

XIV. *The Comparative Anatomy of certain Species of Encephalartos, Lehm.*
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(Plate XLIII.)

Read 16th November, 1899.

THERE may be said to be two types of structure prevailing in the stems of the Cycadaceæ—viz., the one in which there occurs a single vascular cylinder, as in the majority of Dicotyledons; the other in which there is more than one cylinder, often as many as a dozen. There are three genera which present this last type of structure, viz., *Cycas*, *Macrozamia*, and *Encephalartos*. Of these, the first two have already been worked out and described in detail; the third, although the main features of its structure have been superficially touched upon and referred to, has yet to be treated in the same way as the others have been. This detailed account of the structure I propose giving in the following pages.

HISTORICAL SURVEY.

Mohl* in his paper, "Ueber den Bau des Cycadeenstammes," shortly describes the structure of *Encephalartos* under the generic name of "*Zamia*." He distinctly mentions the occurrence of the medullary system of bundles, and states that of a second vascular cylinder there are only very inconspicuous traces. The species described by him under the old generic name were *Encephalartos latifolia* and *E. horrida*.

Miquel's monograph† includes many species of *Encephalartos*, but, naturally, very little information as to the anatomical structure is given.

Mettenius‡, in his excellent work on Cycadean anatomy, treats briefly of the principal features of the stem-structure of *Encephalartos*, as also of *Cycas*, *Dioon*, and *Zamia muricata*.

ENCEPHALARTOS CAFFER, Lehm.

General Structure.

Having obtained from Mr. Wm. Bull, of Chelsea, an old plant of *Encephalartos caffer*, Lehm., with a stem about 9 inches in diameter, I was enabled to carefully investigate its anatomical structure and to compare it with that of *Cycas* and *Macrozamia*. I have found the structure to be extremely similar to that of the latter genus—so similar, in

* Abhandl. der königl. bay. Akad. zu München, i. 1832, pp. 397–442; republished and revised in 'Vermischte Schriften,' 1845, pp. 195–211.

† Monographia Cycadearum, 1842.

‡ "Beiträge zur Anatomie der Cycadeen," Abhandl. der königl. sächs. Gesellsch. der Wiss. vii. 1861, pp. 565–609.

fact, that it appears surprising that the plants should be placed by systematists in distinct genera. In view, therefore, of this fact, it will not be necessary to describe the structure of this plant in any great detail.

The main features of this structure are, as in *Macrozamia Fraseri*, Miq., the possession of a wide pith, traversed by an anastomosing system of vascular bundles and mucilage-canals; a number (4 or 5) of vascular cylinders extremely broken up by medullary rays, so as to be composed of distinct wedge-shaped segments, often widely separated from each other; a thick cortex, traversed by innumerable leaf-trace bundles, and bounded on its outer periphery by the leaf-bases.

I will now proceed to briefly describe the structure in the different regions of the stem, restricting my remarks to those points only in which the structure differs from that of *Macrozamia Fraseri*, Miq.

Cortex.

There is as yet, in this plant, no sign of any formation of periderm at the periphery of the cortex cutting off the leaf-bases; the tissue of these latter is still fresh and directly continuous with that of the cortex.

The mass of tracheides, constituting a large bulk of each girdle-leaf-trace bundle, possess reticulate, but never or rarely spiral thickenings, and thus do not present so great a resemblance to protoxylem as is the case in *Macrozamia Fraseri*, Miq.*. The rest of the secondary tracheides on the lower side of each girdle-trace, which may form a considerable thickness of the bundle, possess scalariform pittings on their walls, which may either extend the whole way across the wall, so as to present the appearance of a close spiral, or may form several rows of short pits as in the Ferns (Pl. XLIII. fig. 1).

The Vascular Zones.

In the lower part of the stem about *five* distinct zones or cylinders of vascular tissue are observed (fig. 2); thus rather more than in *Macrozamia Fraseri*, Miq. These in the upper and younger part of the stem dwindle to two zones. Here and there large segments or bundles can be seen lying, apparently quite out of place and somewhat obliquely, between any two of the rings (fig. 2); these constitute the connections between the successive vascular rings—a function which cannot be discerned from an examination of a single transverse section alone, but can be readily made out from a series of such, as also from a radial section (fig. 3); in the ordinary cross-section these strands appear merely as irregularly-placed segments of the rings. In describing the structure of the *Macrozamia* I omitted to draw attention to their presence, as they were much less obvious in that plant.

Fig. 2 is a diagrammatic view of a portion of a transverse section of an unknown species of *Encephalartos* from the collection in the large Kew Museum, and affords an excellent illustration of the general type of vascular structure of this genus as described above.

* Worsdell, "The Anatomy of the Stem of *Macrozamia* compared with that of other Genera of the Cycadeæ," Ann. Bot. vol. x. 1896.

Throughout the stem and, at least in the upper portion, in more than one of the zones, the younger sieve-tubes of the phloem exhibit on their oblique terminal or radial walls, as seen in transverse section, distinct traces of callus on the sieve-plates, stained with a watery solution of aniline blue, although this substance appears to be much less frequently present in the lower and older than in the upper and younger part of the stem.

Although the character is one found also in *Macrozamia*, I consider it important to state that the curious, irregularly-shaped tracheides described in that plant and in *Cycas* also occur here, scattered amongst the cells of the ground-tissue and the sclerides, *on the inner side of the xylem between two successive vascular rings*. These tracheides I regard as homologous with the tracheides occupying the centre of the concentric vascular strands in the cortex of the stem and root of *Cycas*, and of those strands which constitute the chief vascular structure of the Medulloseæ.

Owing to the early obliteration of the protoxylem elements as seen in the case of the innermost vascular zone, no criterion must be sought from the (apparent) absence or presence of protoxylem in the outer zones as to the primary or secondary origin of the latter. This important point can only be satisfactorily settled by reference to the upper part of the stem near the apex, where the second vascular zone can clearly be observed to originate in cambial divisions arising from the parenchymatous tissue immediately outside the phloem of the primary vascular zone, and which Costantin and Morot determined to be the pericycle*.

A point which was not observed in *Macrozamia* is the fact that the cambiums of most of the vascular zones appear to be all active at the same time, for, in at least three or four out of the five zones, narrow and extremely thin-walled cells, with very conspicuous nuclei, were observed, both cell-walls and nuclei staining deeply with hæmatoxylin. This seems to point to the fact that the cambiums of the older zones, as that of each successive new zone arises, do not cease to be functional (at least in this instance), as has been stated to be the case by various authors for other plants, but rather that new elements are added to all or most of the zones simultaneously for a prolonged period.

An important and, indeed, the only apparent difference between the structure of the stem of this genus and that of the stem of *Macrozamia Fraseri*, Miq., is the absence, or apparent absence, in the former of the highly interesting tertiary strands with inverted orientation, whose character and homologies were fully discussed in my former paper. Although careful search was made, I could detect absolutely no trace of any such structure in this stem. This does not, however, preclude the possibility of their being present in some other species; and it is quite probable that they would not be found in all species of *Macrozamia*.

In the larger meshes of the network exhibited by a tangential section of the phloem of any of the vascular zones are seen the leaf-trace bundles accompanied always by a mucilage-canal, the latter passing right through to the pith, for there is a continuous system of these mucilage-canals throughout the entire parenchymatous system of the

* Bulletin de la Société Botanique de France, xxxii. 1885, pp. 173-175.

plant. The individuality of the leaf-trace bundle is destroyed soon after it enters the xylem of the innermost zone, for it here gives off connections during its inward course to the strands of this tissue, so that a complete transversely-sectioned bundle is not usually observed in the larger meshes of the xylem-network as is the case in the phloem.

The Pith.

The individual bundles forming the complex *medullary vascular system* are similar in form to the segments composing the vascular zones (fig. 4); those in the lower part of the stem are, naturally, by far the largest and equal in size to those segments, consisting almost entirely of secondary xylem and phloem, with a few small, irregularly-placed, reticulate tracheides, which represent the primary xylem of these bundles. Several radial rows of vascular tissue may be formed around a mucilage-canal separated by rows of parenchyma-cells which represent medullary rays (fig. 6).

Mohl* states that the medullary bundles of *Encephalartos* pass through the medullary rays and become connected in the cortex with the leaf-trace bundles. This statement, however, as I have been careful to determine, is an erroneous one. The medullary bundles constitute a vascular system quite independent of that of the leaf-traces. They penetrate the inner vascular zone by the medullary rays (fig. 7), their tracheides uniting with the similar elements of that zone (fig. 8). This latter diagrammatic figure illustrates remarkably well the point above referred to, for a leaf-trace bundle from the cortex is here shown fusing with the same vascular zone and in close proximity to the point of fusion of the medullary bundle, but, it is to be noticed, quite independently of the latter. Fig. 7 represents a tangential section of the xylem of the inner vascular zone with a medullary bundle lying obliquely in the ray and about to fuse with the adjoining strands; a mucilage-canal is seen to be accompanying the bundle.

Structure of the Roots.

The original primary tap-root of the plant had completely died away, and had been succeeded by a number of *adventitious* roots springing from the flattened and partially decayed lower end of the stem.

It appears that these plants, which grow in clefts of rocks in the hilly country of South Africa, have, at a certain season of the year, to endure a dry season, during which their tap-root entirely dies away, along with, presumably, the foliage. During this period the stem, swollen as it is with its massive parenchymatous tissues and protected externally by the thick and coriaceous leaf-bases, probably acts as a water-reservoir by means of the network of mucilage-canals penetrating every part of the organ, the mucilaginous secretion serving to retain every particle of moisture previously absorbed by the root, and thus to preserve the stem from desiccation. It seems to me that this is a very probable explanation of the presence of such a vast system of mucilage-secreting canals in the stems of Cycads. It is a significant fact in this connection that *the roots are*

* Vermischte Schriften, 1845, p. 200

entirely devoid of mucilage-canals. At the end of the dry season adventitious roots are emitted by the stem, fresh leaves are put forth, and growth proceeds as before.

A transverse section through the upper and thickest portion of one of the adventitious roots, close to its junction with the stem, exhibits a very thick cylinder of xylem enclosing a fairly wide pith; the phloem is very much narrower than the xylem and the inner contour of the xylem is almost circular, and I could not discern how many protoxylem-groups were present. Great numbers of sclerotic cells occur in all the parenchymatous tissues and in the phloem. *Mucilage-cells are absent.*

The most interesting feature of the root is the presence, immediately outside the large cylinder, of one or two smaller cylinders or concentric strands, which are possibly not entirely closed on their inner side. Their elements are extremely irregular in position and course, many of the segments composing them running tangentially instead of vertically. Each encloses a pith containing great numbers of sclerotic cells. They are probably entirely secondary in origin, and are doubtless homologous with the similar strands occurring in the roots of *Cycas revoluta* *, Thunb. They fuse with the main cylinder lower down, and thus occur only in the upper and oldest part of the root where it adjoins the stem.

In one thick root examined the pith of the large cylinder is full of tracheides, contorted and involuted in every conceivable direction. They appear to be merely tracheides of the inner part of the xylem, which has, for some strange reason, assumed this unwonted and anomalous course in the pith.

Younger roots are triarch and diarch in structure.

ENCEPHALARTOS HORRIDUS, Lehm.

I examined a plant of this species from the Palm-house at Kew, having an axis 4-6 inches in thickness.

The central cylinder of the stem gradually narrows in diameter as it passes down into the *tap-root*, which in this specimen is preserved. Considerable irregularity prevails in the setting and position of the tissues in the lower region of the stem. On one side of the cylinder, in the transitional region between stem and root, and immediately on its outer periphery, as seen in transverse section, occurs a large vascular strand with a great amount of xylem and phloem, all probably of secondary origin (fig. 9, *cs*¹). This strand evinces a tendency towards a *concentric* structure. It is perfectly similar to and homologous with the semi-concentric strands situated on the periphery of the central cylinder, which some time ago I noted in the transitional region between root and stem of a small plant of *Macrozamia Denisonii*, F. Muell., as also with the similar strands in the same region in *Cycas revoluta*, Thunb. Like those in the latter plants, the strand under consideration has connections with the central cylinder. On the dorsal side of, and closely abutting on, this large strand occur at one level two other smaller ones of the ordinary collateral structure and orientation (*cs*²). At another level two strands are seen, one on each side of the large one, each with a considerable amount of

* Worsdell, "The Comparative Anatomy of certain Genera of the Cycadaceæ," Journ. Linn. Soc., Bot. vol. xxxiii. 1898, p. 440, pl. 20. fig. 5.

secondary thickening, one of which has *inverted orientation*, *i. e.*, with its xylem directed *outwards*, and which, if traced to another level, is seen to fuse with the central cylinder. The strand on the other side eventually fuses with the large semi-concentric one. Further out in the cortex are scattered other much smaller bundles with *inverted orientation* (*cs*³). Another group of three bundles was observed, with *their xylems mutually directed towards each other* (*cs*⁴).

All these smaller strands I regard, with the larger one above described, as being cauline in origin, both on account of their peculiar orientation and grouping, and the fact that no leaf-bundles exhibiting the normal orientation and course are present in the cortex of this transitional region, but only first make their appearance at a higher level.

All these cauline strands are found only in this transitional region between stem and root, and are both above and below this region no longer to be met with. The great importance of this point will be fully dealt with later on. The large strand is, as in *Macrozamia Denisonii*, F. Muell., probably continuous in both directions with the central cylinder, as also, in all likelihood, is the case with the smaller normally-orientated strands immediately abutting on its dorsal side. But, unfortunately, not one of these strands was distinctly traced throughout its whole course.

At the same level at which these cortical cauline strands appear, the central cylinder at one point exhibits a most peculiar anomaly, inasmuch as it there undergoes a curious invagination, so that an arc of bundles, all more or less intimately united laterally, is seen projecting into the pith.

An outer vascular zone has not yet arisen in this stem similar to that in the last species. But there cannot be much doubt that the strands above described represent the first beginning, although on one side of the stem only, of the outer vascular zones, each strand representing in reality a single segment of a whole ring.

At a somewhat higher level the leaf-trace bundles appear in the cortex, so that it is possible, what could not be certainly made out from the structure of the central cylinder, that the region below this level belongs to the root rather than to the stem, although mucilage-canals are there present both in pith and cortex, and medullary bundles are also abundant.

The tap-root is exceedingly thick and swollen in one portion of its length, so that the xylem becomes broken up by the expanding parenchymatous tissues into a large number of scattered fragments.

ENCEPHALARTOS LANUGINOSUS, Lehm.

One out of a number of lateral branches arising low down on the stem beneath the level of the soil was afforded me for investigation. The plant, for the branch had become independent by developing a thick adventitious root simulating very closely both in position and structure a primary tap-root, has about the same thickness of stem as the last species described.

The lower part of the stem, which has a very much less diameter than the major portion, shows, as regards development of vascular tissue, a very great advance on

E. horridus, Lehm. Three or four vascular zones, greatly divided up into distinct segments in places and very irregular in position, are already formed. The pith in the lowest part of the stem is extremely small in area, and traversed by strands running across from one part of the cylinder to the other. Higher up in the stem only two vascular zones are present; the origin of the second one, from cambial divisions taking place in the parenchyma 8 or 10 layers of cells away from the first zone, is very clearly seen in the uppermost part of the stem.

Medullary bundles and mucilage-canals are very sparse in this plant, at least at this stage of its development.

A curious concentric grouping of bundles in the cortex was observed in one transverse section from the lower part of the stem, reminding one of a similar case seen in the cortex of the stem of *Macrozamia Fraseri*, Miq., and of the concentric grouping of the leaf-trace bundles in the *Medulloseæ*.

In some of the radial sections of the vascular zones the large, reticulate tracheides resembling transfusion-tissue are very clearly recognized amongst the parenchyma-cells between the two zones.

Structure of the Root.

The thick adventitious root has a structure which is, doubtless, quite similar to that which the primary tap-root would have presented had it been present. Developed around a small pith are two very thick vascular zones. At one point, immediately on the outer periphery of the second zone, is a thick strand of secondary tissue, curved slightly inwards at each end, similar, although not so far advanced towards the concentric structure, as the large cortical strand described above for *E. horridus*, Lehm. Thus we find here the same structure as in the transitional region between stem and root in *E. horridus*, Lehm., with the exception that in the latter one vascular zone instead of two is developed.

The structure of an adventitious branch of *E. Altensteinii*, Lehm., was also examined, but as it reveals nothing fresh, but exhibits essentially the same structure as that of *E. lanuginosus*, Lehm., a separate description thereof is not deemed necessary.

SUMMARY AND GENERAL CONCLUSIONS.

The following are the chief results, with the conclusions I formulate therefrom, which accrue from the comparative investigation of the above species of *Encephalartos* :—

1. The structure of the vegetative organs, consisting of stem, leaf, and root, of the four species of *Encephalartos* is in almost all respects similar to that of the two species of *Macrozamia*, viz., *M. Fraseri*, Miq., and *M. Denisonii*, F. Muell., already investigated by me.

The difference in the reproductive organs between the two genera, upon which systematists have hitherto founded their classification, appears to me to consist of quite

minor points, the most essential characters being common to the two genera. This fact, taken together with the intimate agreement of the two in their vegetative structure, seems to me to be strongly in favour of the future union of these two genera into a single one by systematists.

I may here remark that the Cycadaceæ afford a striking instance of a case where the anatomy, even more in some instances than the reproductive parts, may afford an important basis for classification, not only with regard to the different genera amongst themselves, but with regard also to living plants of other groups, and especially to fossil forms.

2. The occurrence in three of the species examined of more than one vascular ring, as is the case in *Cycas* and *Macrozamia*. My specimen of one of these species is a plant many years of age; the others are adventitious branches of very old plants; all possess adventitious roots only.

3. The fourth species (*E. horridus*, Lehm.), a seedling plant still retaining its primary tap-root, exhibits as yet but a single vascular ring. But in the transitional region between stem and root occur a single large cauline strand and several smaller ones, such as have been described in the main part of the paper above. With regard to these vascular strands I would here adduce the following considerations:—

a. The plant exhibiting this structure, with its primary tap-root still retained, must necessarily be at a much younger stage of development than any of the other three species.

b. This being so, it is quite natural to find the outer vascular rings as yet undeveloped. But I hold that the large vascular strand cs^1 and the much smaller ones cs^2 of fig. 10 represent the first sporadic and local beginnings of the second and third vascular rings respectively. At a later stage of growth cambial divisions would extend all round and give rise to the second and third rings in their entirety.

c. I have stated that the small *inverted* tertiary strands of *Macrozamia Fraseri*, Miq., are absent or indistinguishable in *Encephalartos caffer*, Lehm. This is true. But in *E. horridus*, Lehm., there exist strands with inverted orientation, of which cs^3 , fig. 10, is an example. This small isolated bundle I regard as a representative of part of the *fourth* vascular ring and perfectly homologous with the inverted strands belonging to the vascular rings in *Macrozamia Fraseri*, Miq.

4. The large, irregularly-shaped, reticulately-thickened tracheides occur, as in *Macrozamia* and *Cycas*, between the xylem of an outer and the phloem of the next inner vascular ring. They are the first-formed, probably secondary tracheides of the former, and may be considered as homologous with the reticulate tracheides occupying the central region of the cortical concentric strands of the stem and root of *Cycas*. I may here add, with regard to these elements, some observations on the first origin of the vascular tissues outside the central cylinder or stele, as noticed in a young stem of *Cycas revoluta*, Thunb., where the second vascular ring was making its earliest appearance, and in the upper hypocotyledonary portion of the primary tap-root of a seedling of the same plant, where one of the small concentric strands was becoming differentiated immediately outside the central stele. In both these cases it was observed that the first-

formed vascular elements arose by tangential division of the large, rounded or angular, cortical or pericyclic cells, resulting in the large, isodiametric, irregularly-shaped tracheides of precisely similar shape to those cells. After one or more of such elements have been cut off, the parenchyma-cells begin to divide radially as well as tangentially, in this way forming smaller and smaller elements with each centrifugal division, until at length the majority of the tracheides are of the same size and shape as those of the central cylinder or stele. The large first-formed tracheides very soon become displaced owing to the pressure of surrounding tissues. This fact, together with that of the great difference in size between these and the later-formed tracheides, renders the determination of their mode of origin, at an older stage of the same vascular tissues, utterly obscure. The similar reticulate tracheides in the cortical concentric strands, more distant from the central cylinder in the stem of *Cycas*, in all probability arise in precisely the same way, but, in that case, I did not succeed in definitely determining their mode of origin.

5. The cambium of several of the vascular zones is, judging from the appearance presented by its cells, simultaneously active.

6. All the secondary tracheides of the leaf-trace bundles possess dense spiral or, more probably, scalariform thickenings, thus differing somewhat from the leaf-traces of *Macrozamia Fraseri*, Miq., where only a certain number of the secondary tracheides are spirally thickened.

7. A medullary system of bundles occurs in all four species, similar in every respect to that of *Macrozamia Fraseri*, Miq. This system is intimately connected with a similarly-anastomosing network of mucilage-canals which is continuous with that of the cortex. The medullary vascular system is, however, quite independent of the leaf-trace system of the cortex. The bundles are *primary* in origin.

Although the presence of a medullary vascular system would appear, so far as one can judge from the examination of but four species, to be universal in the genus *Encephalartos*, the same cannot be said of *Macrozamia*, for no trace of such a system could be detected in the stems of either *M. Denisonii*, F. Muell., or *M. spiralis*, Miq., although it is possible that the latter plant was at rather too young a stage of growth to be able to exhibit the structure.

8. When the plant, growing in its native habitat, has reached a certain age, the primary tap-root dies away as the dry season approaches. The mucilage-canal system then probably acts as a water-reservoir. Next season adventitious roots arise. These exhibit in their upper and older portion a structure similar in many respects to that of the primary root of *E. horridus*, Lehm., viz., either one or two vascular rings and one or more semi-concentric cortical strands.

Finally, after the above observations on the extremely interesting structures in the vegetative organs of *Encephalartos*, I should like, before concluding the paper, to bring forward some considerations with regard to the phylogenetic relationships of the Cycadaceæ, suggested by the contemplation of the various structures in this genus.

In the first place, I wish to restate the generalization made or inferred in my account of the anatomy of *Macrozamia Fraseri*, Miq., viz., that the stem-structure (as also, of course, that of the upper portion of the root) is in all probability derived from the

structure of the same parts in fossil plants identical with or closely allied to the Medulloseæ. The formation of the successive vascular rings would have been brought about as follows:—The original structure in the Medulloseæ “consisted,” to quote my former words, “of rings or layers of concentric vascular strands. . . . As time went on, and greater specialization in the conducting-tissues arose, and a need for the formation of a larger amount of this tissue became urgent, the cambium of the inner portion of each such concentric strand gradually became less and less functional, that of the outer portion, on the contrary, more and more active, so that a much larger quantity of wood and bast became formed on the outer side of each strand than on the inner side, for this was the surest and best means of economizing both space and expenditure in the building up of an efficient conducting-tissue for the stem. The result is, finally, the structure, as we at present know it, in the stem of *Cycas*, *Encephalartos*, and *Macrozamia*.”

Dr. D. H. Scott, in his extremely interesting and valuable paper on the structure of *Medullosa anglica*, holds the above view to be “fallacious,” on the ground that “the primary ground-plan of the stem-structure of a polystelic *Medullosa* was fundamentally different from that of the monostelic Cycadaceæ.” For myself, however, and with all deference to the authority and experience of the author just quoted, the primary ground-plan of the two structures cannot be regarded as “fundamentally different,” inasmuch as I hold (which Dr. Scott does not) that in the “monostelic” genera—*Stangeria*, *Ceratozamia*, *Zamia*, *Bowenia*—there is evidence for the derivation of the central cylinder of the stem from a ring of steles or *concentric* bundles. What I regard as a relic of the ancestral structure is here found in the most primitive cauline organ of the plant, viz., the peduncle, and consists of tracheides occurring in considerable numbers on the inner or ventral side of the protoxylem of each bundle, and, what is more remarkable still, occasionally accompanied, as was seen in the case of *Stangeria*, by phloem on the *inner* side of these tracheides, *i. e.*, on the side nearest the centre of the peduncle. Once or twice an entire bundle, with inverted orientation, was observed on the ventral side of, and in close proximity to, one of the bundles of the cylinder. This centripetal xylem of the central cylinder of the peduncle of the four genera mentioned was first discovered by D. H. Scott, and has been carefully and minutely described by him in a valuable paper*.

The curved, in some cases almost horseshoe-shaped, in one or two cases perfectly *concentric*, contour of the bundles composing the cylinder in the lower part of the peduncle at once suggests the idea of their derivation from concentric bundles or steles. The same may also be said of the bundles of the cylinder in the *axis* of the male cone of *Ceratozamia mexicana*, Brongn. †, and *C. latifolia*, Miq. ‡. Here also occurs another piece of evidence for the Medullosean ancestry of these plants, in the form of *concentric* and collateral bundles in the pith of the same size as the bundles of the cylinder, as also much smaller collateral ones of inconstant orientation. That all these bundles are vestiges of an ancestral condition is shown by their inconstant structure

* Scott, Ann. Bot. vol. xi. 1897, p. 403.

† Thibout, Recherches sur l'Appareil Mâle des Gymnospermes, 1896.

‡ Worsdell, Ann. Bot. vol. xii. 1898, p. 232.

and orientation and their more or less rudimentary development. Scott's explanation of the centripetal xylem in the peduncle of *Stangeria* is that it is a vestige of a structure such as occurs normally in the vegetative stem of such fossil plants as *Lyginodendron* and *Calamopitys Saturni*, Ung., and he parallels the occasional occurrence in *Stangeria* of internal phloem and entire inverted bundles with the case of Seward's *Lyginodendron robustum*, where vascular tissue with inverted orientation also occurs on the inner side of the primary xylem, as it also occasionally does in *L. Oldhamium*. The comparison thus instituted I should distinctly support. But, on the other hand, I regard the vascular tissues with inverted orientation, which occur regularly in *L. robustum*, Sew., and irregularly in *L. Oldhamium*, not as sportive and utterly abnormal, but as a reversion to the typical ancestral condition. That the vascular stem-structure of *Lyginodendron* is really composed of the vestiges of a ring of *concentrically-constructed* strands is distinctly shown, as in the peduncle of *Stangeria*, by the *curved contour* of the bundles composing the cylinder in *L. Oldhamium*. I am very far from regarding the stem-structure of this plant (like Scott does) as derived from that of *Heterangium*, this latter being, with its single large stele, really a variant on that of *Medullosa* with its ring of several steles, just as is also the case with *Colpoxylon*, which latter plant may, in fact, be regarded as a *Medullosa* possessing one or two large steles or concentric strands instead of a number of small ones. Such forms as *Heterangium* are not necessarily the most primitive; a *polystelic* member of the Cycado-filices, *Cladoxylon*, is found at a geological horizon quite as low as that at which *Heterangium* occurs. The latter plant probably represents a distinct phylum of development. *Lyginodendron* more nearly resembles the typical Medulloseæ and existing Cycads, its structure consisting, as in both these groups, of a ring of steles or vestiges of such. Its ancestors never had primary tracheides occupying the so-called "pith."

Scott says again:—"Extrascicular zones occur in the same form in some Medulloseæ as in certain recent Cycads, so it appears unnecessary to derive this part of the structure from a reduced system of rings." But this part of his argument carries but little weight, for it appears almost certain (is, at least, highly probable, in view of the *transitional structures* found in other species of *Medullosa*) that the structure referred to has itself been derived from the definite polystelic arrangement of its own more internal strands and of those of the more typical forms.

I may add that valuable evidence for the origin of the stem-structure of Cycads from that of the Medulloseæ has been observed in the *roots* of several genera—e. g., *Cycas revoluta*, Thunb., *C. Seemannii*, A. Br., *Encephalartos* (described above), and *Macrozamia*,—viz., in the upper or hypocotyledonary part of the organ near the transitional region between stem and root. I would draw very special attention to the fact (for on this depends much of the weight of my whole argument) that this is the region *par excellence* where the *first-formed tissues* are situated and therefore where *ancestral characters* would be sure to preponderate. The vascular tissue arising outside the central stele in this region assumes the form, when it is first laid down, of, in some cases, perfectly *concentric*, in others partially *concentric*, strands or portions of such. These structures in the root are only found in those genera with more than one vascular ring

in the stem; the primary tap-roots of *Stangeria* and *Bowenia*, two genera with but a single vascular ring, do not exhibit these outer concentric strands, as would, in all likelihood, also be the case with *Ceratozamia*, *Zamia*, and *Dioon*, the remaining three genera possessing a single vascular ring in the stem. This is a fact of importance, for it points, with a fair amount of certainty, to the conclusion that *the concentric or partially concentric strands, or the fragmentary portions of such, situated at various radial distances outside the central root-stele, are the homologues of the second, third, or fourth vascular rings in the stem.* And it is probable that, at a later stage of growth, the place of these strands would be occupied by a vascular ring of collateral structure, when the inner portion of each strand would become displaced and isolated as small bundles with inverted orientation of their parts, such as were shown by me to exist in the lower portion of the stem of *Macrozamia Fraseri*, Miq.

Pl. XLIII., fig. 9, I regard as of extreme importance in helping materially to substantiate the views I have put forward as to the phylogenetic origin of the successive vascular rings of Cycads, for it presents within small compass that which, if rightly interpreted, is, to my own mind; at least, a key and clue to the whole question. I hold, then, the significance of this structure to be as follows:—The strand cs^1 represents and is homologous with the second vascular ring of the higher regions of the axis, but it retains (and this is the important point) almost the entire contour of the *primitive concentric constituent* of the ring; the two bundles cs^2 represent two *concentric* strands of the third vascular ring (of which, in each case, all but one of the *outer* segments, exhibiting, of course, the orientation of the first ring or central cylinder, have become obsolete); in the same way the fourth vascular ring has for one of its representatives at this level of the axis the bundle cs^3 , the sole remnant of a *concentric* strand whose *innermost* segment has alone survived. It is highly illustrative of what I have been endeavouring to point out with regard to the meaning and origin of these cortical strands, that cs^4 , at the same distance in the cortex from the central cylinder as cs^3 , affords what I regard as an example of one of these concentric strands which has, happily, retained in more perfect form than the rest its primitive structure. Its parts are, it is true; rather loosely connected together and isolated, thus giving this strand the appearance of a group of bundles rather than of a single one; but it should be remembered that this loose aggregation of the segments is one of the chief and peculiar characters of Cycadean vascular strands. Fig. cs^4 also probably represents, along with cs^3 , one of the primitive constituents of what, in the ancestors of the plant, would have constituted a *ring of small concentric strands*.

The fact that, as in the case of *Encephalartos horridus*, Lehm., and *Cycas revoluta*, Thunb., the concentric strands, or parts of such, in the root are local in their occurrence—appearing sometimes, as in the first-named plant, at one point only of the periphery of the central stele—the greater portion of the subsequent vascular ring being constructed according to the ordinary collateral plan, may be explained by the fact that these ancient types of structure are gradually becoming obsolete and extinct, that they represent, in truth, the last sporadic rudiments of a once dominant *concentric* type of structure, which

is now at length yielding to, and has almost become suppressed by, the modern and more efficient collateral type. In the *later-formed* vascular tissues of the axis, *i. e.*, those in regions other than the transitional one between stem and root, the collateral has entirely superseded the concentric plan of structure, and as such is laid down from the earliest stage onward *all round* the periphery of the central ring.

With regard to the "accessory vascular strands" described by Scott as occurring in the cortex outside the group of steles in the stem of *Medullosa anglica*, and figured in plate 5, photograph 4, and in plate 12, fig. 18, of his paper, I fully incline to agree with the author that they are probably "comparable to the cortical bundles of *Cycas* . . . or to the irregular strands which sometimes occur in the extrafascicular region of *Macrozamia*." But I go further, and say that these accessory strands are homologous, not only with those of *Cycas* and *Macrozamia* mentioned, but, I would add, with those of *Encephalartos horridus*, Lehm., as seen in fig. 9, and therefore, according to my own view, with the successive vascular rings in the stem of *Cycas*, *Macrozamia*, *Encephalartos*, and the *Medulloseæ*. It is exceedingly interesting to note that these "accessory strands" contain in their central parenchymatous portion the same short reticulate tracheides as I have described for the vascular strands of *Cycas*, *Encephalartos*, and *Macrozamia*. This is a point of much importance. Scott says:—"We know . . . that some *Medulloseæ* (e. g. *M. stellata*, var. *gigantea*) formed successive extrafascicular zones of wood and bast outside their stelar system, just as we find in *Cycas*, *Macrozamia*, and *Encephalartos* at the present day. It is therefore not surprising that in our species we should meet with other characteristic Cycadean anomalies." Little wonder, indeed, if, as I believe, these "other anomalies" are entirely homologous with the former ones. The author says further:—"The accessory strands in *M. anglica* are certainly quite different from the normal steles and leaf-traces; neither can they be identified with the strands supplying adventitious roots, which had a more horizontal course. There is no indication of their connection with any other form of lateral appendage." All quite true. But the explanation which I have given of these structures, especially after comparing them with the cortical vascular strands of *Encephalartos horridus*, Lehm., exhibited in fig. 9, will alone avail to save the unsatisfactory process of relegating these "accessory strands" to the category of undefined "anomalous" structures.

The term "anomalous" I hold, moreover, to be inappropriate, as applied to the "extrafascicular" rings of vascular tissue in the three genera of Cycads and certain species of *Medullosa*, for it implies that these structures cannot be classified and defined like the other structures of the order, a supposition which, as I have above tried to show, is false. I hold that there is nothing "anomalous" in these strands, but that they constitute part of the morphologically-inherent structure which has for long ages been characteristic of the group in which they are found. They are thus fundamentally different in nature from the structures, more or less similar in appearance, occurring in the stem and root respectively of such plants as *Tecoma* and *Beta*, which are purely adaptive in character, *i. e.*, have been specially adopted, within a comparatively recent period, to suit the special physiological necessities of the plants in which they occur.

My final conclusion, then, is as follows:—The vascular tissues of the stems of existing Cycads have been derived, with modifications corresponding to the period which has intervened, from the vascular tissues of the stems of the Medulloseæ or plants with closely-allied structure, and along the following lines: the central cylinder of our modern plants is the direct derivative of the primary ring of concentric strands or steles of the fossil forms, while the succeeding secondary vascular rings of the three Cycadean genera which possess them, and the secondary concentric or partially concentric strands, or parts of such, which occur in the cortex of these three plants, have had their origin in the successive outer rings of the Medulloseæ, which (although this point has not yet been definitely ascertained) will probably be eventually proved to be also secondary in origin; for secondary structures can only derive descent from secondary structures and not from primary. Therefore all the secondary vascular tissues of modern Cycadean stems constitute part of the inherent morphological structure, and in this respect differ completely from, and should never be compared with, the secondary extrafascicular structures of such plants as the Sapindaceæ, *Tecoma*, and *Beta*, which, as already stated above, are purely adaptive in character and have been assumed for purposes of nutrition.

In conclusion, I have to thank the authorities of the Royal Gardens, Kew, for so kindly furnishing me with much of the valuable material for this investigation.

EXPLANATION OF PLATE XLIII.

The following are the abbreviations used:—

ph=phloem; *nx*²=normal tracheides of the secondary wood; *px*²=reticulately-thickened tracheides of the secondary wood; *px*=protoxylem; *lb*=leaf-base; *ltb*=leaf-trace bundle; *ct*=cortex; *g*=girdles; *p*=pith; *mb*=medullary bundles; *x*=xylem; *mr*=medullary ray; *vr*¹=first vascular ring; *vr*²=second vascular ring; *vr*³=third vascular ring; *vr*⁴=fourth vascular ring; *mc*=mucilage-canal; *cs*¹, *cs*², *cs*³, *cs*⁴=cortical strands representing the successive vascular rings.

Encephalartos caffer, Lehm.

Fig. 1. Radial section of a girdle-leaf-trace bundle. ×130.

Fig. 3. Diagram of a radial section, showing a connecting strand between two vascular rings.

Fig. 4. Transverse section of a large medullary bundle from the lower region of the stem. ×35.

Fig. 5. Transverse section of a young medullary bundle and mucilage-canal. ×130.

Fig. 7. Tangential section of the xylem of the first vascular ring, showing a medullary bundle and mucilage-canal in the medullary ray. ×35.

Fig. 8. Diagram of a radial section of the first vascular ring, showing the connection with the xylem of a medullary and a leaf-trace bundle.

Encephalartos Altensteinii, Lehm.

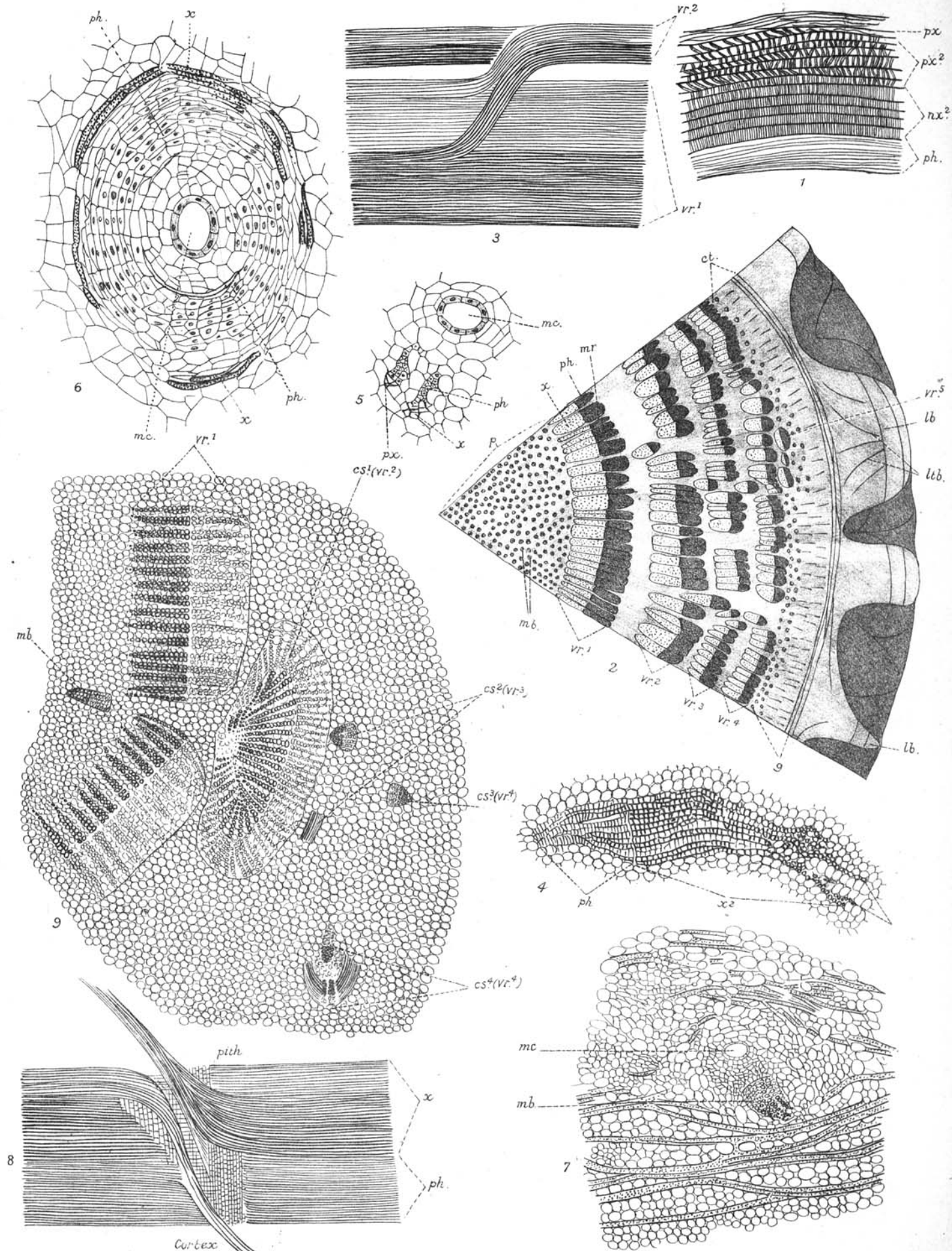
Fig. 6. Transverse section of a mucilage-canal in the pith, surrounded by bundles. $\times 35$.

Encephalartos horridus, Lehm.

Fig. 9. Diagram of a transverse section of a small part of the vascular ring from the transitional region between stem and root, showing a series of more or less primitively-constructed strands in the cortex, which represent the successive vascular rings of the higher part of the stem; also a medullary bundle.

Encephalartos sp.

Fig. 2. Segment of a transverse section of the stem, showing the general structure, viz. medullary bundles, vascular rings, and leaf-trace bundles. Nat. size.



W.C.W. del.

J.N. Fitch lith.

ANATOMY OF ENCEPHALARTOS.