The Anatomical Characters presented by the Peduncle of Cycadaceae.

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With Plates XX and XXI.
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INTRODUCTION.

THE peculiar structure of the vascular bundles in the leaves of Cycadaceae has been well known to botanists since its discovery by Mettenius in 1860¹. The peculiarity depends on the position of the spiral tracheae, which are the first formed elements (protoxylem) of the wood. In ordinary collateral bundles, such as those in the stem of Coniferae, and in both stem and leaf of most Angiosperms, the spiral elements lie at the extreme inner edge of the wood, remote from the phloem. Thus the whole development of the xylem, starting from the spiral tracheae, and advancing towards the phloem, proceeds in centrifugal order. In the foliar bundles of Cycads, on the other hand, the spiral elements are placed in the interior of the strand of xylem, but nearer the outer

¹ Mettenius, Beiträge zur Anatomie der Cycadeen; Abhandl. d. K. Säch. Gesellsch. d. Wiss., Bd. vii, p. 567, 1860.

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than the inner surface. Here, then, the development goes on in two directions; a part of the wood is centrifugal, i. e. developed outwards towards the phloem, but the greater portion is centripetal, i. e. developed inwards, in the direction away from the phloem. This type of bundle may conveniently be called *mesarch*, a term suggested by Count Solms-Laubach¹, implying that the starting-point of the wood, the protoxylem, lies in the interior of the xylem-strand. The structure was thoroughly investigated by Mettenius, to whose observations little has been added by subsequent authors².

The relative development of the two parts of the wood varies considerably; in the finer veins of the foliage-leaves the centrifugal part may die out altogether, while in many sporophylls it greatly exceeds in bulk the centripetal portion, which may even be entirely absent.

Among recent plants typical mesarch bundles have, until the present time, only been found in the leaves of *Cycadaceae*³.

In the stem of these plants only normal collateral bundles have so far been found. Mettenius has shown in detail how the transition from the one type of structure to the other takes place gradually in the base of the leaf⁴.

Among fossil plants mesarch structure was much more widely spread. Not only did it occur in families belonging to the Cycadean stock, as in Bennettiteae and Medulloseae, but it was general in the leaves of the Cordaiteae, a fourth order of Gymnosperms, only known from the Primary Rocks⁵.

The Cordaiteae, like the recent *Cycadaceae*, had normal bundles in their stems, but it is a remarkable fact that in certain other Palaeozoic plants the vascular bundles of the

¹ Fossil Botany, English Edition, p. 257.

² See the well-known figures of this type of vascular bundle in De Bary's Comparative Anatomy of Phanerogams and Ferns, Figs. 158 and 159.

³ Mr. W. C. Worsdell has quite recently shown that the bundles of the cotyledons and other leaves of *Ginkgo biloba*, and of *Cephalotaxus*, are mesarch, and finds reason to believe that in Conifers generally the 'transfusion-tissue' of the leaf is, in part at least, homologous with centripetal xylem. See his preliminary paper 'On the Origin of Transfusion-tissue,' Journal of the Linnean Society, 1897.

⁴ l. c. p. 577.

⁵ Renault, Tiges de la Flore Carbonifère, p. 295, 1879, Plate XVI.

stem had a typically mesarch structure. This was notably the case in *Lyginodendron Oldhamium*, where the very perfect preservation enabled us to examine the anatomy in great detail, and to prove that the bundles of the stem are precisely similar in organization to those of Cycadean leaves¹. The same was the case in *Poroxylon*, as shown by the investigations of MM. Bertrand and Renault².

Heterangium agrees with *Lyginodendron* so far as the leaf-trace-bundles are concerned³; and the *Calamopitys Saturni* of Unger, according to the recent investigations of Count Solms-Laubach, conforms to the same rule⁴.

The frequency of mesarch structure in the stems of Palaeozoic plants showing unmistakable affinities with Cycadaceae, renders it highly probable that this character formerly extended to the stem, as well as the leaf, of the Cycadaceae themselves. This consideration suggested a renewed investigation of the anatomy of recent Cycads, in order to ascertain whether some vestiges of mesarch structure might not still survive in the bundles of the stem. The inquiry thus undertaken at once led to the observation that in the peduncle of both the male and female cone of *Stangeria paradoxa*, T. Moore, centripetal xylem is present, so that the structure of the vascular bundles in these axial organs is of the mesarch type⁵. This discovery has since been extended to the peduncles of certain other Cycads, namely *Bowenia spectabilis*, Hook., *Zamia Loddigesii*, Miq., and *Ceratozamia mexicana*⁶, Brongn.

¹ Williamson and Scott, Further observations in the organization of the Fossil Plants of the Coal Measures, Part III, *Lyginodendron* and *Heterangium*: Phil. Trans., Vol. 186, B, 1895, p. 713, Plates XXI and XXII.

² Recherches sur les Poroxylons: Archives Bot. du Nord de la France, 3^{me} Année, 1886, p. 382.

³ Williamson and Scott, loc. cit. p. 749.

⁴ Solms-Laubach, Pflanzenreste des Unterculm von Saalfeld: Abhandl. d. K. Preuss. Geol. Landesanstalt; neue Folge, Heft 23, p. 65, Plate IV, 1896. The *Calamopitys* of Unger, which evidently belonged to the *Lyginodendreae*, must not be confused with the Calamarian stem described by Williamson under the same name: Mem. Lit. and Phil. Soc. of Manchester, ser. 3, Vol. iv, 1869.

⁵ See Williamson and Scott, loc. cit. p. 768.

⁶ In these three cases the centripetal xylem was first detected by my assistant,

It is in the male peduncle of *Stangeria* that the centripetal wood reaches its greatest development, and this case will therefore be first described.

STANGERIA PARADOXA, T. Moore.

General Structure. The principal vascular bundles of the peduncle, varying from 12 to 18 in number, are ranged in a single ring, which is fairly regular in the upper and middle part of the organ, but becomes much distorted towards its base, where the orientation of the bundles also becomes irregular (cf. Figs. 1 and 2). Lower down still, where the peduncle is about to pass over into the main stem, of which it forms the direct prolongation¹, the vascular ring once more becomes perfectly regular, but with a much smaller diameter, and a reduced number of bundles. Some peculiarities in the course of the vascular strands will be further considered below.

The structure of a normal main bundle is as follows. The centrifugal wood in the mature peduncle reaches a radial thickness of about 12 elements; the scalariform tracheides are closely packed, though the mass is broken up here and there by bands of parenchyma, which do not always form continuous medullary rays. On the inner side of each bundle there are two or more groups of spiral or annular tracheides, constituting the protoxylem. These elements soon become crushed by the growth of the turgescient parenchyma around them (see Figs. 3 and 4, *px*). The elements of the centrifugal wood do not show such regular seriation as in some other Cycads, though their number is certainly added to, for a long time, by the activity of the cambium.

The phloem is extremely well developed, and usually exceeds the xylem in bulk. Many of the individual sieve-tubes are larger than the tracheides, especially in radial

Mr. W. C. Worsdell, who prepared numerous sections of peduncles, at my request.

¹ Solms-Laubach, Die Sprossfolge der *Stangeria* und der übrigen Cycadeen: Bot. Zeit. 1890.

diameter (see Figs. 3, 4, 5, and 7). The compound sieve-plates, chiefly on their radial walls, come out very clearly under appropriate treatment.

The small albuminous cells, which in Gymnosperms represent functionally the companion-cells of the higher plants¹, are very conspicuous, often forming regular tangential bands. On the outer side of the bundle is a band of crushed tissue, consisting of the obliterated elements of the first formed bast, or protophloem. Beyond this there is a small-celled parenchymatous tissue, which is no doubt to be regarded as pericycle. This tissue retains the power of cell-division for a long time, and occasionally gives rise to anomalous formations in connexion with the older bundles.

On the inner side of each bundle is a considerable mass of small, rather thin-walled cells, with conspicuous nuclei, forming a group easily distinguishable from the large-celled tissue of the pith (Figs. 4 and 5, *c*). This group is similar in structure to the pericycle, with which it is in fact connected, round the sides of the bundle. It no doubt comes under the category of M. Flot's internal pericycle, or 'zone périmédullaire,' the present case being one of those in which this zone is only differentiated in connexion with each separate bundle². It is in this tissue that the centripetal xylem is developed.

Centripetal wood. The longitudinal distribution of the centripetal xylem is as follows: it is absent from the actual base of the peduncle, but begins to appear a little higher up, in the region where the irregularity of the vascular ring is most marked (see Fig. 2 *x*¹). Above this point it rapidly increases in amount, and then maintains about the same degree of development throughout the greater part of the peduncle, in the region where the arrangement and orientation of the bundles is normal; in the axis of the cone itself the centripetal xylem again diminishes in amount, disappearing

¹ Strasburger, *Histologische Beiträge*, III, pp. 154, 157.

² See Flot, *Recherches sur la zone périmédullaire*: *Ann. des Sci. Nat. (Bot.)*, Sér. 7, T. 18, p. 107, 1893. For linguistic reasons it seems desirable to substitute *circummedullary* for *perimedullary*.

altogether towards the apex. Fig. 1 gives a fair idea of the extent of its development in the middle part of the peduncle. In this region almost every bundle shown in any transverse section possesses it, and often in considerable amount; at least two dozen elements of centripetal xylem often occur in connexion with a single bundle (see Figs. 3 and 4, x^1). Probably every vascular bundle in the peduncle has centripetal xylem in some part of its course.

The nature of these internal lignified elements is shown in longitudinal sections, which prove that they are, as a rule, scalariform tracheides, like those which form the greater part of the centrifugal wood (see Figs. 5 and 7). The centripetal tracheides are, on the whole, shorter than the centrifugal.

The position of the centripetal xylem is such that its elements are always placed within the circummedullary zone; in some cases they lie at its inner margin, separated by a considerable interval from the spiral tracheides (Fig. 5); in other cases they are situated further to the exterior, and are sometimes almost in contact with the protoxylem (see Figs. 3 and 7).

The extent of the centripetal xylem and the arrangement of its elements in the peduncle of *Stangeria* is precisely comparable to that found in certain foliar organs of Cycadaceae, as, for example, in the stalk of the carpel of *Cycas revoluta* and other species of *Cycas* and of *Encephalartos*. The comparison of the structures, as shown, for example, in Fig. 3, from the peduncle of *Stangeria*, and Fig. 6, from the carpel of *Cycas*, can leave no doubt that the internal tracheides in the former are really homologous with the well-known centripetal xylem of the foliar bundles of Cycadaceae.

The centripetal elements which approach the protoxylem are, on the whole, smaller than those remote from it, just as in the case of the centrifugal wood (Fig. 4). The protoxylem-elements of the peduncle are usually in contact with the centrifugal part of the wood, whereas in the foliar organs of Cycads the reverse is more commonly the case. There are, however, so many exceptions to the latter rule, especially

in the vascular bundles of the sporophylls, that no importance can be attached to this difference¹.

Centripetal xylem was found in all the male peduncles examined—five in number—which approached maturity. It is, however, developed late, as was proved by the comparison of a series of transverse sections, extending from base to top of a young peduncle, with corresponding series from more advanced specimens. The centrifugal wood of the young peduncle had attained a thickness of three or four elements, but in no part was any centripetal wood as yet differentiated. In another peduncle, with centrifugal wood five or six elements thick, the centripetal elements were already fairly numerous; they only attain their full number, however, in nearly mature peduncles, when the centrifugal xylem has from seven to twelve tracheides in each radial series. This late development of the centripetal wood accounts for the shortness of its tracheides, for at the time when they develop the tissue is too mature to allow of any great degree of sliding growth. For the same reason, spiral elements are rare, on the centripetal side, for as growth in length is usually over when these tracheides are differentiated, no provision for extensibility is needed. In one case, however, a very characteristic spiral tracheide, with a fairly close coil, lay between the disorganized protoxylem and the scalariform elements of the centripetal wood (Fig. 7 *x*). Here then there was a gradual transition from the primitive to the definitive tracheides, in both directions, but as a rule the centripetal xylem develops too late for such a transition to be traced.

The more internal tracheides of the centripetal wood are sometimes met with while still in course of development, as is best shown in radial sections.

This belated appearance of the centripetal wood in the

¹ In the pinnae of *Bowenia spectabilis*, Hook., and sometimes in the petiole also, I find the protoxylem in contact with both parts of the wood equally; the same is the case in the pinnae of *Ceratozamia mexicana*, and of *Macrozamia Denisonii*, F. Muell. and *M. heteromera*, as well as in the petiole of *Stangeria*. In the rachis of *Dioon edule*, Lind. the spiral elements often lie midway between the two xylems. Cf. Mettenius, loc. cit. p. 580.

peduncle, is the only point of any importance in which it differs from the corresponding tissue in the leaf. This, however, proves nothing against the homology between the two. In the peduncle of Cycads the centripetal part of the wood is a vestigial structure, and it is well known that vestigial organs, when recognizable in the adult, are usually late in completing their development.

Even in the foliar organs, the relative periods of development of the two parts of the wood is extremely variable, as is indicated by their variable relations to the protoxylem-elements. In the sporophylls of many Cycads the centripetal portion of the wood is excessively reduced and may even be altogether absent. In such cases the spiral elements are always in immediate connexion with the centrifugal wood (see Figs. 12 and 13). In the carpel of *Ceratozamia* the centripetal wood is developed late compared with the centrifugal portion, and no doubt this is often the case, where the former tissue is reduced.

The peduncle and axis of the female cone of *Stangeria*, like those of the male, show centripetal xylem in connexion with some of the bundles. In the specimens available, however, it was much less developed than in the male cone. Here also the elements in question are shown, by longitudinal sections, to be scalariform tracheides.

As a rule, the centripetal wood, whether in the male or female peduncle, is limited to the principal bundles of the stele. No clear case of the presence of this tissue in a leaf-trace passing out to a functional sporophyll has been observed, nor is this surprising, considering the excessively slight development of centripetal xylem in the bundles of the sporophylls themselves. In some cases certain small bundles, passing through the cortex, were found to have a few centripetal xylem-elements; but such bundles appear to be either purely cauline, or to be destined for the bracts or sterile sporophylls which occur at the base of the actual cone. In these the centripetal xylem is somewhat better developed than in the fertile sporophylls.

Vascular System. Before leaving *Stangeria* certain other peculiarities of the vascular system in the peduncle must be considered.

Throughout the whole length of the organ the main bundles fuse and separate again repeatedly, forming collectively a hollow network, with long meshes, as described by Count Solms-Laubach¹. The number of the strands, as seen in transverse section, thus remains approximately constant, except at the base of the peduncle and the apex of the cone, where it diminishes greatly. In the lower part of the peduncle, where the ring of bundles becomes flattened and contracted, every kind of irregularity in their arrangement and orientation may be observed (see Fig. 2)².

Often the xylem forms a horse-shoe, opening inwards, with the phloem in its convex side (see Fig. 2, strand 4). In other cases two bundles lie close together with their phloem-masses in contact (Fig. 2, strands 1, 1). Comparison of successive transverse sections shows that the former arrangement is due to the fusion of two bundles from above downwards, while the latter case indicates that two bundles are about to fuse from below upwards. Occasionally the horse-shoe form becomes exaggerated, so that the xylem appears as a ring, nearly or quite surrounded by phloem. In fact a concentric structure may be acquired for the moment, but this peculiarity is quite local, and dependent simply on the fusion of the bundles; no morphological importance can, I think, be attached to it.

At a still lower level in the peduncle all the irregularities again disappear; the bundles, reduced in number, once more form a perfectly regular ring of small size, with typically collateral structure and normal orientation. The abnormalities of the transitional region are probably due to mechanical causes, the tissues developing under pressure from the leaf-bases, between which this part of the peduncle is wedged in.

On the other hand the small cortical strands which occur in the peduncle, especially in its lower part, present some

¹ Sprossfolge der *Stangeria*, p. 213.

² Cf. Solms-Laubach, l. c. p. 212.

features of interest. They resemble the sporophyll-traces in the fact that each strand, after branching off from the main ring, often divides into two branches, which reunite higher up¹. In many cases these cortical bundles are altogether cauline, not passing out into any kind of appendage. Their course has been carefully followed in series of successive sections, from several peduncles, and it has been proved that they sometimes end blindly in the cortical parenchyma, and sometimes turn inwards again, to reunite with the main vascular bundles of the stele. Probably all the cortical strands, which occur in the lower part of the peduncle, are of this cauline nature. They possibly represent the vestiges of a former leaf-trace system, which, now that the greater part of the peduncle is naked, no longer has any leaves to supply.

Concentric Bundles. In some cases the cortical strands show a typically concentric structure, which they retain for a considerable distance. The longitudinal course of these concentric bundles has been followed in several instances, and one of them was traced through the greater part of the length of a peduncle. Low down, in the region of irregular orientation, a horse-shoe bundle was seen leaving the main ring. As it ascended, the curvature increased, until the structure became truly concentric, with xylem inside and phloem outside. The bundle remained concentric, but diminished in size, until, in the upper, regular, part of the peduncle, it turned in again, coming into contact with one of the main bundles, where it once more increased in bulk, but retained perfectly concentric structure.

The transverse sections of two such bundles (from different specimens) are shown in Figs. 8 and 9, from which their strictly concentric structure, with central protoxylem, is evident. The parenchyma in the centre of the strand is no doubt homologous with the circummedullary tissue accompanying the normal bundles.

These concentric cortical strands are of very inconstant

¹ Cf. Solms-Laubach, l.c. p. 213.

occurrence, some peduncles not showing them at all. So far as I have observed they never split into two, as is so often the case with the collateral bundles in the cortex. Possibly their concentricity is due to this fact, the concentric strand thus representing a double bundle, just as occurs sometimes in the main ring. As we have already seen, a bundle which is collateral below may become concentric higher up; sometimes the change is in the reverse direction.

In any case these cortical strands are of considerable interest, for they constitute, so far as I am aware, the only instance hitherto described of Cycadean bundles with a primarily concentric structure, retained for a considerable distance. They have been observed in quite young peduncles, so there can be no doubt that the concentric structure exists while the tissues are still in their primary condition¹.

The secondary concentric strands, so well known in the cortex of *Cycas*, clearly belong to a different category.

The evidence for the origin of Cycads from Ferns is now overwhelming, Professor Ikeno's discovery of the multiciliate spermatozoids of *Cycas* completing the proof in the most striking manner². Hence one is tempted to look on concentric vascular bundles in a Cycad as a relic of ancestral structure. Such an inference must be received with caution, but I give the facts for what they are worth.

Other Anomalies. One or two occasional anomalies remain to be noticed. In rare cases a cambium arises in connexion with a group of the centripetal xylem, and a little secondary phloem is then found on the side toward the pith. I attach little or no importance to such isolated abnormalities of development, but it may be worth while to point out that similar anomalous formations, on a much larger scale, are frequent in the fossil *Lyginodendron Oldhamium*, and are even

¹ Mr. Worsdell has observed other instances of concentric bundles in Cycads, which he will describe in a forthcoming communication.

² Bot. Centralblatt, Bd. 69, Nos. 1 and 2, 1897; Annals of Botany, June 1897. Dr. Hirase's previous discovery of similar spermatozoids in *Ginkgo* is another decided indication that the Gymnosperms generally were derived from the same source.

more marked in the form which Mr. Seward has named *Lyginodendron robustum*¹.

As already mentioned the cells of the pericycle outside the bundle often become merismatic, dividing tangentially so as to produce a certain amount of new tissue, which usually remains parenchymatous, but which, in very rare cases, may give rise to a rudimentary vascular strand.

The chief point, however, which has been brought out by the anatomical investigation of the peduncle of *Stangeria* is the presence of centripetal xylem which, in the case of the male cone, may attain a development equal to that in such foliar organs as the carpels of *Cycas*, and greatly exceeding that in most other Cycadean sporophylls. The general bearings of this result will be discussed after some other cases have been considered.

BOWENIA SPECTABILIS, Hook.

In the peduncles of both male and female cones of *Bowenia*, centripetal xylem occurs, but only to a very small extent. There is a great difference in the size of the peduncles, that of the female cone being much the thicker, with larger and more numerous vascular bundles than those in the male peduncle: otherwise the structure is identical.

There is nothing peculiar in the centrifugal xylem or the phloem; here, as in *Stangeria*, the phloem is decidedly the more developed of the two tissues. Centripetal wood was only observed in a few of the bundles, and not more than four such elements were found in connexion with any one strand. They are separated from the protoxylem by from one to three layers of cells. Longitudinal sections show that here, also, the elements of the centripetal wood are scalariform tracheides. The tissue is present in such small quantity, that, but for the analogy of *Stangeria*, it might easily be over-

¹ Williamson and Scott, loc. cit. Part III, p. 722, Plate XXIII, Fig. 8: Seward, A Contribution to our knowledge of *Lyginodendron*, *Annals of Botany*, March, 1897.

looked. There is no doubt, however, as to its homologies, but in *Bowenia* the centripetal xylem of the peduncle is evidently in the last stage of reduction.

ZAMIA LODDIGESII, *Miq.*

The peduncle of a female cone of this species was examined, and, next to *Stangeria*, afforded the best example observed of centripetal wood. Towards the base of the peduncle most of the vascular bundles possess this tissue, and in some it is very well developed (see Fig. 10, x^1). The centrifugal wood and phloem show a very regular radial seriation; there are usually several groups of spiral tracheides to each bundle. The elements of the centripetal xylem are, as a rule, found at a little distance from the protoxylem, towards the inner margin of the small-celled circummedullary zone. The elements of the centripetal wood, like those which form the bulk of its centrifugal portion, are scalariform tracheides (see Fig. 11). They have a rather wavy course, and are often quite short, with truncated ends, especially on the side remote from the protoxylem. Both these peculiarities are no doubt due to late development, taking place at a stage when the tissues are too mature to allow of the unrestricted growth in length of the newly differentiated tracheides.

Occasionally a little centripetal xylem occurs in connexion with the small leaf-trace bundles passing through the cortex.

In a male peduncle of the same species no centripetal wood could be detected.

CERATOZAMIA MEXICANA, *Brongn.*

In the peduncle of the male cone of this species fairly well-marked centripetal xylem sometimes occurs in connexion with the principal vascular bundles. It was found best developed in the axis of the cone itself, but it also occurs throughout the whole length of the peduncle down to its base. About half a dozen centripetal tracheides may be

present in connexion with a single bundle, but their occurrence is very inconstant.

The course of the bundles was traced in peduncles which remained attached to a very old stem of this species, embedded among the leaf-traces. They had lost their cones some time before, but were probably of no great age, as they occurred near the apex, and their structure was still intact. The general vascular arrangement in the lower part of the peduncle is essentially the same as in *Stangeria*. Quite at the base there is a small ring (about 3×4 mm. in diameter) of perfectly normal bundles; a little higher up the ring enlarges, and becomes more elliptical, measuring about 10×5 mm. The bundles at the narrow ends of the ellipse are crowded and irregularly orientated—obviously as the result of development under pressure from the leaf-bases¹. A more remarkable anomaly is the presence of inverted cortical bundles immediately outside those of the normal ring. Some of these bundles, where they pass further out into the cortex, show some approximation to a concentric structure.

Further up still, the ring of bundles again becomes regular, but as the cone is approached, new peculiarities make their appearance. The principal bundles are no longer equidistant from the centre but form an irregular double ring, with variable orientation of the individual strands. Small bundles enter the pith; when traced up into the axis of the cone they are found to pass out, usually fusing, as they do so, with the principal strands. The same arrangement was shown in a male cone of *C. latifolia*, Miq., but it does not appear to be constant throughout the genus. In *C. latifolia* also, slight traces of centripetal xylem were observed.

The peduncles of a number of other Cycadaceae of the genera *Cycas* (♂), *Macrozamia*, *Ceratozamia*, and *Zamia* were examined, without, so far, finding any other clear case of centripetal xylem. The instances, however, in which it has

¹ Cf. Solms-Laubach, l. c. p. 212.

been observed, are so widely scattered throughout the Order, that other examples will undoubtedly be added on further investigation.

CONCLUSION.

The most important result of these observations has been to establish the fact that the mesarch type of vascular bundle, hitherto believed to be limited to the leaf in recent Cycadaceae, also occurs in certain axial organs, namely in the peduncles of *Stangeria*, *Bowenia*, and some species of *Zamia* and *Ceratozamia*. Count Solms-Laubach, as the result of his work on the course of the vascular bundles of Cycads, came to the conclusion that in these plants the peduncle shows a primitive organization, as compared with the vegetative stem; he says: 'Sehr merkwürdig aber ist die Art und Weise, wie an einem und demselben Spross unter plötzlicher Verjüngung des Pleromkörpers der complicirte vegetative Spurverlauf ganz unvermittelt in den einfachen der Blüthe überspringt. Dass dieser letztere eine *Reliquie uralter Organisation*¹, dass er den gemeinsamen Vorfahren der Cycadeen und Bennettiteen allgemein eigen gewesen sein wird, dass der vegetative Spurverlauf, wie er jetzt bei ersterer Gruppe vorliegt, eine im Laufe der Zeit erworbene Eigenschaft darstellt, die den Gang der Entwicklung in der Richtung vom Einfachen zum Complicirten uns vor Augen führt, scheint mir eine sehr nahe liegende Annahme zu sein.'

My observations on the structure of the vascular bundles in the peduncle completely confirm Count Solms' conclusions, drawn from their arrangement. In the presence of centripetal wood, so well marked in the peduncle of *Stangeria*, and evident, though less conspicuous, in other cases, we have the same character, in a reduced form, which is presented by the vegetative stem of the fossil plants *Lyginodendron* and *Poroxylon*, as well as by the *Calamopitys Saturni* of Unger.

¹ The italics are my own.

It appears then that the Cycadean type of vascular bundles—one of the most ancient of anatomical characters—was not originally a mere peculiarity of the leaf, but rather represents the vestige of a primitive organization, which was once common to the stem also¹.

In recent Cycads the stem has all but lost this character; it survives, so far as we know, only in certain peduncles, organs which appear to have been less modified than the vegetative stem.

The loss of the centripetal wood was in all probability correlated with the increasing development and earlier appearance of secondary tissues. The earlier the stage at which the formation of wood by the cambium set in, the more would the primary centripetal xylem become superfluous. We can form an idea of the progress of this change by the comparison of some of the fossil forms. In *Heterangium* the secondary tissue-formation set in late, and was, as a rule, comparatively small in amount. In *H. Grievii* especially, the great bulk of the wood is primary, and nearly all the primary part is centripetal, occupying the whole interior of the stele. In *Lyginodendron Oldhamium* the central part of the wood has disappeared, and is replaced by a large pith, around which the bundles are ranged. In each bundle the centripetal portion of the wood is well developed, but secondary growth sets in early, and the secondary wood soon far exceeds the primary in amount².

In *Lyginodendron robustum*, Seward, no primary centripetal wood has been certainly demonstrated as yet; if present, it must have borne a very small proportion to the secondary tissues. In *Cycadoxylon* the former tissue seems to have all but disappeared, much as in recent Cycads³.

¹ This view has already been stated in the joint paper on *Lyginodendron* and *Heterangium* by the late Dr. Williamson and myself. See p. 768, l. c.

² For *Heterangium* and *Lyginodendron* see Williamson and Scott, loc. cit., and the earlier papers by Williamson there cited; also Seward, Palaeobotany and Evolution, Science Progress, October, 1896.

³ See Seward, A Contribution to our knowledge of *Lyginodendron*, Annals of Botany, March, 1897. The author constantly uses the term 'centripetal wood'

As regards the development of the centripetal xylem, *Poroxylon* is about on a level with *Lyginodendron Oldhamium*; but in the former this tissue dies out towards the lower end of each leaf-trace bundle, about seven or eight internodes below the point where it enters the stem¹. *Poroxylon* seems to show distinct affinities with the *Lyginodendreae* on the one hand, and the *Cordaiteae* on the other.

Ultimately the stem retained centrifugal wood only, as in the *Cordaiteae*, and in recent Cycads, with the exceptions recorded in the present paper. We must not suppose that the whole of the centrifugal wood was secondary in origin. In *Lyginodendron* and *Heterangium*, the primary xylem has a well-marked centrifugal portion². The same is clearly the case in many foliar bundles of recent Cycads, though sometimes the limit between primary and secondary tissue may be impossible to define.

The view maintained in the present paper as to the evolution of the vascular bundles in Gymnosperms has much in common with that put forward by MM. Bertrand and Renault in 1886³. These authors, however, assumed that the whole centrifugal part of the wood is secondary, an assumption which hangs together with their attempt to derive Cycads, *Poroxylon*, and *Lyginodendron* from Lycopods and not from Filicineae. This view is no longer tenable. Both recent Cycads and their fossil allies (*Bennettiteae*, *Lyginodendreae*, *Medulloseae*) abound in Fern-like characters, and have simply nothing in common with Lycopods. *Lyginodendron*, for

for the secondary tissue, sometimes developed at the margin of the pith in *Lyginodendron* and *Cycadoxylon*. This terminology is of course quite legitimate, but it is important to avoid confusing this anomalous secondary formation with the centripetal xylem which forms part of the primary structure of the bundle. The latter is simply termed 'primary wood' by Mr. Seward. On *Cycadoxyleae* see Renault, *Flore fossile d'Autun et d'Épinal*, Part 2, 1896.

¹ Bertrand et Renault, *Recherches sur les Poroxylons*, *Archives Bot. du Nord de la France*, 1886-7; also *Remarques sur les faisceaux foliaires des Cycadées*, loc. cit. p. 238.

² Williamson and Scott, loc. cit., pp. 713 and 749.

³ *Remarques sur les faisceaux foliaires des Cycadées*, loc. cit.

example, had in all respects the foliage of a Fern, and so had *Heterangium*¹; in the latter the structure of the stem, apart from the secondary growth, is exactly that of a monostelic fern, while the supposed resemblance to *Lycopodium* is merely fanciful. Recent work has completely confirmed Williamson's original view as to the Fern-affinities of these fossil genera.

While the origin of the Cycadean stock—in the widest sense—from Filicineae is now well established, it is not possible in the present state of knowledge to determine more exactly the line of descent of our recent Cycadaceae. Though they retain many primitive characters, they form but one special group, of what was once an extensive and varied class, which we may call Cycadales. The best known of the abundant Cycadeoid remains which have come down to us from the Secondary Period, are those of Bennettiteae, a group very distinct from the living Cycadaceae. Much additional palaeontological evidence will be required before the geological history of the latter family can be revealed.

The Cycadales generally may even be polyphyletic, having perhaps sprung from the Filicineae at various points. The Lyginodendreae, Protopityeae, and Medulloseae all combine Filicinean with Cycadean characters, but they appear to join on to very different groups of Ferns. In the light of Count Solms-Laubach's recent remarkable observations on the Cladoxyleae of the Culm², it seems highly probable that the Medulloseae sprang from polystelic Ferns, each of the well-known rings of wood in the Medullosean stem corresponding to a distinct stele, with its own secondary zone. On the other hand, the Protopityeae³, and the Lyginodendreae,

¹ It is extremely probable that *Sphenopteris Höninghausi*, Brongn., was the foliage of *Lyginodendron Oldhamium*, and *S. elegans*, Brongn., that of *Heterangium Grievii*. Cf. Kidston, On the Fructification and Internal Structure of Carboniferous Ferns; Trans. Geol. Soc. Glasgow, Vol. ix, Pt. I.

² Pflanzenreste des Unterculm von Saalfeld, above cited.

³ Solms-Laubach, Bot. Zeitung, 1894, Abth. I, p. 206.

especially the latter, are essentially monostelic, *Heterangium* directly connecting *Lyginodendron* with the type of stem-structure now represented by *Gleichenia*, &c.

Recent Cycads and, so far as I am aware, the Mesozoic Bennettiteae also, have evidently monostelic stems, and the observations recorded above tend to connect them with the Lyginodendreae rather than with the other intermediate groups. On this point, however, it is necessary to speak with great caution, for the distinction between polystely and monostely—so striking in the extreme forms—is one on which it is quite possible to lay too great stress¹. We may, however, safely go as far as this: the discovery of mesarch bundles in certain axial organs of Cycadaceae, establishes a new link between that family and the Lyginodendreae, though by no means excluding the possibility of relationship in other directions.

The other point of interest recorded above, is the occasional occurrence of concentric vascular bundles in the cortex of the peduncle. This is a very inconstant phenomenon, and I hesitate to attach great importance to it, for we know that concentric structure sometimes appears in the foliar bundles of various Angiosperms, where there can be no question of phylogenetic significance².

The cortical bundles of the peduncle in *Stangeria* appear to represent a vestigial leaf-trace system, no longer connected with leaves. It is possible that a primitive structure has sometimes been retained by these now rudimentary strands. The concentric structure suggests a comparison with Medulloseae, but a better analogy can be found among the Lyginodendreae, for the leaf-traces in the cortex of *Calamopitys Saturni* appear to have been perfectly concentric³. In *Lyginodendron* the leaf-traces were collateral, only becoming concentric in the leaf itself.

¹ On this point see, for example, Mr. Gwynne-Vaughan's paper on Polystely in the genus *Primula*, Annals of Botany, June, 1897.

² Cf. Gwynne-Vaughan, loc. cit.

³ Solms-Laubach, Pflanzenreste des Unterculm, Plate IV, Fig. 11.

The main results attained may be briefly summed up thus:—

1. The peduncles of certain Cycads (*Stangeria paradoxa*, ♂ and ♀; *Bowenia spectabilis*, ♂ and ♀; *Zamia Loddigesii*, ♀; *Ceratozamia mexicana* and *latifolia*, ♂) have mesarch vascular bundles, comparable in structure to those of the leaves. This is, in my opinion, a primitive character, indicating affinity with the fossil *Lyginodendreae* and *Poroxyaleae*.

2. Some of the primary cortical bundles of the peduncle of *Stangeria* show concentric structure. Possibly this also may be a relic of ancestral organization.

In conclusion I desire to express my thanks to Mr. W. C. Worsdell, to whose skilful aid in the investigation I am greatly indebted. The illustrations are also from his hand.

EXPLANATION OF FIGURES IN PLATES XX AND XXI.

Illustrating Dr. Scott's paper on the Peduncle of Cycadaceae.

The following abbreviations are used throughout the figures:—*px.* protoxylem; *x*¹. centripetal xylem; *x*². centrifugal xylem; *ph.* phloem; *cb.* cambium.

PLATE XX.

Fig. 1. *Stangeria paradoxa*. Diagrammatic transverse section of the peduncle of a male cone, taken about half way up, showing the arrangement of the vascular bundles, and the distribution of the centripetal wood, indicated by dots; *c. s.* cortical strands. The numerals indicate corresponding bundles in this section and the next. × about 12.

Fig. 2. *Stangeria paradoxa*. Similar section from the lower part of the same peduncle, at the level where the centripetal wood first appears. Note the irregular orientation of the bundles in this region. *c. s.* cortical strands, one of which is concentric. × about 12.

Fig. 3. *Stangeria paradoxa*. Transverse section of a vascular bundle from the upper part of a male peduncle. The centripetal xylem is well developed, and abuts on the compressed protoxylem. × 85.

Fig. 4. *Stangeria paradoxa*. Similar section from the middle part of another male peduncle. *c*. small-celled tissue in which the centripetal xylem is situated; *p*. pith. $\times$ about 85.

Fig. 5. *Stangeria paradoxa*. Radial section through a vascular bundle in a male peduncle. The centripetal xylem is here shown at the border of the pith, *p*, separated by narrow-celled tissue, *c*, from the spiral tracheides, *px*. $\times$ about 85.

Fig. 6. *Cycas revoluta*. Transverse section of a vascular bundle from the stalk of a carpel, for comparison with Fig. 3, from the peduncle of *Stangeria*. To the left a small inverted cortical bundle is shown. $\times$ 85.

PLATE XXI.

Fig. 7. *Stangeria paradoxa*. Radial section through a vascular bundle in a male peduncle. The centripetal xylem begins with a spiral tracheide. $\times$ 130.

Fig. 8. *Stangeria paradoxa*. Transverse section of a concentric cortical bundle from the middle part of a male peduncle. $\times$ 130.

Fig. 9. *Stangeria paradoxa*. Similar bundle, from the lower part of another peduncle. There is here a central parenchyma in which the protoxylem is embedded. Sieve-plates are indicated on the radial walls of some of the sieve-tubes. $\times$ 130.

Fig. 10. *Zamia Loddigesii*. Transverse section of a vascular bundle from the peduncle of a female cone, showing centripetal xylem. $\times$ 85.

Fig. 11. *Zamia Loddigesii*. Radial section of a similar bundle. $\times$ 85.

Fig. 12. *Stangeria paradoxa*. Transverse section of a vascular bundle from a carpel. The centripetal xylem is very slightly developed. $\times$ 110.

Fig. 13. *Stangeria paradoxa*. Similar bundle from a stamen. $\times$ 110.

Fig. 1.

Fig. 2.

Fig. 4.

Fig. 5.

W.C. Worsdell del.

Fig. 3.

Fig. 6.

Fig. 1.

Fig. 2.

Fig. 3.

Fig. 5.

Fig. 4.

Fig. 6.

Fig. 7.

Fig. 8.

Fig. 9.

Fig. 10.

Fig. 11.

Fig. 12.

Fig. 13.

Scott, Dukinfield Henry. 1897. "The anatomical characters presented by the Peduncle of cycadaceae." *Annals of botany* 11, 399–419.

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