cotyledon became bifurcated.

The cotyledons then gradually dry up and wither away. They have already withered in the seedling shown in Pl. 34. figs. 2 *a*, 2 *b*; their ragged bases are seen at C (fig. 2 *b*). There is no definite absciss layer formed, but the cotyledons wither and gradually drop off, owing to the slow decay of the tissue at their base; the continuity of the two primary vascular bundles is preserved for a considerable period.

Stage 2.—At this stage the upper portion of the hypocotyl is much swollen and fusiform (Y, fig. 2). In this particular seedling the feeder could no longer be distinguished, but it was still present in the larger seedling drawn in fig. 3; here it is clear that only the upper part of the hypocotyl has swollen. The unswollen portion of the hypocotyl (U, figs. 3 & 4) is usually of considerable length, as in this seedling (fig. 3), but it is occasionally quite short; one case was examined in which its length was somewhat less than that of the swollen portion; and in another example, at about the stage shown in fig. 3, the feeder was placed immediately beneath the swollen

* Bower, I. pp. 15–20.

† It will be seen that there is a special vascular supply to these swellings, a fact which adds to the interest already awakened by their outward appearance (Pl. 35. figs. 15 *a* & *b*).

‡ Bower, I. and II.; cf. also Henriques, J. A., Bot. Centralbl. (1909) no. 47, p. 68.

hypocotyl and no unswollen portion was present (Pl. 34, fig. 6). The meagre development of the hypocotyl in this seedling is probably correlated with the fact that the plumular leaves were not properly grown, and were still contiguous by their upper surfaces, thus reducing assimilation and retarding growth.

The top of the fusiform hypocotyl (Pl. 34, X, fig. 2) is slightly flattened between the ragged remains of the cotyledons, and it is apparent that some intercalary growth must have taken place in this region, separating the once continuous margins of the two cotyledonary bases. The method of growth will be more easily understood on reference to figs. 1 *a* and 3, where the downward sloping scars (C) represent the margins of the bases of the old cotyledons, now separated from one another by a further growth between the cotyledons, resulting in the formation of a more or less triangular portion (T). It will be seen that this intercalary growth has taken place just below the swellings (R) shown in fig. 1; by means of the upward and lateral growth of these swellings a still more noticeable change has taken place, resulting in the development of a very definite and swollen ridge continuous round the top of the enlarged hypocotyl. From an examination of the intermediate stages referred to (figs. 1 *a* & 3) it is clear that the accelerated meristematic growth which first began in the swellings (R) has afterwards spread from these swellings round the projecting edge left after the withering of the cotyledons, until it forms two elongated ridges which finally fuse in the median plane of the cotyledons so as to form a continuous ridge. In fig. 2 a small indentation, at each of the two ends of the ridge, is the only sign of its double origin. In many of the older seedlings it is found that even this has disappeared (see also O, fig. 9 *a*).

Consequent on the upgrowth of this narrow ridge and immediately internal to it there is a groove, already of some depth, from the base of which spring the two plumular leaves. Between the leaves on their inner side is the depressed apex, which remains inactive. On either side of the apex the conical processes, or cotyledonary buds, have become considerably enlarged (Pl. 34, B, fig. 2); they are much elongated in a plane at right angles to the planes of the two cotyledons, a fact which makes their appearance unlike that commonly distinctive of buds, but which is probably to be attributed to the effect of lateral pressure, exerted on them during their development by the closely appressed plumular leaves.

Stage 3.—In fig. 4 *b* it will be seen that the upper part of the fusiform hypocotyl has become further swollen, so that it is now globular (K). A few seedlings of this age, or even older, were observed in which the fusiform shape was retained, but the globular upper portion has been more or less developed in all the mature plants which have been observed. In many seedlings of this stage there is a flattened portion (*cf.* X, fig. 2) intercalated by the continuation of growth between the cotyledonary bases and extending laterally beneath the ridge, but in the seedling shown in fig. 4 there was no definite flattened portion developed. The ridge is now still further enlarged, and by its smooth white appearance is rendered very conspicuous against the rough brown surface of the rest of the hypocotyl. The upward growth of the ridge has deepened the leaf-groove; it is deepest at its ends opposite the original position of the cotyledons, while at the flanks its floor is raised up by the meristematic division continually taking place

at the base of the leaf. On the inner side of the leaf-groove a second prominent white ridge is now to be distinguished, resulting from the intercalation of a second elongated area of meristematic growth, internal to the leaves. This second ridge forms the inner lip of the groove and is shown in fig. 4 *c* (Br.), where it appears as a narrow band encircling three sides of the base of each of the cotyledonary buds: its growth has already raised up the cotyledonary buds above their original level. It is from this inner ridge that the inflorescences commonly arise.

Further Growth.—The general form attained in Stage 3 is but little modified in the mature plant. The method of growth from this stage has been carefully described by Bower. The changes in form are chiefly brought about by cell-divisions at the base of the leaf-groove, by means of which the inner and outer ridges grow in size and become still further raised *.

The uplifting of the cotyledonary buds by the growth and expansion of the inner ridge gives the growing plant a very remarkable appearance. The buds, or lobes of the crown, as they have been called, become much enlarged and flattened, forming the well-known "table-top" so characteristic of old *Welwitschia* plants; they are usually merged in one another on their contiguous sides, the line of fusion (F, fig. 9) being often hardly or not at all distinguishable. It is obvious that in these cases the apex of the plant has become buried by the growth of the "crown" and is incapable of further growth.

Pl. 34. fig. 9 represents a young plant which has attained to the mature form. The growth of the cotyledonary buds and the intercalation of the inner ridge has pushed apart the two sides of the leaf-groove, and has consequently separated widely the formerly closely approximated leaves. Both inner and outer ridges still show traces of their double origin (O^1 , O^2 , fig. 9 *a*).

Origin of the Inflorescences.—The origin of the inflorescences in young and mature plants has been described by Bower † and Pearson ‡. Among my young plants were some very early stages in which only one or two inflorescences had as yet been developed. In each case they were borne on the inner lip of the groove, *i. e.* the inner meristematic ridge, and the first-formed inflorescences always occurred opposite the line separating the two cotyledonary buds, in what appears to be always the oldest portion of the intercalated region (fig. 9). Their formation is generally confined to the inner ridge, but Pearson has recorded as not uncommon cases in which the outer ridge becomes much enlarged and zoned, and gives rise to inflorescences.

Modifications of the Normal Development.—It has been remarked above that in normal cases the apex is buried by the growth of the crown and no further development is possible.

In quite a large number of instances it is found that the *lobes of the crown* are *not merged in one another*, at any rate up to a considerable age. In these cases meristematic growth produces transverse continuations of the inner ridge so that each bud is completely encircled. Fig. 7, although drawn for a different purpose, may, if A be

* Bower, II. pp. 583–585, pl. 33. fig. 10.

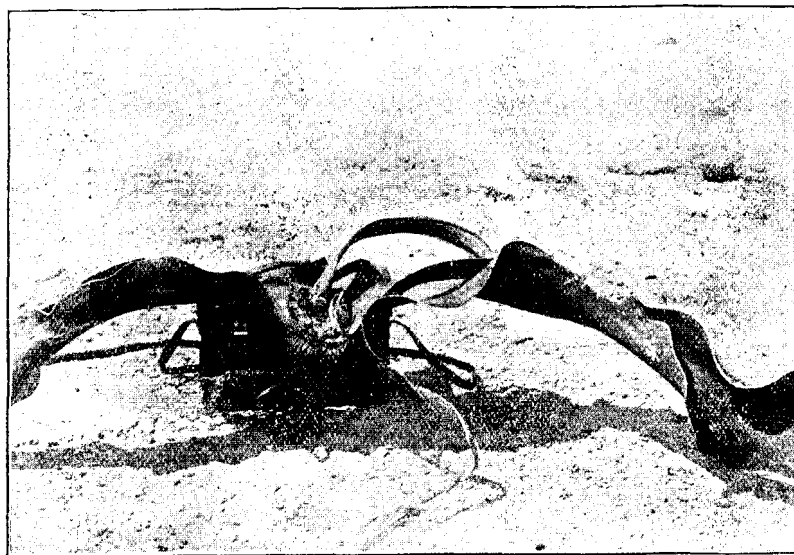
† Bower, II. p. 590, figs. 13 & 14; see also Hooker, 1863.

‡ Pearson, II. pp. 332–333.

omitted, be regarded as representing such a case. It is in fact almost duplicate of another plant in which A was not present. It will be seen that in such plants the apex is not buried and might well be able to undergo further development.

Cases have been recorded in which the first pair of leaves remained small and later growth of the apex produced *extra leaves* *.

Fig. 1.



Among my material was only one case, a mature plant (text-fig. 1) †, in which a *single extra leaf* had been produced by an individual otherwise quite normal. This extra leaf takes its origin deep down between two cotyledonary buds, and must have been produced by growth at or near the depressed apex. It decussates with the members of the first pair, but is considerably narrower, and its width is much less than the width of the cotyledonary buds. The cotyledonary buds diverge considerably at the centre, where this leaf originates, but are contiguous on either side of the leaf. The line of fusion between them is even here, however, quite distinct, and it appears that, owing probably to the unusual extra growth at the apex, they remained separate until a late stage.

In one of my young plants (Pl. 34. fig. 7), already referred to as having its two cotyledonary buds remaining unfused, a curious *elongated projection* (A, fig. 7) occurred between the buds in the position occupied by the apex in the young plant. This projecting object was shown by anatomical examination to be in organic continuity with the plant, having its origin between the lobes of the crown, from the apex of the stem; but I do not feel qualified to give any decided opinion as to its morphological nature. It is oval in transverse section, and at its base it is composed of parenchymatous tissue without a vascular supply; higher up the central portion is still parenchymatous, while a number of groups

* C. Naudin, 'The Gardeners' Chronicle,' Aug. 13, 1881 (*ex* Bower, II. p. 593).

† This photograph was taken near Mossamedes by Professor Pearson, who has kindly lent it to me.

of fibres are seen to be developing just internal to the epidermis (Pl. 34. fig. 10 *a*). Higher still these fibres are fully mature (fig. 10 *b*): they are thick-walled unlignified cells, exactly resembling those borne in groups under the epidermis of the leaf in *Welwitschia* and occurring in many other parts of the plant. A few lignified elements occur on the outer edge of some of the groups of fibres, chiefly at the ends of the oval, but it is not possible to affirm that these are of the nature of xylem and they were lignified only for a very short part of their course (fig. 10 *a*, L). The upper part of the object is composed entirely of loose corky cells with suberized walls, and there can be little doubt that it is in a degenerating condition.

It may be that the structure is to be regarded as axial in nature, produced by the further development of the apex itself. I am more inclined to consider it as representing another pair of leaves fused by their contiguous surfaces and never having attained to mature development. This possibility was suggested to me by an examination of the seedling shown in fig. 6, in which the first two plumular leaves were still contiguous by their inner and upper surfaces, and the hypothesis is supported by the presence of regular peripheral groups of fibres, but there is no trace of a double origin *. The parenchymatous nature of the base is probably evidence that it has been added to in that region by meristematic growth, as is the case with the leaves. It would certainly appear that the apex of the structure is older than the base.

A very remarkable development of one of the leaves of a young plant is to be seen in fig. 8 *a*, *b*. While one of the leaves was normally developed from the groove on one side of the plant, the other was only partially confined to the groove on the other side. Half of its width originated from half of the groove, but its other half from a deep groove between the free cotyledonary buds, leaving unoccupied the other half of the normal groove. It was considerably torn, and from its position was at first taken for an extra leaf such as that shown in text-fig. 1. That part of the inner ridge which surrounded the cotyledonary bud encircled on two sides by the leaf in this abnormal fashion was unusually well-developed and zoned; meristematic division had evidently been very active there. On the outer side of the leaf a small extra lobe (B 3) was also present and another lobe, not shown in the figure, occurs at B 4.

A transverse section through the hypocotyl (of the specimen represented in fig. 8) at the level of entry of the leaf-bundles shows a straight row of bundles entering from one leaf, and an L-shaped series from the other, the hook of the L passing between the bases of the two main buds (Pl. 35. fig. 23).

The fact that half of one side of the "leaf-groove" is here unoccupied by a leaf appears to me to be a fact of some interest. It makes more evident the independent growth of the two ridges (the two lips of the groove), a fact more surprising here than in the normal plant, where they are separated from one another by the base of the leaf.

The presence of *extra lobes to the crown* was found in one other case besides that recorded above. In this example one lobe was divided into three (fig. 5), but

* It is also interesting to notice that this seedling, like the one with the extra leaf, was found by Professor Pearson near Mossamedes, a comparatively damp district, in which *Welwitschia* manifests unusually active growth.

the three portions had a common base. The two main lobes were widely separated and were each surrounded by the well-developed inner ridge.

Cases in which one lobe or bud is more strongly developed than the other are fairly common.

In conclusion, it will be obvious from this description of the development in seedlings of *Welwitschia* that the epicotyledonary stem is extremely reduced in this plant, and that practically the whole tuberous mass, commonly known in the adult plant as a stem, is morphologically the swollen hypocotyl which bore in rapid succession the two cotyledons and the two plumular leaves. The stem apex gives rise only to these two leaves and is suppressed early in the life of the seedling. It is finally in most cases even buried by the growth of the cotyledonary buds.

The only portion of the plant which can be regarded as the epicotyledonary stem is that which undergoes intercalary growth above and below the leaf-bases. In the early stages the leaves originate at practically the same level as the cotyledons; it is only later that they become widely separated by further growth, which begins between the margins of the cotyledons as a small projection and finally develops into the outer ridge. But it must be noted that this ridge does not elevate the leaf-bases in a manner which can be compared with the separation of two nodes by the ordinary elongation of an internode. The ridge is a quite independent structure and has from the beginning a special vascular supply. It appears very doubtful whether either it, or the inner ridge, which originates later by intercalary growth on the inner side of the groove, can really be regarded as normal epicotyledonary stem. These ridges are rather of the nature of specialised placental outgrowths on either side of the leaf-base.

In any case the extent of this growth-region is extremely small in comparison with the large swollen hypocotyl, which may also grow considerably in length (E marks the level of the feeder in fig. 4 b); the many peculiarities of the vascular structure and transition are probably to a large extent attributable to this remarkable elongation of the hypocotyl.

The plant is really an "adult seedling"; and there are few forms with which it can strictly be compared. It presents some points in common with seedlings of *Araucaria Bidwillii*. At that stage in the growth of a seedling of *Araucaria Bidwillii* at which the cotyledons wither, the plant "is capable of resisting drought, and may be sent to Europe without losing the power of germination. It has been suggested that the first stage of germination may correspond with a short rainy season, while the resting stage coincides with the period of drought"*. *Welwitschia*, living in a climate in which the period of drought is indefinitely prolonged, appears to have got very little further in its development than has such a seedling!

It will be seen later that in its anatomy, especially in the transition region, it has other points of still more striking resemblance to various species of *Araucaria* †.

* Seward and Ford, 1906, p. 331; see figs. 13, B (*Araucaria Bidwillii*) and C (*Araucaria imbricata*).

† Attention has been called by Prof. Pearson to another striking resemblance between *Welwitschia* and *Araucaria* (Pearson, 1909, p. 370).

Section II.—THE ROOT SYSTEM.

Occurrence of Branching.—In most of my plants the root system was not preserved intact, and the portion of the tap-root still attached to the plant, although in some cases of considerable length, was quite unbranched.

In the one case of branching found in the West African material a large stone was wedged in between the two portions, and it would appear probable that in this case the root had bifurcated owing to injury by the stone. In some of the West African seedlings there were remains of minute lateral roots, but they were very few and were sparsely distributed.

The seedlings from the Botanic Garden had been raised in stony soil in long drain-pipes. In one of them an early bifurcation of the root had taken place (Pl. 34. fig. 1, B); here also it had come into contact with a stone, and forked in consequence. In the other and older seedling there were several such bifurcations, and in each case anatomical examination showed that some injury had happened to the root at the point of bifurcation. Professor Pearson agrees with me in thinking it probable that bifurcation and the formation of strong lateral roots in this plant is always due to the influence of some such obstacle.

The two seedlings just referred to were strikingly different in one particular from the seedlings obtained growing in their natural habitat. The younger seedling in the lower parts of its root system, the older seedling throughout a large portion of its length up to within two inches of its feeder, bore numerous minute hair-like lateral rootlets. These rootlets (see H, Pl. 34. fig. 1) received a small vascular supply from one pole of the diarch main root. As the younger portion of the root system has been broken off, all the rootlets are unfortunately of considerable age and have lost their cortex by disintegration; they are protected by two or three layers of corky cells, internal to which is the minute stele, which contains two phloem groups and a very small diarch plate of xylem (Pl. 35. fig. 12).

These fine lateral rootlets have not been found in seedlings examined before. Bower records one case of the formation of a lateral root in consequence of injury*, and Chev. D. J. N. de Monteiro found cases of repeated branching in roots about eighteen or twenty inches long†; but these lateral roots appear to have belonged to an entirely different category from those just described. The occurrence of the fine rootlets, few in the desert plants, but numerous in these artificially grown seedlings, is a feature of some biological interest: it is probably dependent on the conditions under which the plant is grown. In the habitat normal to the plant the surrounding surface soil is absolutely bereft of moisture, except during that brief period of rainfall during which the seeds first germinate‡; the development of absorbent organs by the descending tap-root would therefore be worse than useless, its one aim necessarily being to reach the underground sources of water. In the case of seedlings reared in the moister atmosphere of

* Bower, I. p. 26.

† Gard. Chron. 1880, p. 690; Bower, II. p. 571.

‡ Pearson, 'Nature,' 1907.

the xerophyte house at the Botanic Garden, the soil conditions cannot but be somewhat different; hence the production of the fibre-like rootlets for the absorption of the small amount of moisture thus presented to the root. It is probable that in this plant the formation of lateral roots is conditioned by the amount of moisture present.

Anatomy of Forking Root.—The anatomy of the normal elongated root and hypocotyl of *Welwitschia* has been described by other authors*, and full accounts have been given of their external appearance and internal structure and of the development of the ground-tissue, lignified fibres, &c. I have little further to add to their descriptions.

The forked root system described in the young seedling (Pl. 34. fig. 1) is, however, of some interest and seems worth a short description, since it affords an excellent illustration of the powers of endurance of this remarkable plant.

Text-fig. 2 (p. 336) represents a series of transverse sections from above downwards through the region of the root injured by contact with the stone. In text-fig. 2, A, the transition from hypocotyl to root structure is not quite complete, and the two groups of xylem in the stele are each monarch; while attached to each are two separate groups of secondary xylem and phloem, from which the normal diarch plate of the root has not yet been formed. Just above the place of injury it is seen that the secondary xylem and phloem of both poles of the root are laid down in four groups (text-fig. 2, B); the first sign of disturbance is seen in one of the protoxylem groups (*b*), which becomes elongated and irregular in appearance. The small bundle (*c'*) seen in connection with *b* in A, has died out; but the small bundle *c* in connection with group *a* is still present, accompanied as before by two others.

Immediately after the appearance of this irregularity in the group of protoxylem *b*, the whole group is destroyed, and this half of the vascular tissues is represented only by a decayed mass (*b*, text-fig. 2, C).

The other and larger plate *a*, with its small secondary bundles, still persists. The fact that similar small bundles are not present in connection with the plate *b*, as they are in all normal seedlings, shows that the injury to the root on that side must have taken place at an early stage before the age at which the additional peripheral bundles could have been laid down.

The single remaining protoxylem group is now surrounded by four large and several smaller groups of secondary xylem and phloem. The peripheral smaller groups move outwards, evidently in another attempt to supply a branch. This attempt meets, however, with the same fate as the first, and another dead plate of vascular tissue thus results (*c*, text-fig. 2, D).

The four remaining bundles are now arranged symmetrically round the group of protoxylem, and the root makes a third attempt: it divides at right angles to the plane of the two previous divisions, and a small portion of the vascular tissue is separated off from the larger portion which remains in the original main root. The root thus formed is successful in its development, but a small part of the remaining tissue subtending the rootlet in the main root is destroyed (*d*, text-fig. 2, E & F).

* Hooker, Bower, Bertrand, *ll. cc.*

† See Bower, I. & II.; also text-fig. 3 of this paper, p. 342.

At a level very little below the area of disturbance the two roots formed at this third attempt are found to be nearly of the same size and to have quite normal diarch structure (text-fig. 2, G).

There is one point of some interest shown in this figure which may be referred to here: a small mass of lignified elements, generally much stretched and ruptured, is seen on the

Fig. 2.

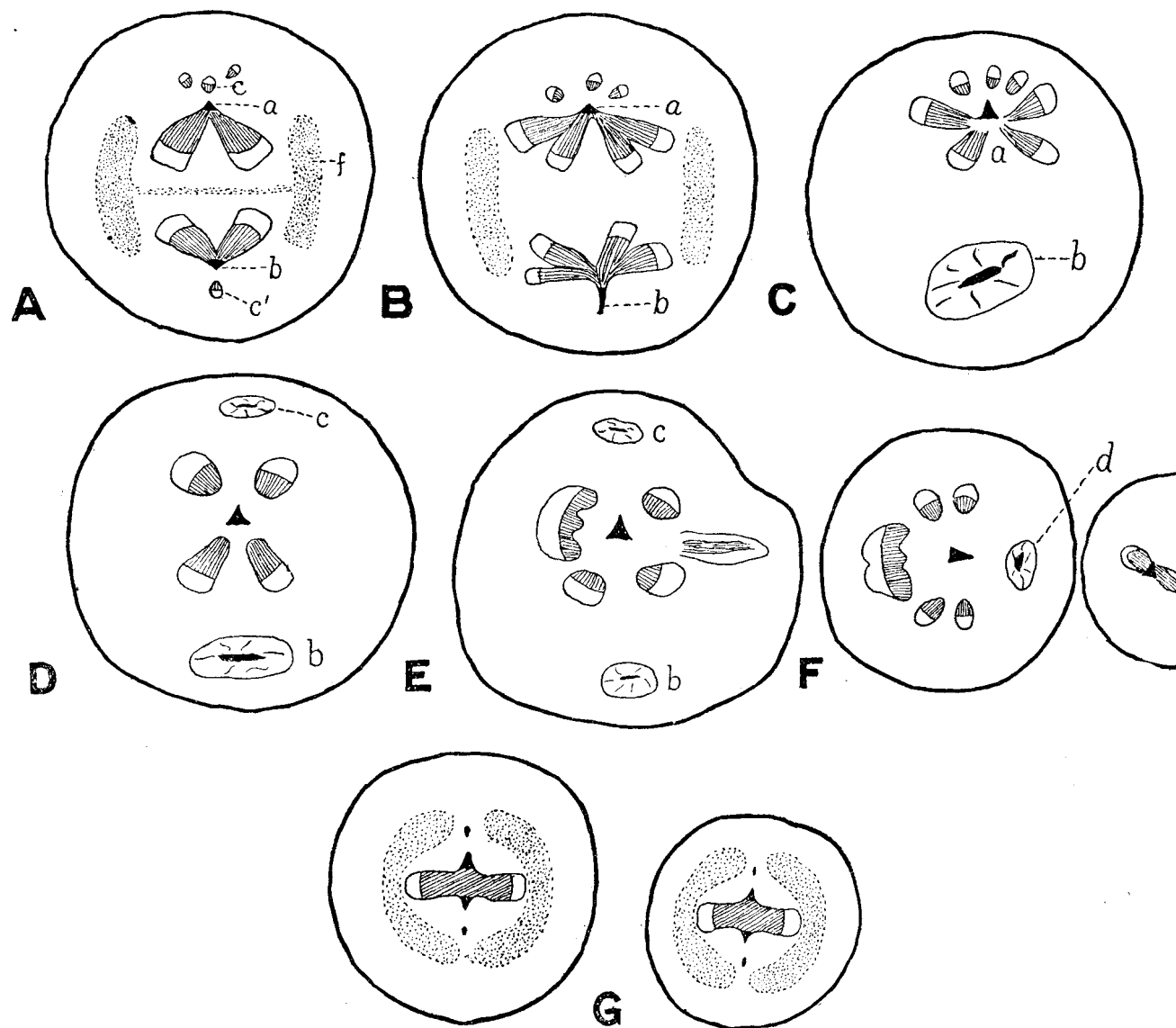


Fig. 2, A-G.—A series of transverse sections through the bifurcating root of the seedling shown in Pl. 34, fig. 1 (secondary xylem=shaded, primary xylem=black, dotted area=fibres (*f*), phloem outlined).

outer side of each of the protoxylem groups, separated from it by several layers of parenchymatous cells (Pl. 35, fig. 14). In text-fig. 2, G, these elements are very few in number, but in some cases they form a very considerable group and are often arranged in a triangle having its apex directed towards the apex of the triangle formed by the protoxylem of the main group. In such cases there is little doubt that the protoxylem

is to be regarded as mesarch; Bower, however, in his study of the early development of the seedling, did not come to this conclusion and merely points out the fact that the protoxylem is "long drawn out" *.

Section III.—THE STRUCTURE OF THE RIDGES AND YOUNG INFLORESCENCES.

Some of the most interesting facts disclosed in this investigation are concerned with the development of the vascular elements in the ridges on either side of the leaf-bases, and their connection with the bundle-system of the hypocotyl.

General Structure of the Ridges.—In the young seedling (Pl. 34. fig. 1) the ridges, each as yet represented only by a small protuberant outgrowth (R), are made up of rapidly dividing parenchymatous cells, among which are scattered a few fibres with thickened and lignified walls: the epidermis is thin-walled and without stomata.

In the older seedling, fibres become very numerous in both ridges, and cork-formation extends over the base of the outer ridge on its outer surface. Numerous stomata are present in the epidermis of the upper free portion of both ridges; these stomata resemble those of the mature leaf, and the epidermis (also like that of the leaf) is composed of conical cells with a thick cuticle impregnated with calcium oxalate. This region with stomata extends over the outer surface of the outer ridge for some distance towards its base, but stomata are absent on its inner surface, where it forms one side of the leaf-groove, and the epidermis is there made up of small, closely packed, cubical cells unprovided with a cuticle. Stomata and cuticle are similarly absent from that part of the inner ridge which forms the other side of the leaf-groove.

Vascular System of the Ridges.—(a) In the seedling shown in Pl. 34. fig. 1 the vascular supply of the ridge primordium consists of a small group of bundles, which form a more or less concentric ring and end freely upwards (Pl. 35. figs. 15 a & b). Each bundle composing the ring is collateral, and all its elements appear to be secondary in origin. No transfusion-tissue is present at this stage. When the bundles are followed downwards in a series of transverse sections, it is seen that while one or two from each group join on to the pairs of primary bundles in the hypocotyl, the greater number end freely in the parenchyma separating the two pairs from one another †.

At this stage the inner ridge is as yet undeveloped, and there is no sign of a vascular supply either to it or to the cotyledonary buds.

(b) In the older seedlings, in which the outer ridge is elongated (*e. g.* in Pl. 34. figs. 1 a, 2) and the inner ridge is just beginning to be apparent, the latter has still no vascular supply, but the simple ring of bundles which formerly terminated at the base of the outer ridge has now undergone some considerable change. The central mass of parenchyma is greatly enlarged, and the bundles are widely separated from one another and are more irregularly distributed; it can, however, still be seen that they constitute two series which together form an ellipse, the bundles of the two series being orientated inversely to one another. A good deal of transfusion-tissue accompanies all the bundles and is scattered

* Bower, I. p. 20, pl. 4. fig. 15, &c.

† See text-fig. 3, F, G, H, p. 342.

throughout the parenchyma (Pl. 35. fig. 19); and as the termination of the bundles is approached, this transfusion-tissue increases in amount. The bundles have kept pace with the upward growth of the ridge: in the upper and now free and elevated portion of the ridge the bundles of the outer series run inwards and terminate together with the inner series in a common irregular mass of scattered transfusion tracheids (Tr, Pl. 35. fig. 16). Anastomoses are frequent, so that the ridge is provided with a peripheral network of bundles running a little way beneath its surface. This is incomplete and open below, where the bundles run down into the hypocotyl and there join the main stele of the seedling. At this stage free endings are rare, most of the bundles having now become joined up with the four groups of vascular tissue found traversing the hypocotyl. The bundles of the ridge join on to the same two groups which supply the bundles of the subtending leaf.

(c) In the later stages (*e. g.*, Pl. 34. fig. 4) no important change takes place in the structure of the outer ridge. A large number of new bundles are intercalated by the rapid meristematic divisions of the parenchymatous tissue; these are chiefly added to the outer series, where they are often arranged in two or more rows, all with the xylem on the inner side of the bundle*.

In many cases the first-formed elements of the xylem in these additional bundles are not the innermost ones; but while a large portion of the later-formed xylem is centrifugally developed, a few tracheids are produced centripetally. Sometimes the centripetally developed xylem even exceeds the centrifugal in amount (Pl. 35. fig. 20). Nearly all the bundles are accompanied on the centripetal side by transfusion elements. There is an increased number of small transverse bundles at this stage, connecting the two series in the outer ridge.

The inner ridge is now traversed by a number of bundles (Pl. 35. fig. 18), most of which are connected with the inner series of bundles belonging to the outer ridge. In many cases they can be seen originating from this inner series and running in between the leaf-bundles at the base of the leaf-groove; they then bend upwards and form the irregular series of bundles which traverses the inner ridge and surrounds the cotyledonary buds: like the bundles in the outer ridge, they end in groups of transfusion-tissue.

Finally, in the oldest plant examined (Pl. 34. fig. 7) the following was the course of events as seen in a series of transverse sections:—In the uppermost portion of the outer ridge there is no sign of vascular bundles; about a centimetre from the surface are a number of groups of transfusion-tissue, which represent the endings of vascular bundles. These vascular bundles are mostly horizontal and are all very irregularly distributed, but followed downwards they are seen to become separated into two series orientated inversely to one another, between which run transversely a number of connecting bundles. Lower down these cross-connections decrease in number. At each end of the ridge a bundle, which represents one of the pair of bundles formerly passing out into a cotyledon, is still conspicuous and now functions as part of the vascular supply to the ridge. At the base of the outer ridge the inner series is much distorted, and its bundles twist round and anastomose with one another. Some of them join on to the outer series

* *Cf.* concentric rings in Cycads; also *cf.* trunk of *Cycadella*, Wieland, p. 66, fig. 35.

and pass down into the hypocotyl. Others pass out between the leaf-bundles under the base of the groove and supply the inner ridge and its inflorescences. On their way some of these bundles form connections by means of secondarily developed vascular elements with the secondary tracheids &c. of the leaf-bundles.

In these later stages it is not possible to follow accurately the course of the common bundle-supply of the two ridges in a downward direction. Free endings are rarely met with, but some of the bundles can be traced down below the level of the feeder before they fuse with the bundles of the hypocotyl.

Vascular Supply of the Young Inflorescence.—I was able to investigate the vascular supply of the young inflorescence* seen in Pl. 34. fig. 9. Its axis received a number of separate bundles (Pl. 34. fig. 11), which, in connection with the bundles of the inner ridge, had branched off from the vascular system of the outer ridge and passed under the groove between the leaf-bundles. Transverse sections of the axis of the young inflorescence showed its bundles to be distributed in two more or less irregular whorls*. In the outer whorl there were several cases of three, four, or more bundles arranged to form a concentric group†. No transfusion-tissue was yet present, and the pith was parenchymatous. It was quite clear that all the bundles were entirely composed of secondary elements produced by the tangential divisions of the meristematic parenchyma (Pl. 35. fig. 21).

It is interesting to notice that the bundles were better developed and the xylem more strongly lignified in the upper portion of the young inflorescence-axis. The bundles are therefore probably older in this region, a fact which would suggest that they develop first here and later become extended downwards. Similar facts were observed in the newly intercalated bundles in the young leaves.

It will be seen from this account that the vascular system in the young ridges and inflorescences is entirely secondary in origin, all the bundles being derived from the growth and further extension of the small concentric ring of secondary bundles which arises first in the outer ridge and later supplies vascular tissue to the inner ridge and the inflorescences.

Section IV.—THE COTYLEDONARY BUDS.

The young cotyledonary buds are composed entirely of parenchymatous tissue and have at first no vascular supply.

In the stage represented in Pl. 34. fig. 2, numerous fibres are distributed throughout the tissue of the now flattened cotyledonary buds, and corky tissue has been developed at their pointed ends. Each bud receives a number of small vascular bundles arranged to form an elongated series. In Pl. 35. fig. 17 it can be seen that the end bundles of the series are collateral and much curved, having their xylems regularly orientated towards the rest of the bundles. The remainder are, on the contrary, very irregularly distributed and may be collateral or concentric. At the apex of the bud the bundles tend to become

* A full description of the adult inflorescence axis is in course of publication by Sykes, in Phil. Trans. Roy. Soc. 1910.

† Worsdell, 1901, p. 768.

arranged into two groups: towards the base the series forms an almost continuous stele. It is not possible certainly to ascertain whether there be any primary elements in these bundles; but by far the greater number of their constituents are entirely of secondary origin.

The group of bundles running up into a cotyledonary bud originates from the two bundles of the cotyledon in the axil of which the bud is borne: it is interesting to find that the vascular supply of the cotyledonary bud bears the same relation to that of the cotyledon as does the vascular supply of one of the flowers of the inflorescence or of one of the inflorescence-branches to the bract in the axil of which it is borne*.

In the older cotyledonary buds—or lobes of the crown, as they are often called in the later stages—cork-formation has extended over the whole surface. The original vascular supply does not seem to have undergone much change†, except that the bundles forming the elongated series have become more or less separated from one another by the growth of the parenchyma, and may in some cases appear to be arranged in a ring. At the base of the bud the inner ridge has now grown up‡, and its bundles form a very irregular ring round the original bundles of the bud (Pl. 35. fig. 18); they run in all directions, and in some cases they appear to establish connections with the bud-bundles.

Section V.—TRANSITION PHENOMENA.

I have now to describe various facts connected with the transition phenomena in *Welwitschia*, chiefly relating to the behaviour of the special bundle-system supplying the ridges. For this purpose it is necessary to give an account of the transition process in the main bundles, which traverse the root and hypocotyl and run into the cotyledons and leaves; this process is in itself of considerable interest in this plant, but Bower's clear description makes it superfluous to give a second full account, and I propose merely to give the outlines, laying especial stress on peculiarities which are here for the first time demonstrated, or which are important in the light of recent research.

Outlines of Transition.—The main facts in the youngest seedling are as follows:—Two bundles enter from each cotyledon, and almost immediately rotate to form the four exarch collateral bundles of the hypocotyl. After a considerable interval, the protoxylems of each pair fuse to form one of the poles of the root, the two phloems of the two groups thus produced remaining separate. Finally, one of the phloem groups from one pole joins one of the phloem groups from the adjoining bundle of the other pole, and there is thus produced a normal diarch root in which two phloem groups alternate with two xylem groups. There is no primary xylem in the hypocotyl, save that which passes out into the cotyledonary traces; similar facts have been described in *Araucaria* §.

Text-figure 3 (pp. 342–343) represents a series of transverse sections taken at intervals

* Strasburger, 1872, pp. 144, 145.

† Bower, II. pl. 32. fig. 9, p. 583.

‡ Bower, II. pp. 581, 582. Professor Bower's material did not make it possible to distinguish between the original vascular system of the bud itself and those later-formed bundles supplying the tissue of the rapidly enlarging inner ridge, by the growth of which the lobes of the crown are upraised.

§ Seward & Ford, 1906, pp. 333–336.

from an older seedling (Pl. 34. fig. 1) intermediate in age between that figured by Bower in his first paper* and the youngest of those described by him in his second paper†. Text-fig. 3, A, shows the diarch root; in B the two poles of the root have separated, and in C two separate collateral groups of vascular tissue are present at each pole; the two groups are connected with one another by meristematic tissue (text-fig. 3, C, *m*). The levels at which these sections are taken can be judged by reference to the older seedling drawn in Pl. 34. fig. 4 *b*, where A indicates the upper level of the diarch-root structure and the stage at which the separation of the two poles of the root begins, and C is the stage corresponding with text-fig. 3, C. The four groups of vascular tissue present at this stage are continued upwards into the hypocotyl; they remain collateral past the level of the feeder (Pl. 34. fig. 4 *b*, E, and text-fig. 3, E), up to the level F in Pl. 34. fig. 4 *b*, when they become concentric. The formation of four concentric groups, characteristic of the upper portion of the hypocotyl of *Welwitschia*‡, is gradually brought about by the addition of small secondary bundles round each of the four original main collateral bundles. The beginning of this process is seen at F, text-fig. 3, where meristematic division has spread outwards from each group and produced a large inner bundle (*l*) and a number of small peripheral bundles. In G and H, text-fig. 3, the gradual establishment of the four concentric groups is seen. It is these four groups (reminiscent as they are of the concentric steles of the *Medulloseæ*§) which give to the vascular structure of the so-called "stem" of *Welwitschia* its very striking appearance||.

One of these concentric groups is drawn in detail in Pl. 35. fig. 22. A number of isolated tracheids are scattered throughout the parenchyma in the centre of the group. A single and fairly regular row of cells defines the limits of each of these groups, but it was not possible either here or at any other level to make out any of the characters which distinguish a definite endodermis, so that it does not appear correct to designate them as "steles."

In the short space intervening between levels G, I, text-fig. 3 (F and K in Pl. 34. fig. 4, *b*)¶, the four separate groups are not so clearly defined. At I, text-fig. 3, the four main bundles have rotated on their own axes, and are now endarch; in K, L, M is seen their further rotation and the division of each bundle into two, so that four bundles run up into each cotyledon. The other bundles which made up the concentric groups supply the plumular leaves, K, L, text-fig. 3. Each leaf thus receives at this stage a number of bundles, some of which have been connected with one cotyledon trace, some with the other. One leaf-bundle from each concentric group is at these stages, text-fig. 3, E–I, remarkable for its greater size, and it appears probable that these four bundles represent the original leaf-supply, two to each leaf, before the intercalation of the secondary bundles began. In older seedlings the ever-increasing numbers of leaf-bundles often become distributed in rings more or less concentrically arranged

* Bower, I. pl. 4. fig. 15.

† Bower, II. pl. 32. fig. 6.

‡ Cf. the folding of the cambium in the bundles of the peduncles; Sykes, 1910.

§ Weber & Sterzel; cf. Sykes, 1910, Phil. Trans. Roy. Soc. ined.

|| Cf. the four groups of vascular tissue in *Convolvulus Scammonia*; Solereder, p. 572, fig. 131.

¶ In an older seedling the four hypocotyledonary groups were traced up to $\frac{3}{4}$ in. from the apex.

Fig. 3.

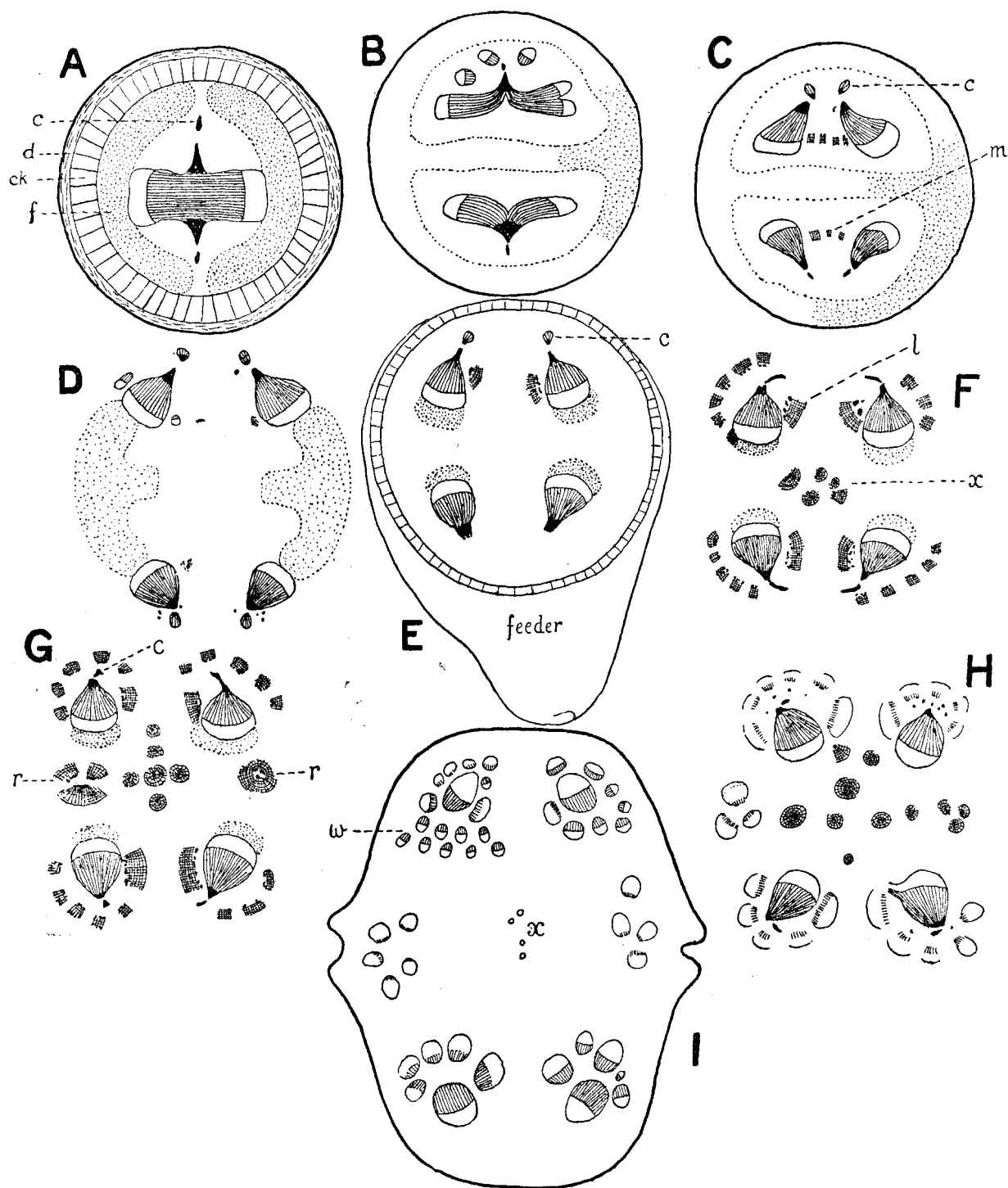
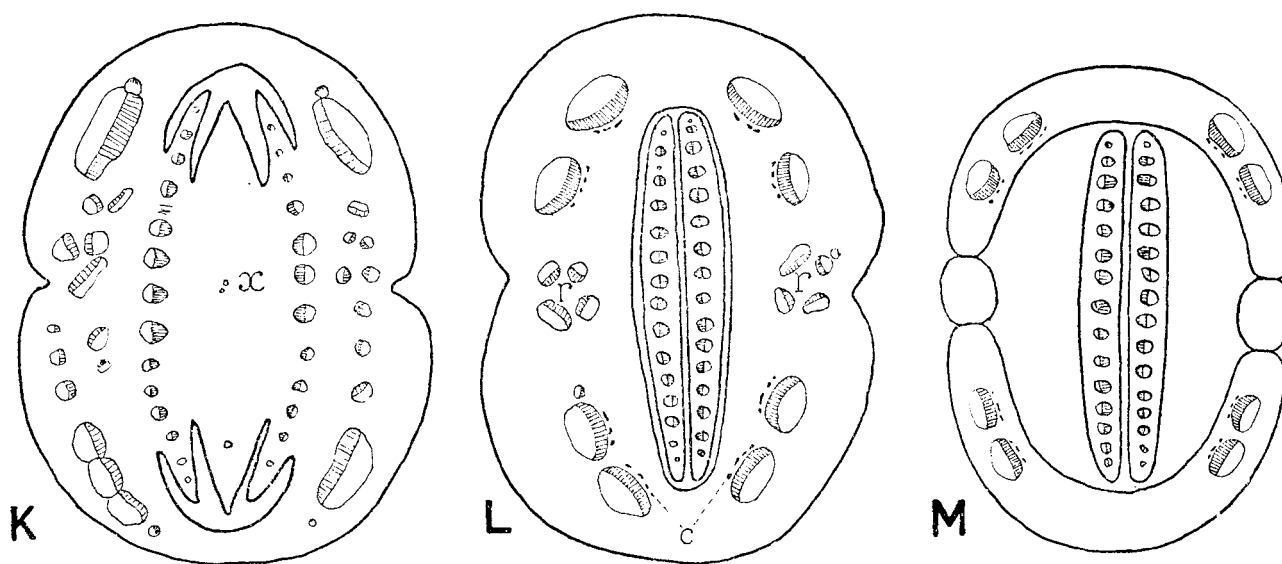


Fig. 3, A-M (described in text). *d*=dead cortex; *ck*=cork; *f*=fibres; *c*=outer isolated portion of xylem; *m*=meristematic divisions; *x*=bundles from ridges and cotyledonary buds &c., ending freely in pith; *r*=concentric series of bundles supplying ridges; *l*=main leaf-bundle. (Phloem=blank; xylem=shaded with fine lines; when a bundle consists merely of meristematic divisions it is represented by a cross-hatched area; fibres=dotted.) (K, L, M are inserted on the next page.)



in the hypocotyl *. Some suggestions of this arrangement are already visible at W, text-fig. 3, I.

The Vascular Supply of the Ridges.—In older seedlings this growing complexity makes it difficult to distinguish the four original cotyledonary bundles. This difficulty is increased and the distribution of the bundles made more irregular by the entrance of a large number of bundles from the ridges. It remains to draw attention to the presence of a few of these even in the young seedling just described.

At X, text-fig. 3, F, several bundles are seen ending freely in the pith. When these are traced upwards they tend to form two groups on the periphery of the hypocotyledonary vascular cylinder. These groups become (*r*, text-fig. 3, G) distinctly concentric, and their concentric arrangement is later still more obvious as they are traced upwards to their termination at the base of the developing outer ridge † (L, text-fig. 3).

Some of the bundles seen in the pith in F, G, H, text-fig. 3, end freely upwards; at their termination they are represented only by a few meristematic divisions (*x*, text-fig. 3, I, K). They probably represent the rudimentary vascular supply of the stem apex and cotyledonary buds ‡; in older seedlings no bundles were seen at the apex of the plant, but they were all prolonged into the cotyledonary buds. In a seedling in which the cotyledonary buds were very unequally developed (Pl. 34. fig. 6) the bundle-supply first appeared much lower down on one side than on the other.

In the older seedlings the elliptical series of numerous bundles § then supplying the ridge (text-fig. 4) becomes secondarily connected with the bundles in the hypocotyl; half of the bundles from the ridge joining one pole of the hypocotyledonary system, and half joining the other pole. Bower's material did not make it possible for him to trace the development and origin of the ridge-bundles, and he does not appear to have clearly

* Cf. concentric rings in the Cycadaceæ, Worsdell, 1896 &c., and in *Cycadella*, Wieland, p. 66, fig. 35.

† A similar concentric series of bundles was followed downwards and found to end freely in the hypocotyl of the rather older seedling shown in Pl. 34. fig. 6.

‡ Bower, II. p. 581.

§ *Ante*, p. 338.

distinguished the ridge-bundles from the later intercalated bundles of the leaf: he included both together in the "peripheral series" *.

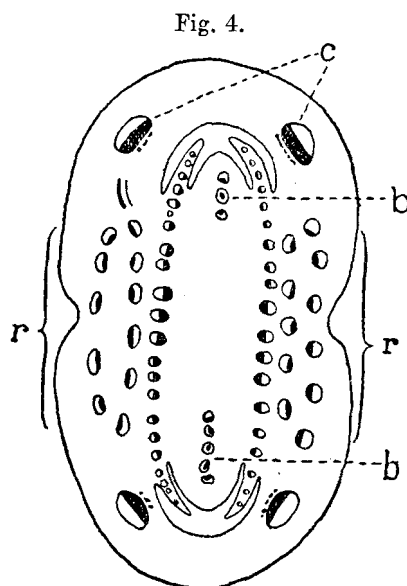


Fig. 4 represents a transverse section through the base of the leaf-groove in the seedling shown in Pl. 34. fig. 2. *r, r* represent the two elliptical series of bundles supplying the outer ridge; *b, b* = the row of bundles at the base of the cotyledonary buds; *c* = pair of bundles originally supplying a cotyledon. The bundles of each bud have a double origin from the two bundles supplying the cotyledon, in the axil of which the bud is borne.

It is of some interest that the bundles supplying the ridge originate in a manner so similar to those supplying the leaf which the ridge subtends. Both leaf and ridge receive a series of bundles which have a double attachment, being joined to one of the two bundles supplying each of the two cotyledons. There thus appears to be somewhat the same relation between the leaf and ridge-bundles as between the cotyledon and bud-bundles †.

Section VI.—COMPARISON OF THE TRANSITION PHENOMENA IN *WELWITSCHIA* WITH THOSE IN OTHER GYMNOSPERMS.

The peculiarities in the behaviour of the vascular system in *Welwitschia* depend largely on the extraordinary slowness of the transition from the four endarch collateral bundles entering the upper part of the hypocotyl to the characteristic radial structure of the normal diarch root, and it is probable that they are chiefly due to the unusual length of the swollen underground hypocotyl in this plant.

In this connection it is interesting to refer to the seedling (Pl. 34. fig. 6) already described, in which the remains of the feeder were present immediately beneath the swollen part of the hypocotyl, and there was thus no elongated unswollen part of the hypocotyl developed. Here the transition was much more rapid than in the normal

* Bower, II. pp. 581, 582.

† *Ante*, p. 340.

cedling, but still retained its distinctive features. In the figures * A indicates the upper level of the normal diarch root, at B x the two poles of the root have diverged, C is the level of the formation of four separate groups, and E is the level of the feeder. Above the feeder the four groups are rapidly separated by the increase in amount of parenchymatous tissue, at H they begin to assume their concentric character.

It has been seen that the main features of the transition-region are the rotation of each cotyledonary bundle as a whole, and the fact that, while the exarch structure characteristic of roots is thus at once established, the collateral structure characteristic of stem-bundles is still maintained throughout the hypocotyl and the upper part of the root.

The transition phenomena in *Araucaria* † present the strongest resemblance to those in *Welwitschia*. Here also two bundles enter from each cotyledon and, finally, form one pole of the diarch root. The four cotyledonary bundles rotate as a whole, but it is only for a very short time that the four exarch bundles thus formed retain their collateral structure. The four xylem groups rapidly fuse in pairs, and the four phloem groups, becoming detached from the xylem, also fuse in pairs, thus establishing a normal diarch root-structure.

In *Podocarpus* ‡ the process is similar in essentials, but is still more rapid. Here again two bundles enter from each of the two cotyledons, and begin to rotate as a whole. Almost immediately, however, the xylem groups fuse in pairs and the phloem groups separate from them, and also fusing form two bands alternating with the xylem groups.

In *Sequoia* § the general plan of the transition is somewhat different, but in this case also the cotyledonary bundles rotate as a whole, retaining for a short time their collateral structure.

A few other isolated cases occur in which the bundles rotate as a whole, so that they are for a short part of their course exarch and collateral ||, but in most Gymnosperms the transition is more rapid ¶; the xylem usually rotates alone, while the phloem group associated with it is separated from it before the bundle becomes exarch.

These few examples appear to suggest that the character of the transition phenomena is partly governed by the length of the hypocotyl, a factor probably to a large extent dependent on the habit of the plant; the long stage in *Welwitschia* in which the four collateral bundles have their xylems turned outwards is probably a special modification, and it does not appear that in this series a resemblance in such characters can be taken to denote phylogenetic relationship.

In the general features of their transition the Cycads do not resemble *Welwitschia*, but there are some remarkable points of comparison which appear to be of considerable interest. It will be remembered that the four collateral cotyledonary bundles in *Welwitschia* each form in the hypocotyl one constituent of a concentric group; such concentric groups are unique in character, but some parallel is afforded by the three

* Compare the relative levels in Pl. 34. fig. 4 b, described on p. 341.

† Hill, T. G., and De Fraine, II. 1909, p. 213.

‡ Hill, T. G., and De Fraine, I. 1908.

|| E. g. *Pinus contorta*; *Ibid.* I. 1908, p. 205.

§ *Ibid.* I. 1908, pl. 35. fig. 13.

¶ *Ibid.* I., II., III., 1908, 1909.

concentric steles found in the hypocotyls of *Encephalartos Barteri* * and of *Cycas siamensis* †.

An abnormal seedling of *Araucaria Bidwillii* ‡, in which Shaw found four concentric steles, should also be mentioned in this connection.

The smaller concentric bundles scattered in the parenchyma of the hypocotyl of *Welwitschia* may be compared with the anomalous concentric cortical strands which are a characteristic feature of the roots of some Cycads §.

Section VII.—CENTRIPETAL XYLEM IN THE SEEDLING.

Cotyledon and Ridge Bundles.—At the base of the cotyledons there are differentiated on the centripetal side of the cotyledonary bundles a small number of rather short broad tracheids with reticulately pitted walls (*cf.* L, M, text-fig. 3), which are often transversely connected with the bundles supplying the outer ridges. This centripetal wood dies out almost at once, before the bundles branch to form the parallel series which traverses the cotyledon: there is then no trace of centripetal elements.

In the 13 months old seedling no transfusion tissue was yet developed, and only a small amount of this tissue is present in connection with the bundles traversing the withering cotyledons of seedlings two to three years old. The transfusion tissue here first arises and is always best developed on the phloem side of the bundle, and it is not possible to trace any continuity between it and the centripetal xylem ||.

A varying number of transfusion tracheids accompany the ridge-bundles during the upper part of their course; these occur mainly on the centripetal side of the xylem. The centripetally-developed tracheids both here and in the cotyledonary bundles are somewhat intermediate in character between the centrifugal xylem and the short wide transfusion-tissue elements scattered throughout the parenchyma of the ridges ¶. There were no unmistakable indications of centripetal xylem in the young bundles of the leaf.

Hypocotyl.—It is not easy to follow the exact behaviour of the centripetal xylem when the cotyledonary bundles rotate and become exarch in the upper part of the hypocotyl. Scattered tracheids are present throughout the parenchyma in the centre of each of the four concentric groups of vascular tissue which are there formed, and a small group of primary xylem is also present (Pl. 35. fig. 22) on the outer edge of the protoxylem **. The primary xylem is indeed often separated into two distinct portions, both of which are more or less triangular in cross-section, the apices of the triangles being directed towards one another.

In the lower unswollen portion of the hypocotyl, after the concentric character of the

* Worsdell, V. pp. 136–137.

† Matte, p. 189, fig. 248.

‡ Shaw, F. J. F.; see also Seward & Ford, p. 334, fig. 16, and p. 344, fig. 19.

§ *Cf.* Hill, T. G., and De Fraine, III. p. 442, for concentric strand in young root of *Macrozamia*.

|| *Cf.* Scheit, who considers that the origin of the transfusion-tissue is always in the xylem (*ex* Worsdell, II. p. 303).

¶ *Cf.* Worsdell, V. p. 768.

** Bower remarks that the protoxylem in the hypocotyl is much elongated in a lateral direction, I. pl. 4. fig. 15, &c.

four groups has been lost, the differentiation of the primary xylem into two groups is still present. In some cases a little secondary xylem and even phloem are developed in connection with the smaller and outer portion (*cf.* C, text-fig. 3, E).

Root.—Still lower down the additional phloem group thus formed ends freely (*c*, text-fig. 3, C, p. 342), but the small mass of xylem extends much further downwards and appears and reappears throughout the root *, sometimes dwindling to a single tracheid †.

Text-figure 5, A–F, shows the changes which take place in this additional mass of xylem (*c*) in a portion of the root-system of the seedling shown in Pl. 34. fig. 2.

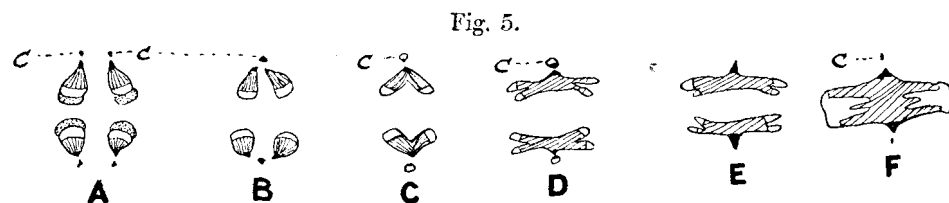


Fig. 5, A–F.—Phloem white; secondary xylem diagonally shaded; primary xylem black; fibres dotted.

It is to be noticed that at the fusion of the four hypocotyledonary bundles in pairs (B–C, text-fig. 5), the small outer masses of primary xylem fuse first, and the larger portions with the secondary xylem and phloem fuse later. At D the inner and outer groups of the primary xylem are seen to come into contact, and at E to fuse, but lower down at F a small group of four or five primary xylem elements is again separated off from the main bundle. At C and D a little phloem has been laid down in connection with the small outer group of primary xylem.

Section VIII.—ANATOMY OF THE ADULT HYPOCOTYLEDONARY STEM.

General.—Concerning the anatomy of the adult hypocotyl, I have little to add to the account given by previous authors ‡.

The four concentric groups are still visible in very old plants. Newly intercalated bundles entering from the leaves are arranged more or less definitely with relation to these four centres, often forming a series of concentric rings. It is not, however, easy to define the outer limits of the leaf-series, as it is at a late stage indistinguishable from the series of numerous bundles supplying the ridges and inflorescences. The two series together compose Bower's "peripheral series."

Histology of the Xylem.—In the root and lower regions of the hypocotyl the tracheids of the protoxylem are reticulate (Pl. 35. fig. 14), while those of the secondary xylem have a single or double row of bordered pits (Pl. 35. figs. 13 & 14). The bordered pits are not contiguous.

In the upper portion of the hypocotyl, and in the ridges and leaves, many of the tracheids have both reticulate thickening and oblique or horizontal bordered pits § (Pl. 35. fig. 24, C).

* *Cf. Ginkgo*, Hill & De Fraine, III. 1909.

† *Ante*, p. 337.

‡ Hooker, 1863; Bertrand, 1874; De Bary, 1884; Bower, II.

§ Compare Cupressineæ and some Leguminosæ.

Throughout the plant, except in the minute hair-like lateral rootlets *, there are also found wider elements, with three rows of bordered pits on their longitudinal walls, and having their transverse walls absorbed (Pl. 35. fig. 24 *a*, & Pl. 34. fig. 24 *b*) †, except for a small peripheral ridge ‡.

Comparative.—Since all the main essentials of seedling structure are preserved in the adult *Welwitschia*, it is obvious that the most important comparisons with other plants are those already made with various seedlings. I know of no recent plants whose stem anatomy can profitably be compared with the anatomy of the hypocotyl in *Welwitschia*; its whole adult structure is, however, strikingly reminiscent of that of the stems of some of the Medulloseæ.

The four concentric groups of secondary vascular tissue, each with tracheids scattered throughout its pith, are very like the large central steles of *Medullosa stellata* and the smaller but more irregularly arranged steles of *M. Solmsii*, while the peripheral series of secondary bundles, arranged as they often are in several concentric rings, may be compared with the outer rings of secondary elements in *M. stellata*, var. *gigantea*, &c. §

Resemblances in other respects between *Welwitschia* and the Medulloseæ have been indicated by the author elsewhere ||.

Section IX.—GENERAL CONCLUSIONS.

1. The mature plant may well be described as an “adult seedling”; the main axis is differentiated into root and hypocotyl, and bears, in addition to the two cotyledons with buds in their axils, only two plumular leaves at the base of a deep groove. On either side of this groove there is a ridge made up of rapidly dividing parenchymatous tissue. A study of the development of these ridges shows that the outer ridge arises as a small projection between the margins of the cotyledon bases; the accelerated growth producing the projection afterwards spreads laterally and gives rise to the long ridge. Similar accelerated meristematic growth, at the bases of the cotyledonary buds, produces the inner ridge on which the inflorescences are usually borne. Further development in this region causes the apex to be completely buried by the enlarged cotyledonary buds or lobes of the crown.

2. The small projection from which the *outer ridge* is developed receives at first a concentric ring of secondary bundles which end freely downwards in the hypocotyl. As the ridge grows, numerous additional bundles are intercalated, and secondary connections are established between the bundles of the hypocotyl and those of the ridges. The bundles of the inner ridge and inflorescences are connected with those of the outer ridge.

3. Owing probably to the great length of the hypocotyl, the *transition* from the structure at the apex of the plant to the root-structure is remarkably slow. The two bundles of the diarch root fork and give rise to two pairs of bundles; each of these original pairs supplies one of the cotyledons in the seedling; they are still prominent even in plants of

* *Ante*, pp. 334–5.

‡ De Bary, p. 335; Bertrand, 1874, p. 16 (*Ephedra* and *Gnetum*).

|| Sykes, 1910, I. p. 625, and II. *ined.*; cf. Worsdell on the Peduncle, IV. pp. 768–770.

† Cf. Gwynne-Vaughan.

§ Worsdell, V. pp. 133, 134.

considerable age, where they terminate in the outer ridge. The four collateral cotyledonary bundles are joined in the upper portion of the hypocotyl by the bundles which enter from the buds, ridges, and later from the leaves. The rotation of all the bundles takes place almost as soon as they enter the hypocotyl, and there is therefore not at any time a characteristic stem-like structure. The associated bundles form at once four concentric groups, but many of the more newly intercalated bundles of the leaves, &c., may be separately prolonged downwards for a greater or lesser distance before they become connected with one of these groups.

The bundles entering from a bud are joined on to both the constituents of the double trace of the cotyledon subtending the bud; but each ridge receives bundles which are connected with one member of each pair of cotyledonary bundles, and the same is true of the leaf, one half of each leaf-trace being associated with a member of each of the double cotyledonary traces.

4. The *method of transition* in *Welwitschia* is found to be most closely comparable with that in *Araucaria*. *Welwitschia*, *Araucaria*, *Podocarpus*, and some other forms make up a series, in all of which two bundles enter from each cotyledon and form one pole of the diarch root; in each case the collateral cotyledonary bundles rotate as a whole, and after a time the xylems of a pair of bundles fuse together, while the phloems leave them and fuse with the phloems of the other pair. The members of the series differ in the distance over which this process extends, according to the length of the hypocotyl. In other Gymnosperms the transition is still more rapid and the cotyledonary bundles do not rotate as a whole. It is thought probable that in this series the resemblance in the form of the transition is thus dependent on habit and not on relationship.

5. One of the most remarkable characteristics of the anatomical structure of *Welwitschia* is the *small amount of primary vascular tissue* in this plant. The development of primary xylem and phloem is limited to the poles of the root and the four main hypocotyledonary bundles, which are derived from the two poles, and which supply the cotyledons. The bundles supplying the two ridges and the inflorescences are clearly entirely derived from meristematic divisions of the parenchyma, and it is only later that they are connected by cambial divisions with the primary bundles.

The small size of the bundles in the cotyledonary buds makes it impossible to be certain whether or no there is any primary xylem present, but it appears most probable that there is none. The possibility remains that there is primary tissue in the two original pairs of bundles which first supplied the leaves. I have no material young enough in which to investigate this, as the first-formed xylem elements in quite young leaf-bundles get disrupted and separated from one another in consequence of the tension exerted by the rapid growth going on at the base of the leaf. But in the newly intercalated leaf-bundles all the xylem elements are arranged in tangential rows, and are continued downwards into the hypocotyl by secondarily developed elements, which connect them with the cotyledonary bundles (*m*, text-fig. 3, C). In the younger seedlings this connection is established by means of a meristem only, no xylem elements having yet been lignified.

In the young plant the bundles are all better developed and the xylem more strongly lignified in the upper part of their course through the ridges, inflorescences, and leaves than in their downward extensions into the hypocotyl. It would appear that vascular bundles are differentiated in the earlier stages of these organs, and are later continued downwards and become associated with the four original cotyledonary bundles, thus giving rise to the four concentric groups so characteristic of the hypocotyl of *Welwitschia*.

Such a series of facts appears to me to indicate that in this plant no distinction between primarily and secondarily developed vascular tissue is possible for purposes of morphology*.

6. *Centripetal xylem* is developed in connection with the four bundles in the bases of the cotyledons, and after the bundles have rotated a small isolated group of primary tracheids accompanies the four exarch bundles down the hypocotyl; and is also associated with the bundles of the root during the greater part of their course. It is obvious that this separate peripheral mass of primary xylem occupies the same position relative to the protoxylem as did the centripetal xylem in the cotyledonary bundles before they rotated, although its position relatively to the centre of the hypocotyl is now exarch.

In many of the outer series of bundles in the outer ridge, although these are entirely secondary, the first-formed elements are not the innermost ones, and some xylem is formed in both centrifugal and centripetal directions. In longitudinal section transfusion tracheids can also be seen on the centripetal side of many of the ridge-bundles: these merge gradually into the transfusion-tissue which is profusely scattered among the parenchyma.

7. It is difficult to make any close *comparison with other plants*. The retention of the seedling characters in the adult plant makes comparison with other seedlings of most interest, but since the vascular structure of seedlings probably depends to a remarkable extent on their habitat and environment, such comparison is probably not the most profitable for indicating relationships. The most remarkable character in *Welwitschia* is its four concentric groups of vascular tissue, with primary xylem tracheids scattered in their pith. Concentric steles are found in the hypocotyls of the seedling of some Cycads, and have been described in an abnormal seedling of *Araucaria Bidwillii*.

Such concentric groups are, however, most comparable with the several central steles of the Medulloseæ, and the peripheral series of secondary vascular bundles also recalls the outer rings of secondary vascular tissue in these plants.

8. The *method of branching* of the root when injured by stones or other obstacles has been described, and its investigation has afforded fresh evidence of the remarkable vitality of this plant. A seedling grown under conditions damper than the natural was found to develop a number of minute lateral rootlets.

9. Certain interesting *abnormalities* have been recorded in which (1) extra leaves have been produced in cases where the apex has not been completely buried, (2) one of the two normal leaves has been abnormally developed, or (3) further lobing of the cotyledonary buds has taken place. These have not thrown much light on the morphology of the plant.

* Worsdell, V. p. 141.

This investigation of seedling and adult plants of *Welwitschia* has served still further to confirm the previous impression of the aberrant nature of its structure, correlated as it doubtless is with its peculiar habitat and mode of life.

BIBLIOGRAPHY.

- BERTRAND, C. E.—Anatomie des Gnétacées et des Conifères. Paris, 1874; and Ann. Sc. Nat., Bot. sér. 5, tom. xx. (1874) p. 8.
- BOWER, F. O.—I. On the Germination and Histology of the Seedling of *Welwitschia mirabilis*. Q. J. M. S. vol. xxi. (1881) p. 15.
 II. On the further Development of *Welwitschia mirabilis*. Q. J. M. S. vol. xxi. (1881) p. 571.
- DE BARY, A.—Comparative Anatomy of Phanerogams and Ferns. Engl. ed. by F. O. Bower and D. H. Scott. Oxford, 1884.
- GWYNNE-VAUGHAN, D. T.—On the real Nature of the so-called Tracheides in Ferns. Ann. Bot. xxii., 1908.
- HENRIQUES, J. A.—*Tumboa Bainesii*. Trabalhos da Academia de Sciencias de Portugal, 1^{er} série, i. Lisboa, 1908; and Bot. Centralbl. 1909, No. 29.
- HILL, T. G., and H. DE FRAINE.—On the Seedling Structure of Gymnosperms.
 I. Ann. Bot. vol. xxii., 1908.
 II. „ „ vol. xxiii., 1909.
 III. „ „ vol. xxiii., 1909.
- HOOKE, J. D.—On *Welwitschia*, a new Genus of Gnetaceæ. Trans. Linn. Soc. Lond. vol. xxiv., 1863.
- MATTE, H.—Recherches sur l'appareil libéro-ligneux de Cycadacées. Thèse. Caen, 1904.
- MONTEIRO, D. J. N. de. *Welwitschia* Germination. Gard. Chron. n. s. xiv. (1880) p. 690.
- MONTEIRO, J. J. Angola and the River Congo, vol. ii. (1875) p. 228, pl. 15.
- NAUDIN, C. Gard. Chron. n. s. xvi. (1881) p. 217.
- PEARSON, H. H. W.—I. Some Observations on *Welwitschia mirabilis*. Phil. Trans. B, vol. cxviii., 1907.
 II. The Living *Welwitschia*. Nature, vol. lxxv., 1907.
 III. Further Observations on *Welwitschia*. Phil. Trans. B, vol. cc., 1909.
- SEWARD, A. C., and S. O. FORD.—The Araucariæ, Recent and Extinct. Phil. Trans. B, vol. ccxcvii., 1906.
- SHAW, F. J. F.—The Seedling Structure of *Araucaria Bidwillii*. Ann. Bot. vol. xxiii., 1909.
- SOLEREDER, H.—Systematic Anatomy of Dicotyledons. Engl. ed. by L. Boodle and F. E. Friisch. London, 1908.
- STRASBURGER, E.—Die Coniferen und die Gnetaceen. Jena, 1872.
- SYKES, M. G.—The Anatomy and Morphology of the Leaves and Inflorescences of *Welwitschia mirabilis*.
 I. Proc. Roy. Soc. vol. lxxxii. II. Phil. Trans. B, vol. cci., 1910. (Ined.)
- WEBER, O., and J. T. STERZEL.—Beiträge zur Kenntnis der Medulloseæ. Chemnitz, 1896.
- WIELAND, G. R.—American Fossil Cycads. Carnegie Inst., Washington, 1906.
- WORSDELL, W. C.—I. Anatomy of the Stem of *Macrozamia* compared with other Genera of Cycadaceæ. Ann. Bot. vol. x., 1896.
 II. On Transfusion Tissue. Trans. Linn. Soc. ser. 2, Bot. vol. v., 1897.
 III. The Vascular Structure of the Flowers of the Gnetaceæ. Ann. Bot. vol. xv., 1901.
 IV. Contribution to the Comparative Anatomy of the Cycadaceæ. Trans. Linn. Soc. ser. 2, Bot. vol. vi., 1901.
 V. The Structure and Origin of the Cycadaceæ. Ann. Bot. vol. xx., 1906.

EXPLANATION OF THE PLATES.

PLATE 34.

Figs. 1 & 1 *a* are drawn from seedlings grown in the Botanic Garden, Cambridge ; the other seedlings figured were obtained from Professor Pearson's material.

(Except when otherwise mentioned, the drawings are life-size.)

Fig. 1. Seedling about 13 months old. C=cotyledon ; P=leaf ; R=small swelling projecting from the common bases of the cotyledons at their point of junction ; F=feeder still enclosed in seed-coat ; B=bifurcation of root ; H=minute lateral rootlets.

1 *a*. A young seedling of about 24 months. A small ridge (R) is here shown, and is evidently derived from one of the processes (R) seen in fig. 1. A triangular portion (T) beneath the ridge has been intercalated between the bases of the old cotyledons, which are, however, still marked by a small projecting edge (*c*), which is prolonged for a short distance in a downward direction. L=back-turned plumular leaf ; C', C'=bases of old cotyledons.

2 *a* & *b*. Older seedling. Y=the swollen portion of the hypocotyl ; X=slightly flattened top of hypocotyl, with the ragged remains of the base of the cotyledons (C) ; L=one of the plumular leaves (the other has been removed) ; B=buds in the axils of the cotyledons ; G=groove at the base of which the leaves take their origin ; R=ridge formed partly from the bases of the old cotyledons and partly from the further growth of the swellings seen in fig. 1.

3. Seedling a good deal larger and probably somewhat older than that shown in fig. 2, but in some respects less advanced in development. K=upper cylindrical portion formed by the further swelling of the fusiform hypocotyl ; U=unswollen part of hypocotyl ; C=downward sloping scars, which represent part of the areas of attachment of the two old cotyledons, now separated from one another by the growth of the region between the cotyledons, which has resulted in the formation of a more or less triangular portion (T), the triangle having its apex directed downwards ; the ridges (R) are still separate and do not extend round the ends of the groove, but are limited to its two sides. Other letters as before.

4 *a*. An older seedling. Br=a small ridge, the inner lip of the leaf-groove, which has now grown up round the base of each of the buds (B).

4 *b*. The same seedling, seen in another position. Letters denote levels determined by sections :— A=the upper level of the diarch root-structure ; between A and C a gradual separation of the two poles of the diarch root takes place which is complete at Bx ; C=the level at which the separation of the xylem and phloem groups at the two poles begins, resulting in the formation of four exarch collateral bundles ; E is the probable original level of attachment of the seed, as judged by the drawing out of two of the bundles opposite the point of attachment of the feeder ; at F the four groups become more or less concentric ; H is the level of the base of the ends of the groove and the origin of the cotyledonary buds ; L, a little higher, is the level of attachment of the base of the plumular leaves at the sides of the groove. It is seen that the groove is deeper at the ends where the buds arise than at the sides, where it is raised up by the growth of the bases of the leaves.

4 *c*. The same seedling seen from above, after the removal of the tops of the buds. The inner ridge (Br) at the base of the buds is seen to be continuous round the two buds, but not to pass in between them. Other letters as before. (× 2.)

5. Top of a young plant, showing one of the cotyledonary buds divided into three lobes.

- Fig. 6. Young seedling in which the hypocotyl is unusually short, the feeder being still present immediately beneath the swollen portion. The two leaves of the seedling were contiguous by their adjacent faces and the cotyledonary buds were very minute. Letters as in fig. 4 *b*. For description see text, pp. 343-4.
7. Young plant with widely diverging cotyledonary buds, each surrounded by a separate inner ridge. Between the two buds is seen the structure A, which is described in the text, p. 332.
- 8 *a*. Top of a young plant with unfused cotyledonary buds seen from above. One leaf has been removed, the other is torn and part of it only is present. This part (p^2) is in an abnormal position, between the two cotyledonary buds. In fig. 8 *b*, drawn from a side view of the plant, the whole of the base of this abnormal leaf is visible, and it is seen that, while half of it is situated in the leaf-groove (G_1), the other half passes round one of the cotyledonary buds and takes its origin from the groove separating the two buds. The other half of the "leaf-groove" (G_2) is unoccupied by any portion of the leaf. B_3, B_4 = extra lobes of the crown, originating from the base of the groove, *outside the leaf*. The ridge (Br) round the left lobe of the crown is unusually well developed and is zoned.
- 9 *a*. Top of a plant seen from above. All trace of the original separate development of the two lobes of the crown is lost, except for some indications of the line of fusion seen at F. Indentations at O, O' still afford evidence of the double origin of the two ridges. A young inflorescence is seen.
- 9 *b*. Same plant, seen from the side. A portion of the lower ridge has been removed, in order to show clearly the origin of the young inflorescence from the inner ridge.
- 10 *a*. Transverse section through structure *a* in fig. 7, taken about halfway between its base and apex. F = fibres; L = cells with lignified walls. $\times 116$.
- 10 *b*. Ditto, higher up than 10 *a*, showing fully developed group of fibres. $\times 116$.
11. Diagram of section through young inflorescence and inner ridge in fig. 9 *a*. Shows origin of inflorescence from base of pit, supplied by several vascular bundles. B = section through brown upper portion of the crown. $\times 2$.
- 24 *b*. (See explanation to Plate 35.)

PLATE 35.

- Fig. 12. Transverse section of minute hair-like lateral rootlet, from seedling grown in the Cambridge University Botanic Garden. B = decayed cortex, &c.; C = corky cells; P = phloem; X = xylem. $\times 170$.
13. Part of longitudinal section through similar but older rootlet. F, F = thick-walled unlignified fibres; P = sieve-tube; X = xylem. $\times 170$.
14. Part of longitudinal section of main root. Pxy = protoxylem; C = tracheid separated from the protoxylem by two layers of parenchyma. $\times 170$.
- 15 *a*. Transverse section through concentric ring of bundles at the base of small protuberant outgrowth (the ridge primordium) shown at R in Pl. 34. fig. 1. C = point of junction of the bases of the cotyledons. $\times 116$.
- 15 *b*. Transverse section of the other similar outgrowth on the same plant. $\times 116$.
16. Transverse section not far from the top of the outer ridge of the plant shown in Pl. 34. fig. 2. Tr = transfusion-tissue at the common endings of the bundles of the two series; F = fibres; St = stomata; C = corky tissue. $\times 50$.
17. Transverse section of young cotyledonary bud in Pl. 34. fig. 2, showing elongated series of vascular bundles. C = cork; A, a' , a'' end in a common concentric bundle; B and b' in a second ditto. $\times 170$.

- Fig. 18. Transverse section of lobe of the crown in fig. 4. O = original bud-bundles ; R = irregular bundles supplying inner ridge. $\times 75$.
19. A small part of a transverse section through the outer ridge of the plant in Pl. 34. fig. 2. F = calcium oxalate fibre ; Tr = transfusion tracheid. $\times 170$.
20. Bundle from outer series in the outer ridge of plant drawn in Pl. 34. fig. 2. Cf = centrifugal side of bundle ; Cp = centripetal side of bundle ; Pxy = protoxylem ; Ph = phloem ; Tr = transfusion tracheid. $\times 116$.
21. Transverse section of bundle from young inflorescence axis, showing all the elements to be arranged in radial rows. $\times 170$.
22. One of four concentric groups of vascular tissue in the hypocotyl of the young seedling shown in Pl. 34. fig. 1. C = bundle supplying cotyledon ; L = bundles supplying leaf ; the other bundles probably represent the newly intercalated secondary leaf-bundles and the bud-bundles. Note the scattered tracheids in the centre of the group and the protoxylem group at the apex of bundle C. (See text, p. 341.) $\times 170$.
23. Diagram of C-shaped leaf-trace supplying the abnormal leaf in the plant drawn in Pl. 34. fig. 8. LG = boundary of leaf-groove.
- 24 a, c, & 24 b (see Pl. 34). Various elements of the xylem showing pitting and thickening. V = vessel ; T = tracheid.



