The Vascular Structure of the Sporophylls of the Cycadaceae¹.

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With Plates XVII and XVIII.

ONE of the most marked characters of the plants comprising the order Cycadaceae is the sympodial nature of the development of the stem, whereby the main axis usually terminates in a peduncle bearing a cone with sporophylls, while the vegetative axis is continued as a lateral branch. An exception, however, is found in the female plant of *Cycas*, where sympodial branching does not obtain, the vegetative axis growing continuously through; here the sporophylls, instead of being borne on differentiated portions of the axis known as cones, occur in whorls intercalated amongst the ordinary foliage-leaves of the stem.

The structure of the peduncle in this order has recently been described², and has been found to possess certain structures not known in the vegetative axis, such as the primary concentric strands in the cortex and in the central

¹ From the Jodrell Laboratory, Royal Gardens, Kew.

² Scott, Ann. Bot., Vol. xi, 1897.

cylinder, and the centripetally-formed xylem of the bundles composing the latter. These are, I think, ancestral characters which, in the vegetative part of the stem, have been lost owing to special modification of its tissues for functional purposes, and which in the peduncle, as having undergone much less modification in structure, have been retained. This more primitive structure of the peduncle has been emphasized by Solms-Laubach¹ as a result of his observations on the course of the vascular bundles in this organ, and also by Scott², who first discovered the presence of centripetal xylem here.

Precisely as in the case of the peduncle, we shall find that the *sporophyll*, the normal foliar appendage of the former, has also retained certain primitive characters which are not found in the foliage-leaf. But in the following pages two factors have to be considered in the structure of the former—the presence of these primitive characters, and the modification of its general structure in connexion with the sporangiferous function.

In order to throw light upon the structure of the sporophyll I shall proceed to compare it with that of the foliage-leaf.

In the base of this latter organ, which is the first-formed portion, the vascular bundles have a purely endarch structure; higher up in the petiole, however, a mesarch structure of the bundle obtains, the centripetal xylem gradually increasing, and the centrifugal xylem gradually decreasing, in quantity from below upwards, until the former is almost entirely predominant. The number of the bundles is almost uniform in every part of the petiole. The difference in structure between the bundles in the leaf-base and those in the remaining portion of the petiole is explicable from the fact that a transition occurs in the bundles of the lower region of the petiole from the structure peculiar to the stem to that which is peculiar to the leaf.

When the structure of the bundle-system in the *sporophyll*

¹ Die Sprossfolge der Stangeria und der übrigen Cycadeen, Bot. Zeit. 1890.

² Loc. cit.

is examined, a similar phenomenon, as might be expected, prevails. Here also in the base of the organ, near the point of its attachment to the axis of the cone, the bundles are, or tend to be, endarch in structure, while in proportion as they pass higher up towards the lamina the endarch is gradually replaced by the mesarch character, until, in the lamina of the organ, the latter predominates. Thus the same general structure obtains here as in the foliage-leaf.

Now the sporophyll has a function to perform which is entirely different from that of the foliage-leaf. Whereas the function of the latter is to elaborate food-material for the supply of the various parts of the plant, to aid in the conduction of water through the stem, and to discharge the surplus quantity of this water from its expanded surfaces, the function of the sporophyll is to bear the sporangia, and to act as channels for the conduction of nutriment of all kinds to these latter; it also, in some cases, takes a small part in assimilation.

Though both foliage-leaf and sporophyll are morphologically of foliar nature, and possess essentially the same structure, their physiological relations are seen to be widely divergent. It is the special sporangiferous function of the sporophyll which has induced those modifications in the structure and arrangement of the vascular bundles of this organ which are considered worthy to form the subject of a separate paper.

There exists a considerable range of variation as regards the external development of the sporophyll in the different genera, and sometimes also within the same species between the two sexes. They may be either large and leaf-like or very much reduced and modified in shape, so as no longer to bear much resemblance to ordinary foliar organs.

In the *male sporophyll*, as is known, the sporangia are thickly arranged in sori on the lower surface of a large flattened area situated between the extremely short stalk and the terminal, swollen, sterile portion; the function of the latter is to afford protection to the sporangia within; the apex

of this part is often prolonged into a short acuminate blade, recalling its foliar nature, or it may be produced on each side into two reflexed horns.

The numerous bundles which are found in the stalk of this organ usually have their origin in a single bundle which is given off as a lateral branch from one of the members of the central cylinder of the axis of the cone; this bundle, while traversing the cortex, divides into two, and these in the base of the sporophyll split up at first into three and very soon after into a larger number. Occasionally the two bundles may arise separately and independently from the cylinder of the axis. The bundles of the stalk are usually of small size, their xylem being mainly of *centrifugal* origin, sharply defined and deeply staining with safranin, and often, but not always, accompanied by a (usually) much smaller quantity of *centripetal* xylem, which, however, is not so sharply defined nor so brightly stained, the tracheides of the centrifugal portion being evidently better lignified and chiefly functional in conduction. In proportion as the bundles pass up into the flattened portion of the sporophyll bearing the sporangia, the centripetal increases and the centrifugal xylem decreases in significance and quantity, until, in the sterile portion above, the former predominates. In this latter portion the structure of the bundles is essentially the same as that in the foliage-leaf. The centripetal xylem is as sharply defined as, and often even of a brighter colour, than the centrifugal, and is usually present in greater quantity. The bundles are of very varying sizes; they have no definite orientation, lying in all directions. They arise from successive branching of those in the stalk. They have no longer any important conducting function to perform, the xylem being probably chiefly serviceable as a strengthening framework, so that the phloem is usually reduced in quantity and definiteness. The change of function of the bundles in this region and their relative unimportance will probably have much to do with the inconstancy of structure displayed, for the two kinds of xylem are very unequally developed in different bundles, the one often

entirely supplanting the other, and vice versa. The very frequent presence here of the bundles with an endarch structure probably indicates the far-reaching influence of the special physiological function of the sporophyll, which causes, even in the region where it can no longer have any meaning, the suppression of the centripetal in favour of the centrifugal xylem. In the extreme portions the bundles are often reduced to a few irregular large tracheides. Transfusion-tissue is of very frequent occurrence in connexion with the bundles, and is sometimes of considerable development.

In the *female sporophyll* there are usually about four, sometimes a larger number, or only two bundles to be seen in the stalk. Two bundles arise independently, as a rule, from two distinct members of the central cylinder of the axis; these, where a larger number supplies the sporophyll, divide up in the cortex before entering the latter.

The structure and behaviour of the bundles in the female sporophyll are essentially the same as has been described for those in the male organ; but the difference in sex of the sporangia, necessarily involving a difference in their function, a great reduction in their number, a considerable increase in their individual size, and an altered position on the sporophyll, goes hand in hand with a certain difference in the development of the bundles. The bundles which are told off to supply the sporangia are, in most cases, two in number, one at either side of the much elongated stalk; each of these branches in the base of the expanded portion, sending off one or two bundles for the sporangium, which in nearly all genera is situated at the margin of the sporophyll in the sinus formed by the reflexed lateral portion of this part of the sporophyll, or on the tip of the reflexed portion, so that its apex is directed towards the axis of the cone. There is considerable variation in the number of the bundles which enter the sporangium and in the amount of branching which takes place after the one or two strands have been given off from the bundle proceeding from the stalk. The two lateral bundles in the stalk which supply the sporangia are always

much larger than, often extremely large as compared with, the other intermediate bundles which run right through into the sterile portion without taking any part whatever in the conduction of substances to the sporangia. These latter bundles are always quite small, their xylem and phloem being but poorly developed. The lateral bundles, on the other hand, have a great development of centrifugal xylem and phloem, as would, from their function, be expected. For each one has to supply a large megasporangium, and this over a protracted period, during which the processes of sporangial development, fertilization, and embryonic growth must supervene, demanding a constant and adequate stream of nutritive substances through the tissues of these bundles. Hence is the difference in structure and development between the bundles of one and the same female sporophyll, and between these and the bundles of the male sporophyll, easily explained. These larger bundles very often have an element or two of centripetal xylem, while this tissue is usually absent in the smaller bundles, the large development of the bundle seeming to go hand in hand with the presence of centripetal xylem, as will be seen more clearly when the individual genera are treated of.

The structure of the bundles in the thickened, expanded portion of the female sporophyll agrees essentially with that of the same region in the male organ. An exception to the general structure prevailing here is found in the bundles, or a certain number of them, which enter the megasporangium, and occur immediately below the base of the latter; these bundles assume, in many cases, a perfectly *concentric* structure, which may or may not enclose a central pith, and may be large or quite minute in size; others are not completely but only partially concentric, while others again are quite collateral in structure. All these kinds of structure may occur in the same group of bundles entering the sporangia. These concentric strands I regard not as purely adaptive structures connected with the radial symmetry of the sporangium they supply, for though this idea might explain the structure of

the single large concentric strand entering the central chalazal portion of the sporangium, and which breaks up into a group of bundles radiating from the common centre to the different parts of the organ, it will hardly entirely account for the extremely small concentric bundles occurring in no very definite position in the group, and which must necessarily take a subsidiary part in supplying the sporangium. I am inclined, on the other hand, to regard these *concentric* structures and the constancy with which they occur in the region concerned, as relics of the original primitive structure appearing in what must be considered as the most primitive tissue of the sporophyll.

It is the *function* of the individual bundles of the sporophyll, both on the male and female side, which readily explains their various degrees of development and varying types of structure. The bundles of the male sporophyll, at the level of the insertion of the sporangia, are small and insignificant in appearance because each one is told off to supply one of the numerous small sori scattered over the surface of the sporophyll, the microsporangia composing each having but a very temporary existence, insomuch that the function of the bundle supplying them ceases with the dispersion of the spores. Even in the lowest region of the stalk, before much branching of the bundles has occurred, and where they are therefore somewhat larger and fewer in number, the latter have quite a small development of centrifugal xylem as compared with that of the bundles supplying the megasporangia, this being clearly correlated with the respective functions of these bundles. But why in some genera the bundles in the basal region of the stalk of either male or female sporophyll should possess centripetal xylem, while in the case of other genera this tissue should be quite absent, and why this variation should exist both between the bundles of sporophylls of opposite sexes and between the bundles of one and the same sporophyll, is no more obvious than the reason why the same variation in structure should prevail in the bundles of the peduncle, not only of different genera, but also of different

species, as has recently been clearly observed¹. The greater or less development of the centrifugal portion of the bundle does not appear to be the sole or even the principal conditioning factor in determining the amount of centripetal xylem present, for where the latter is fairly well represented, the centrifugal portion may be better developed than in those cases where it is absent. There is evidently in these organs, as in the peduncle, the axis of the cone, and the foliage-leaf, a tendency, in spite of other prevailing influences, for the primitive mesarch characters to appear in the bundles, this tendency being stronger in some genera than in others, notably in those in which the sporophylls are of large size, this latter being doubtless indicative of their more primitive character as compared with the smaller and more highly modified sporophylls of other genera.

In the cones of both sexes of all genera there are always, at the base of the cone, a number of sterile sporophylls, which may either have the form of the fertile organs and be crowded together like these, or may be elongated structures more like bracts in shape and position; frequently a gradual transition occurs between these latter and the normal fertile sporophylls. It is interesting to note that the vascular structure of these barren sporophylls, while partaking in a general way of that of the fertile organs, exhibits a more primitive character, owing chiefly to the fact of the absence of the sporangiferous function in these organs, whereby these primitive structures, which consist of the more frequent presence of concentric structures and the occasional abortion of parts of the vascular system, have not been so much interfered with and altered as in the case of the fertile sporophylls. The small bundles in the cortex of the upper portion of the peduncle of both sexes, which are usually observed in pairs, and which supply the sterile sporophylls, possess very often a small quantity of centripetal xylem², which is frequently developed as trans-fusion-tissue both in a ventral and lateral position.

¹ Scott, loc. cit.

² Cf. Scott, loc. cit., p. 406.

I will now proceed to describe the structure of the vascular bundle-system of the sporophylls of the various genera of the order.

CYCAS REVOLUTA, Thunb.

Male Sporophyll. The few sporophylls available for investigation were supplied from a male cone preserved in spirit in Museum No. I in the Royal Gardens. On this account the course of the bundles from the central cylinder of the axis of the cone to their entry into the sporophyll was not observed; but this has been adequately followed in *C. siamensis* Miq. and *C. circinalis* L. by Thibout¹, who finds that a single bundle enters the cylinder from the sporophyll. The sporophyll does not assume such a perpendicular position with regard to the axis of the cone as in most genera, but is more or less curved. It is also larger, not being quite so reduced in size as in other cases. There are a number of bundles in a row whose size is in correspondence with that of the sporophyll. They possess sharply defined centrifugal xylem in fair quantity. Most of them have an almost equal quantity of centripetal xylem; but the latter, in one or two cases, far exceeds the centrifugal, consisting of a great number of elements extending some distance from the protoxylem. The tracheides of the centripetal are often far larger than those of the centrifugal xylem. But in every case the centripetal is less brightly and sharply stained than the centrifugal portion, this fact indicating that the latter is more strongly lignified and thus chiefly functional in conduction.

The chief feature of the structure of these male sporophylls of *Cycas* is the appearance, in the bundles of the lower portion of the stalk, of centripetal xylem. In no other genus is this tissue so well-developed in this region of the sporophyll, and it affords an instance of the way in which the centripetal tracheides may form the chief part of the xylem quite low down in the stalk. In the sterile portion the centrifugal

¹ Recherches sur l'Appareil Mâle des Gymnospermes, 1896.

xylem of the bundle is greatly reduced in quantity, its elements less sharply defined, and less brightly stained. The centripetal xylem usually exceeds it in quantity.

Female Sporophyll. This organ is situated on the main axis of the vegetative stem, and not on a strobilus as in all the other genera. It occurs in whorls alternating with the foliage-leaves. It is larger in size than the sporophyll of any other genus, and more nearly resembles a foliage-leaf in external conformation; herein lies probably a more primitive and less modified character; the sporophylls of other genera, from their crowded arrangement on a cone, having undergone a much greater modification in form. These sporophylls differ also from all others in possessing a very long stalk, and in bearing a larger number of megasporangia than two, these being situated, not on the terminal expanded portion of the sporophyll, as in other genera, but at regular intervals on short projections from the stalk. The size of the sporangia is in correspondence with that of the sporophyll, being the largest of the whole order.

The structure of the vascular bundles of the sporophylls is remarkable and interesting; it is precisely that which is found in the bundles of the peduncle of *Stangeria*. The strands, as seen in transverse section, are arranged laterally in groups which form a single row (Fig. 1). Some bundles or groups of bundles are entirely or partially surrounded by a thick zone of cells, probably pericyclic, filled with dense protoplasmic contents and conspicuous nuclei. This, again, is surrounded by a belt of stone-cells, possibly representing an endodermis, which have conspicuous reticulate thickenings on all their walls. But these two tissues are of inconstant appearance.

The *centrifugal* xylem and the phloem are of very great development, which is quite equal to that of the bundles in the peduncle of other genera, and is in evident correlation with the size and number of the sporangia which they have to supply. The *centripetal* xylem, either in contact with the protoxylem, or as scattered tracheides or groups of

tracheides lying some distance away, is always present; in position and development it is the exact counterpart of that in the peduncle of *Stangeria*. It sometimes occurs opposite a gap between the bundles.

Transfusion-tissue, of quite small tracheides with bordered pits or close reticulations, occurs in proximity to the centripetal xylem both in a ventral and lateral position, and its derivation from this tissue is obvious. It is present in connexion with the cells containing dense protoplasmic contents surrounding the bundle; where these cells are absent the transfusion-tissue is also no longer to be found. Some of the bundles are curved into a semi-concentric shape. On the dorsal side of nearly all the bundles are small strands with inverted orientation, their phloem being directly in contact with that of the main bundles. Each has an active cambium with (usually) a fair amount of xylem and phloem developed. Some have protoxylem; other smaller ones have none, so that they are not all secondary. In this respect they resemble the similar strands observed in the peduncle of *Ceratozamia*. In one case, on the dorsal side of the protoxylem, i.e. on the side towards the periphery of the sporophyll, two tracheides occur which have evidently been formed by a cambium centrifugally, for regular radial rows of cells are seen on the dorsal side of these two tracheides. Also, on the ventral side of some of the tracheides of the centripetal xylem of the main strand, evidence of cambial divisions occurs such as I have also seen in the peduncle of *Stangeria*; these were always observed in sister-cells of such tracheides lying on the inner (ventral) side of the latter towards the pith. Such division-walls were noticed nowhere else in the surrounding parenchyma-cells.

Two strands are observed to pass off to a sporangium and enter it without previous branching. One of these is almost completely *concentric* in structure; it has a large amount of secondary centrifugal xylem, and about three groups of protoxylem are observed around the inner margin of the latter. In the greater part of its contour the strand is

evidently of primary origin, but a small segment of the cylinder is probably formed of purely secondary tissue, though this is not perfectly certain; but no crushed phloem-elements are observed at the periphery of this part. In the central parenchymatous tissue, or pith, of the strand occur a few tracheides isolated or in groups, some of which are attached to the protoxylem; they do not extend to the centre, but quite a small central free space is left; they evidently belong to the primary centripetal system (Fig. 4).

This concentric strand, for about three-fourths of its contour, has small inverted strands attached to it, whose tissues appear to be mostly secondary; there is no sign of primary phloem anywhere, no crushed elements of the latter being visible, most of the elements in this region occurring in the same radial rows with cambial cells. But the xylem of these strands, besides the numerous layers of secondary tracheides, has in all cases some primary xylem, some of the elements being small, others large and developed as transfusion-tissue with reticulate thickenings on the transverse wall, which occur both in a lateral and a ventral position, often in great quantity. In only one of these small bundles could I discern any sign of protoxylem, in most this tissue appears to be absent. In one or two cases there seems to be a considerable quantity of primary centrifugal xylem. In the tissue below the place of insertion of other megasporangia the strands are quite collateral, with a few centripetal tracheides, of which, in one instance, a radial row of three was attached to the protoxylem; a sheath of stone-cells extends round close to this row of tracheides. In some of the bundles a large amount of transfusion-tissue runs out amongst the cells with conspicuous nuclei and dense protoplasmic contents occupying the region between the strands and the sheath.

In the sterile region of the sporophyll, above the insertion of the sporangia, the bundles are much reduced as regards their centrifugal xylem and their phloem, so that the former approximates more to the dimensions of the centripetal xylem,

while in the pinnae of the organ the bundles undergo a still greater reduction, and resemble there in their structure those of the ordinary foliage-leaf.

CYCAS CIRCINALIS, L.

Female Sporophyll. In this plant the same structure of the strands prevails, but the latter are usually much elongated tangentially (Fig. 2). Some of these tend to become revoluted towards the dorsal side, a phenomenon similar to that occurring in the root of *C. Seemannii*, Al. Br.¹

A single strand passes off to the sporangia, and in so doing divides into 3-5 strands which enter the latter; some of those have a perfectly concentric structure. Fig. 3 represents a bundle from the lamina in transverse section.

The sporophylls are much more slender and the sporangia smaller than in the last species.

STANGERIA PARADOXA, Th. Moore.

Male Sporophyll. In the stalk are a number of bundles in a row (except at the very base where there are only two). In the well-developed centrifugal xylem the tracheides are clear and well defined, taking the stain brightly. Centripetal xylem is quite absent. In the sterile portion the centrifugal xylem is much reduced, its elements being inconspicuous and not so brightly stained as in those of the stalk; in many bundles one, three, or four elements of centripetal xylem occur, in other bundles there are none seen at all.

Female Sporophyll. Two bundles leave the cylinder of the axis of the female cone, each from a separate strand, and may either enter the sporophyll without dividing further, furnishing to that organ two large bundles of equal development, or they may previously divide so as to form three or four bundles, of which the outer one on each side supplying the sporangium is considerably larger than the one or two

¹ Gregg, Ann. Bot., Vol. i, p. 4, Fig. 1, 1887.

intermediate ones (Figs. 6 and 7). Only in one or two bundles are two or three very small centripetal tracheides seen. The bundle at either side which supplies the sporangium forks just on entering the base of the lamina, one branch passing upwards, the other bending off towards the reflexed lateral lobe, between which and the stalk the sporangium is seated. Before this bundle assumes its downward course into the lobe, however, and opposite the place of insertion of the sporangium, it gives off a branch which forks: of the two bundles thus formed, one enters the sporangium without further change, the other, immediately before entering the latter, divides into two (Fig. 5).

The bundles of the *lamina* are characterized by a great reduction in the centrifugal and a corresponding increase in the centripetal xylem, so that the two parts are about equal in development (Fig. 8). The lamina of a female sporophyll at a very young stage was examined; in this is a number of very small bundles, most of which have an element or two of centripetal and one or two of centrifugal xylem. A few of them have no centripetal xylem besides the protoxylem. It is difficult to make out which is primary and which secondary centrifugal xylem in some bundles; the smaller elements in connexion with the protoxylem are probably primary. The centrifugal and centripetal xylem appear to be developed simultaneously. Many of the elements of the latter are very small and closely united to the protoxylem, two or three together, and would most likely have the same spiral thickenings as the latter; others usually single, lie some distance away.

Scale Leaves and Barren Sporophylls. At the base of the peduncle of the male cone are large, narrow, elongated scales, consisting of a fleshy central portion, with a wing on either side. They contain at the base three bundles which are collateral in shape, and possess secondary centrifugal xylem; a tracheide belonging to the centripetal xylem is here and there seen. In the upper part of the scale the bundles increase to four or six, becoming very much reduced in size,

and exceedingly small. They are here seen to possess one or two centrifugal and one or two centripetal tracheides; there is a very small quantity of phloem; no definite cambium can be distinguished, so that it is possible that the centrifugal tracheides are primary. The bundles are arranged in an arc. Sclerotic cells are scattered about in the ground-tissue.

The uppermost scales are more leaf-like and much broader than the lower scales, and represent sterile sporophylls, resembling in shape the fertile organs. One of these, whose structure was examined, has an extremely long foliar base, running ridge-like, a considerable distance down the peduncle. About half way up this foliar base a minute concentric bundle becomes differentiated from the ground-tissue, arising quite independently of any other strand (Fig. 10). Higher up it gradually increases in size, and in the upper free part of the organ is observed to give rise to an imperfect branching system forming the nervation of one side of the sporophyll. About three or four branches occur, all very imperfect, interrupted for considerable spaces in different parts of their course, and dying out before reaching the margin of the sporophyll; they appear to have a very reduced structure, and their tracheides are much twisted and contorted. From their evident progress towards extinction and the concentric structure of the bundle from which they spring, they may be said to represent part of the original primitive bundle-system of the sporophyll which has long since ceased its connexion with that of the peduncle. A portion of the system, however, has still retained this connexion, and after a large part of the sporophyll became fused with the peduncular tissues, the bundle constituting the base of this system assumed a more direct course into the axis, passing in in the upper part of the foliar base, instead of, as in the case of the small concentric bundle, running down in the latter towards its lower extremity. This bundle, which enters the barren sporophyll from the peduncle, possesses, whilst still in the latter, two distinct and well-marked groups of centripetal xylem. The subsequent course and branching of this bundle

and the nervation to which it gives rise, though imperfect, are not nearly so rudimentary and reduced in character as the one above described, for the bundles composing it are perfectly functional and nearly everywhere continuous; the tip of the organ is occupied by 3-5 bundles formed by the division of one of the two main branches of the bundle coming from the axis; these bundles have the structure characteristic of those in the sterile portion of the sporophyll, while the large bundle in the lower part has an endarch structure. The presence of these bundles in the cortex supplying the barren sporophylls was observed in two or three female and also in several male peduncles; they were most abundant in the former, where they often occur in longer or shorter and very straight tangential rows in the outer part of the cortex, but may also occur quite isolated. Most of these bundles possess, besides the usual endarch portion, two, often very large, groups of centripetal xylem, lying each slightly to one side of the median ventral line, and with tracheides of which those farthest towards the ventral side are three or four times the size of those composing the centrifugal xylem. Protoxylem is seen to be attached to each group (Fig. 9). But there is considerable variation in the development of these centripetal xylem groups, for they may be very much more reduced than those shown in Fig. 9, or even almost entirely absent; they may be also in much closer connexion with the centrifugal xylem, or even, as in the case of one such group belonging to a bundle in a male peduncle, *perfectly continuous therewith*.

The reason why I attach special importance to these bundles arises from the fact that I regard each such bundle, with its three distinct groups of xylem, as the vestige of a primitive *concentric* leaf-trace bundle which was probably characteristic of the ancestors of these plants. Now in the cortex of the stem of certain species of *Medullosa* just such concentric leaf-traces are known to occur, which during their course outward become split up into three portions, the concentric structure becoming thereby lost. My Figure 9

may be aptly compared with Fig. 8 (in the text) of Weber and Sterzel's work¹, and with Fig. 9, Plate V of Solms' paper. It will be seen that in the bundles of the fossil plants secondary xylem is present in all three parts in considerable quantity, while in those of modern plants this tissue occurs in small quantity in the complete dorsal portion only. In a male peduncle of *Stangeria* one of the bundles with its two groups of centripetal xylem was traced into the elongated barren sporophyll, as above described, when the centripetal xylem-groups were found to gradually die out as the bundle passes into the sporophyll, so that a purely endarch structure of the strand remained. I regard the two ventral groups of xylem each with its inner protoxylem-strand, as the remnants of two distinct bundles, whose phloem has disappeared and which are now more or less separated from each other and from the dorsally-placed complete bundle with which, in the ancestors of the plant, they formed a compact whole as a concentric leaf-trace bundle.

In the same female peduncles groups of three bundles some little distance apart, with their xylems converging, are often seen close to the central cylinder. These appear to me to represent, in a rather different way, the same phenomenon of a vestige of an ancestral concentric strand; in this case, however, the three parts have not become in any way reduced, but they have, however, undergone much more complete separation from each other than in the previous case.

BOWENIA SPECTABILIS, Hook.

Male Sporophyll. A single bundle leaves the vascular cylinder of the axis of the male cone and very soon, almost immediately, divides into two. These run through the cortex and enter a sporophyll, where they forthwith begin to divide up into a number of bundles.

In the stalk of the sporophyll the bundles are nearly all

¹ Weber u. Sterzel, Beiträge zur Kenntniss der Medulloseae, Chemnitz, 1896; pp. 17 and 18, Figs. 7 and 8 of text, and Plate III. Solms-Laubach, Ueber Medullosa Leuckharti, Bot. Zeit., 1897.

extremely minute, with centrifugal xylem only, the tracheides of which are well defined and thick-walled. The bundles are very irregular in position and orientated in different directions. In the sterile portion the centrifugal xylem is much reduced and quite insignificant. The centripetal xylem is fairly well developed and its tracheides much scattered and wandering. In some of the bundles the phloem is scarcely developed, and the parts of the xylem cannot be properly orientated.

Female Sporophyll. Two bundles leave the central cylinder of the axis of the female cone; in the outer part of the cortex each of these divides into two, so that four bundles are produced. In those cases where other bundles, besides these four, occur, in the stalk of the sporophyll, these are cut off by the two original bundles just before entering the latter, and passing off towards the ventral side of the sporophyll, they, in the majority of cases, twist on their axes, assuming thereby a more or less abnormal orientation (Fig. 11). The number, orientation, and structure of these ventral bundles in the stalk varies greatly; the following are the principal cases met with:—

1. One large bundle with inverted orientation.
2. Three bundles, two with inverted orientation, and the median one concentric (Figs. 11 and 12).
3. Two bundles, closely contiguous, lying sideways with their xylems facing each other.
4. Two bundles, one of which lies sideways, the other obliquely.
5. One bundle, lying close on the ventral side of one of the normal bundles, and with normal orientation, but placed rather obliquely.
6. One bundle, lying sideways.
7. One bundle, with normal orientation.

All the ventral bundles pass up into the lamina, without taking any part in supplying the sporangia; those which in the stalk were inversely orientated, in the lamina twist on their axes once more to assume approximately the normal orientation. Here the same change as regards the relative

development of the centrifugal and centripetal xylem occurs as in previous cases.

Of the four normally orientated bundles in the stalk, the two lateral ones which supply the sporangia are considerably the largest. One or two small elements of centripetal xylem may occur in any of the four bundles, but are nearly always present in the large lateral ones. From each of these latter, as they enter the lamina, two bundles branch off to the sporangium; and each of these, immediately before entering the latter, may divide up into two or three. In transverse section of the part immediately below the insertion of the sporangium, one of the two bundles is seen to be divided into three.

Scale Leaves and Barren Sporophylls. At the base of the male cone are a number of scale leaves similar to those in *Stangeria*. They contain a row of many bundles with endarch structure and very small in size; a few bundles also occur on the ventral side of this row and appear to be normally orientated. Immediately below the compactly-arranged sporophylls of the male, are two or three elongated, barren sporophylls (Fig. 13). In the case of one cone, each barren sporophyll contains, in its lower portion or stalk, a row of four or five bundles, of which the two end ones of the row are concentric in structure (Fig. 14), one of these being very small, the other of normal size. The intermediate bundles are rather larger in size than those of the fertile organ, this being due, possibly, to the smaller number of the former; their structure is similar, the centrifugal xylem being sharply defined and the phloem well developed; in the upper part, or lamina, the smallest concentric bundle dies out, while the larger one assumes a collateral structure; while, as regards the other bundles, a similar change in their structure takes place as in the fertile sporophyll.

DIOON EDULE, Lindl.

Male Sporophyll. In the narrow stalk is a single row of bundles. All are of quite small size and of nearly equal

development as regards the centripetal xylem, which is quite small in amount. Nearly all the bundles have three or four (one bundle had seven or eight) tracheides of centripetal xylem; these are, however, always faint, rounded, and weakly stained compared with those of the centrifugal xylem. In the sterile portion the usual structure of this part prevails; some of the centripetal xylem is developed as transfusion-tissue which is both lateral and ventral in position.

Female Sporophyll. Two bundles leave the cylinder of the axis of the female cone, and on their way through the cortex divide up into a considerable number of bundles, so that in the stalk of the sporophyll a row of about nine bundles occurs. Though the sporophyll is one of the largest in the order (equal in size to that of *Encephalartos*), the megasporangia are not nearly so large as in that genus; consequently, the bundles have also a considerably less development, and are all regularly orientated. In those sporophylls which bear two well-developed sporangia, the one or two bundles at either end of the row are larger and have better-developed phloem and centrifugal xylem than the intermediate ones (Fig. 15). In those with one abortive sporangium, the most external bundle of the row on the same side of the stalk is scarcely better developed than the rest. In those with both sporangia abortive, the same applies to the external bundle on both sides. The bundles of the lamina exhibit the ordinary structure (Fig. 16). The external bundle of the row on one side of the stalk and a branch from the bundle next to it bend off in the lamina and pass down to supply the sporangium; each of these divides into three, so that six bundles enter the latter (Fig. 17). Of these two or three of the smaller ones are perfectly *concentric* in structure. Some of the bundles of the inner portion of the integument of the sporangium have also a *concentric* structure, the protoxylem occupying the centre of the bundle and enclosed by primary tracheides; the phloem, however, on the ventral side is rudimentary in character; the occurrence of these bundles in the integument seems to show that the

concentric structure of those occurring in the sporophyll below the insertion of the sporangium and in the base of the latter is not entirely due to the radial symmetry of the sporangium which they supply.

ENCEPHALARTOS VILLOSUS, Lehm.

Male Sporophyll. In the winged stalk is a row of bundles, of which the one on either side situated between the wing and the central region is the largest, and has a large amount of centrifugal xylem; a certain small amount of centripetal xylem occurs at the sides of the bundle and is continuous with the centrifugal portion. The smaller bundles in the rest of the stalk have also very conspicuous centrifugal xylem of fairly large elements.

Female Sporophyll. The axis of the cone to which these sporophylls were attached was not available for investigation, so that the course of the bundles therein could not be traced.

The sporophylls are the largest of any in the order except those of *Cycas*. Their vascular system is, consequently, very well developed, and much resembles that of *Cycas*. As in that genus, the bundles have a large amount of centrifugal xylem, and many possess besides a considerable quantity of centripetal xylem, though others have less of the latter or even none at all. As in *Cycas* also, there are inverted strands on the dorsal side of many of the bundles, some of which have a small amount of centripetal xylem, while others have none; most, if not all, appear to have protoxylem; two strands placed back to back may be of equal size. But the bundles have a very irregular arrangement, being orientated and grouped in all kinds of ways, resembling somewhat the arrangement of the bundles in the basal region of the peduncle in *Stangeria*. At each side of the stalk there is an aggregation of bundles in close proximity and with variously orientated parts; these are the strands which supply the sporangium; the other bundles are smaller. In shape the bundles of the sporophyll are rounded and often very much curved, so as to

form an almost *concentric* structure (Fig. 18); indeed, in another species, *E. horridus*, Lehm., a primitive concentric structure for these bundles appears to be indicated by the peculiarity presented by some of them, as, for instance, one bundle which is curved into a horse-shoe shape so that the xylem from opposite sides almost meets at the open part of the strand so as to enclose a pith with protoxylem round its periphery; in another larger, tangentially-elongated strand which is but slightly curved, there occur on the ventral side of two groups of centripetal xylem, and intimately connected therewith by radial rows of cells, two distinct groups of crushed phloem-cells, with a slight indication of these latter having at one time been united by similar tissue; thus the combination of this phloem with the groups of centripetal xylem affords the phenomenon of two small strands with inverted orientation on the ventral side of the main strand; other groups of centripetal xylem occur belonging to the same strand, but isolated and without any sign of phloem near them (Fig. 19).

In the *lamina* the strands have about the same general structure; but here the centrifugal xylem is extremely reduced as compared with that in the stalk, its tracheides also being usually much smaller; it is about equal in development to the centripetal which occurs in considerable quantity, and in some bundles extends as transfusion-tissue, with scalariform thickenings on the transverse walls of the tracheides, both laterally, and even quite on to the dorsal side of the phloem. In *E. horridus*, Lehm., protoxylem was only seen on the side of the centripetal xylem.

The megasporangium receives 4-5 bundles, some of which have a very distinct *concentric* structure (Fig. 20).

MACROZAMIA FRASERI, Miq.

Male Sporophyll. There are about a dozen bundles in the stalk lying in a regular row and somewhat unequal in size. They all have sharply-defined and brightly-stained centri-

fugal and an entire absence of centripetal xylem. They arise from the branching of three bundles (which really represent two, of which one has undergone premature division) which enter the sporophyll from the axis of the cone, these three originating in the cortex from the single bundle which leaves the central cylinder. Owing to this premature division of one of the bundles entering the sporophyll, there are at first a larger number of bundles on one side of the organ than on the other.

In a rather young male sporophyll of *M. spiralis*, Miq., there are about nine bundles in the stalk.

Female Sporophyll. This is one of the large types of sporophyll. Owing to the fact that the material at my disposal was dead and withered, the arrangement of the bundles in the stalk could not be ascertained, as the sections broke up into small fragments. The strands appear to be of the same type, in form and structure, as those in the female sporophyll of *Encephalartos*, as they possess a large amount of centrifugal and also a small but well-marked quantity of centripetal xylem. In the lamina some of the bundles are a good size, the centrifugal and centripetal parts of the xylem being of about equal development, though the former seems to stain rather more sharply than the latter.

ZAMIA LATIFOLIA, Lodd.

Male Sporophyll. In the lower part of the stalk are three bundles with the typical centrifugal and no centripetal xylem. A little higher these divide up into a rather larger number, of which one from each side is seen to pass off to the dorsal side of the sporophyll. One of the bundles in this region show a good example of primary centrifugal xylem; it has a single, minute, flattened tracheide of secondary centrifugal xylem separated from the other portion of this tissue by a layer or two of roundish parenchyma-cells; next, towards the ventral side succeeds a row of four or five tracheides, very well-defined, and with brightly-coloured walls, and then

a second row of as many, but rather smaller and less clearly-defined tracheides, these two constituting the primary centrifugal xylem; these tracheides do not lie in the same radial rows as the cambium-cells further out, but are separated therefrom by the parenchymatous cells afore-mentioned, some of which overlap in position two of the cambium-cells. In the sterile portion the mesarch structure of the bundles is very pronounced.

Female Sporophyll. In the stalk, besides the four bundles which exhibit the usual structure and no centripetal xylem, there is a very small one on the ventral side with inverted orientation and almost concentric structure, which has evidently sprung from one of the four bundles opposite to which it lies.

ZAMIA PUMILA, Linn.

Male Sporophyll. In the stalk is a row of about six bundles, quite small in size, one or two having only a single tracheide of centrifugal xylem. Of these small bundles, two occur on the dorsal side of the row, one of them lying sideways and being semi-concentric in shape. That there is a tendency for a concentric structure to appear in the bundles is shown also by one in which a rudimentary phloem occurs on the ventral side of the protoxylem. In one of the bundles two elements of centripetal xylem occur.

In the sterile portion the bundles have the usual mesarch structure.

ZAMIA SKINNERI, Warsz.

Male Sporophyll. In the stalk are three bundles with well-developed secondary tissue, of which the tracheides, especially in the median bundle, are of considerable size and very brightly coloured. To each bundle a single tracheide of centripetal xylem is seen to be attached. In the region just above where the bundles pass off to the sporangia, occur two large bundles with well-developed, typical mesarch

structure, both the centrifugal and centripetal xylem having each its distinct group of protoxylem. Higher up in the sterile portion these bundles split up into a larger number, some of which are partially concentric in structure like those in the female sporophyll of *Encephalartos*.

ZAMIA MURICATA, Willd.

Male Sporophyll. There are three very small bundles in the stalk, with the usual structure, the two outer ones of which have a sidelong position. But at a certain level there occur in close proximity to two of these the rudiments of a bundle lying obliquely towards the ventral side of the normal bundle; in one case the rudimentary bundle appears to have a mesarch structure, a minute protoxylem-group intervening between the reduced phloem and two rather scattered tracheides. In the sterile portion many of the bundles exhibit a structure intermediate between mesarch and endarch, tracheides occurring at the sides of the protoxylem of which it is not easy to say whether they belong to the centrifugal or centripetal portion of the xylem; in the same region are other bundles with a definite mesarch structure, some of which have no centrifugal xylem at all.

ZAMIA LINDENI, Regel.

Male Sporophyll. In the stalk is a short row of four bundles which are normal in every respect (Fig. 21). In the sterile portion are a great number of bundles orientated in every direction and with the usual structure.

Barren Sporophyll. The smaller compactly-arranged barren sporophylls at the base of the male cone, which are similar in conformation to the fertile organs, present a very interesting structure. The bundles in the stalk, sometimes one, sometimes several in a row, are all more or less to be interpreted as having a partially *concentric* structure; in some

cases the appearance is as if two distinct bundles were closely united, but not completely fused, by their ventral faces; in others the bundle has a curved, or horse-shoe shape. The bundles are all irregularly orientated, mostly assuming a sidelong position (Fig. 22). But these structures are of importance from the fact that they exhibit more primitive characters than the bundles of the fertile sporophyll, the latter differing entirely therefrom, both in structure and arrangement, being perfectly collateral and normally orientated. It is owing to the absence of the sporangiferous function in these barren sporophylls that this primitive structure has been retained.

ZAMIA LODDIGESII, Miq.

Female Sporophyll. Two bundles leave the cylinder of the axis of the female cone, each from a distinct strand thereof. On their way through the cortex each divides into two, thus forming four bundles. The small bundles which occur in pairs in the cortex of the peduncle and which supply the barren sporophylls at the base of the cone have, many of them, centripetal xylem, of the normal kind and in the form of very distinct transfusion-tissue, both in a ventral and a lateral position (Fig. 24).

Of the four bundles in the stalk of the sporophyll, the smaller, newly-formed ones move somewhat forward towards what becomes the ventral side of the organ. The two lateral bundles are somewhat larger, though not so strikingly so as in other genera. All these bundles have several elements of centripetal xylem which are often larger than the tracheides of the centrifugal portion; in this respect this plant affords quite an exception to the general rule.

One bundle turns off to the megasporangium on each side, dividing into two main branches; one of these, the proximal one, before entering the sporangium, divides in different directions into three branches; the distal bundle, which

passes obliquely away to the far side of the sporangium, remains undivided. As seen in transverse section, a bundle about to enter the sporangium has a curved contour, with very well-developed centrifugal and often a large amount also of centripetal xylem; the occurrence of this latter is perhaps correlated with the evident tendency of these bundles to revert to a concentric structure.

In many of the bundles in the most distant portions of the lamina, transfusion-tissue is very markedly developed, resulting from the extension, even on to the dorsal side of the phloem, of the centripetal xylem (Fig. 23). As in nearly all other cases, the tracheides of the centrifugal are always much smaller than those of the centripetal xylem.

ZAMIA FURFURACEA, Ait.

Female Sporophyll. In the stalk are four bundles with the usual structure; no centripetal xylem occurs here; the two lateral bundles are rather better developed than the others and have larger centrifugal tracheides. A little higher up in the sporophyll one of the middle bundles gives off a very small branch which gradually, in passing upwards and towards the ventral side, turns on its axis, assuming directly afterwards a perfectly *concentric* structure, which again, higher up, opens out and becomes collateral; there may be more than one bundle on the ventral side of the normal row; these bundles pass up into the lamina without again assuming a normal orientation. In this latter region of the sporophyll transfusion-tissue is well developed in many of the bundles.

Two bundles enter each megasporangium; one of these, the largest, being the lateral, unbranched bundle of the stalk on the same side which passes up round the axil of insertion of the sporangium; the other, which is very much smaller, as a descending branch from a bundle which has passed a considerable distance up into the lamina; there is thus

a difference in this respect from what occurs in the case of *Z. Loddigesii*. The smaller bundle is collateral in structure and somewhat curved in shape, with two or three elements of centripetal xylem, the other larger one has well-developed centrifugal and no centripetal xylem, and is curved inwards so as to assume an almost *concentric* structure; in the base of the sporangium this bundle begins to separate into two, as a result of which two almost distinct bundles come to lie in close contact, with their xylems facing each other.

ZAMIA FISCHERI, Miq.

Female Sporophyll. The arrangement and structure of the bundles here is very similar to what obtains in the last plant; a small ventral, inverted bundle also being present.

ZAMIA LEIBOLDII, Miq.

Female Sporophyll. The sporophyll examined bore *three* megasporangia (Fig. 25); as a consequence of this the arrangement and structure of the bundles in the stalk are somewhat modified to suit this abnormality. On the side on which the two sporangia occur is a bundle much larger than is usually the case, and close to it another bundle almost or quite as large, but lying somewhat obliquely and with inverted orientation. The bundle at the other side of the sporophyll is very much smaller, corresponding more in size to the bundles supplying the sporangia in previous species. At a slightly higher level the inverted bundle on the side of the two sporangia turns on its axis and becomes united laterally, in the normal position, with the adjacent bundle, so as to form a single exceptionally large bundle, considerably elongated in the tangential direction, and with very well developed centrifugal but no centripetal xylem. The unusual size of this bundle is obviously correlated with the extra sporangium attached to that side of the sporophyll.

At a somewhat higher level still, this large strand divides up into a row of four, of which the two end-bundles are larger, and have their centrifugal xylem developed in such a way as to indicate that they are the bundles which are to supply the sporangia. Hence, probably on account of the lop-sided character of the sporophyll, owing to the extra sporangium being present on one side, the vascular system, to counterbalance this, is concentrated on this side, the normal row of four bundles, instead of being evenly spread over the tissues of the sporophyll, as in all other cases, is limited to the side on which this extra sporangium occurs. The smaller bundle on the other side of the stalk has nothing to do with any of the sporangia, but passes up into the lamina. In the upper part of the stalk about three smaller ventral bundles are seen, one of which is *concentric* in structure, the others irregularly orientated; tracing these downwards, one of them is seen to spring from one of the four bundles of the row, the other two, of which the concentric one opens out and becomes collateral, end blindly each close up against the rim of a mucilage-canal. Higher up, the two end-bundles of the normal row are seen to pass off respectively right and left to the sporangia (the one supplying the two sporangia much earlier than the other). The extra sporangium may be fed by subsequent branching of the bundle passing off to the normal sporangium on that side; but the exact course of the bundles to each sporangium was not followed. The bundle passing off to supply the single sporangium on the other side appears to give off a small branch while doing so; this does not happen in the case of the bundle supplying the two sporangia. The large bundle found entering the sporangium is almost concentric, as in other cases; on entering the sporangium it splits up into a number of parts which radiate out from the common centre.

Fig. 25 *a* and *b* represent respectively ventral and lateral views of the sporophyll.

CERATOZAMIA LATIFOLIA, Miq.

Male Sporophyll. The course of the bundles from the central cylinder of the axis of the male cone to the sporophyll has been thoroughly described by Thibout in *C. mexicana*, Brongn.¹ The occurrence of medullary bundles in the axis has also been mentioned and figured by him², and by Scott³ in that species. In the present species I observed in one case three small bundles lying in the pith immediately within the normal ring which, one after the other, end blindly upwards. In another case a single large bundle in a similar position was traced upwards for a long distance; in one part of its course it split into two bundles which directly afterwards again fused together into one. It twice partially fused with a bundle of the ring during its course, but was not seen to completely fuse therewith. A similar large bundle, which at first was collateral, became higher up *concentric*, and at a still higher level again collateral; it eventually ended blindly in the pith. These characters are confined, in this species, to the male cone; they do not, however, occur in the male cone of *C. Miqueliana*, H. Wendl.

In the lowest part of the stalk of the sporophyll three bundles occur, of which the median one is much smaller than the others; the centrifugal xylem is clearly defined and brightly coloured, and there is no sign of any centripetal xylem. For the rest, the structure is similar to that of the bundles in the male sporophyll of other genera.

CERATOZAMIA MEXICANA, Brongn.

Male Sporophyll. In the lowest part of the stalk are three bundles, the median one as in the last species, being much smaller than the others, and lying out of the row or a short distance towards the dorsal side (Fig. 26). In the sterile

¹ Loc. cit. p. 23.² Loc. cit. p. 24.³ Loc. cit. p. 412.

portion of a young sporophyll in which the parts of the bundle are not as yet fully developed, the xylem consists of protoxylem, on the ventral side of which are two or three elements of centripetal, and occasionally, on the dorsal side, one or two elements of primary centrifugal xylem, and in the lateral region are primary elements intermediate between the two kinds. In one or two bundles one tracheide was seen which appears to be secondary in origin, and which was deeper in colour and larger than the others, and isolated, lying quite apart from the group of primary tracheides.

Female Sporophyll. Two bundles arise independently from a distinct strand of the central cylinder of the axis of the female cone; on their way outward through the cortex they each divide up into a number of bundles, some of which pass up on to the ventral side of the others, turning on their axes as they do so, so that in the stalk of the sporophyll there is a ring or double row of bundles with their xylems all pointing towards the centre. The ventral bundles of the stalk with inverted orientation nearly all, in the lamina, turn on their axes and become normally orientated, so that two rows of bundles pass upwards through this region; one or two bundles, however, lying somewhat out of the ventral row, towards its inner side, retain their inverted orientation. As the sporophyll was very young, the bundles had not yet attained their full development; but in the stalk, centrifugal and no centripetal xylem was developed.

C. MIQUELIANA, H. Wendl.

Female Sporophyll. In the lowest part of the stalk there is a row of three or four bundles, of which the two outer lateral ones are of great size, with a very well-developed mass of centrifugal and two or three quite small elements of centripetal xylem. The one or two intermediate bundles are quite small, elongated radially, and may have an element or two of centripetal xylem. In some sporophylls there occur on the ventral side of and lying usually some distance away from

the normal row, several small normally-orientated bundles whose origin, owing to the cone being in a state of decay and the tissue therefore connecting the sporophylls with the axis being partially destroyed, could not be ascertained (Fig. 27). In the case of a small bundle with inverted orientation, lying on the ventral side of one of the large lateral bundles, this was observed to be cut off from this latter, whose phloem gradually extended round the xylem, so as to render the bundle partially concentric in structure, when part of it became severed towards the ventral side, which part, twisting on its axis, formed the small inverted bundle.

In the lamina, the bundles have usually an equal quantity of centrifugal xylem, but in some the latter is absent.

In the young female sporophyll the developing bundles of the lamina appear to *form centrifugal and centripetal xylem at the same time*; in some bundles both kinds are seen together (Fig. 28), in others centripetal alone; in others, again, centrifugal alone; in some there is an intermediate stage where the tracheides lie at the side of the protoxylem. This variation in the respective development of the centrifugal and centripetal xylem coincides with what is found in the mature sporophyll.

In the *barren sporophyll* of this genus the bundles are all of uniform development, and none are so markedly developed as those supplying the sporangia in the fertile sporophyll.

SUMMARY.

The result of my investigations into the structure of the sporophyll for each genus may be thus summarized:—

Cycas, ♂ : in lower part of stalk (though probably not at extreme base) centripetal xylem of bundles is equal to, or greater in amount than, centrifugal xylem.

——— ♀ : borne directly on vegetative axis; larger and more leaf-like than in any other genus; bundles of large size, with large development of centrifugal and

considerable and constant quantity of centripetal xylem, with small inverted strands on their dorsal side, structure exactly resembling that of bundles in peduncle of *Stangeria*; large strand supplying megasporangium has almost completely concentric structure with few primary tracheides in central pith.

Stangeria, ♂ : two bundles in stalk with purely endarch structure.

————— ♀ : two to four bundles in stalk, of which two lateral ones supplying sporangia are much larger in size; centripetal xylem of two or three tracheides only in one or two bundles.

Bowenia, ♂ : number of very small bundles in stalk, irregularly orientated, and with purely endarch structure.

————— ♀ : four principal bundles in stalk, of which two lateral are largest; few tracheides of centripetal xylem always present in latter and may also occur in smaller bundles; besides these, occur small bundles on ventral side very differently orientated in different sporophylls, and sometimes quite *concentric* in structure.

Dioon, ♂ : number of small bundles in stalk; most have three or four or more centripetal tracheides.

————— ♀ : one of the largest in order, but megasporangia relatively small in size; number of bundles in stalk, but extreme base not represented. Lateral bundles of row more strongly developed than rest only when sporangia they supply are not abortive; small quantity of centripetal xylem present in some bundles.

Encephalartos, ♂ : row of bundles in stalk, of which some are larger than others, and have small amount of centripetal xylem.

————— ♀ : one of the largest in order; bundles in stalk resembling those of ♀ of *Cycas* in structure, but very irregularly orientated and grouped, and more curved in shape, some having almost *concentric*

structure. Centrifugal xylem nearly always present, often in large quantity. Small inverted strands attached to dorsal side of bundles, as in *Cycas*.

Macrozamia, ♂ : two to three bundles in lowest part of stalk, which rapidly divide up into larger number with usual endarch structure ; no centripetal xylem.

————— ♀ : one of the largest in order ; bundles have very well-developed centrifugal and well-marked quantity of centripetal xylem ; bundles resemble very much those in ♀ of *Encephalartos*.

Zamia, ♂ : three to four bundles in stalk with rather irregular arrangement and orientation ; centripetal xylem sometimes present ; some bundles are partially *concentric* in structure.

Z. Loddigesii, Miq., ♀ : four bundles in stalk, of which two lateral are largest. All bundles have centripetal xylem, whose elements are often larger than those of centrifugal portion.

Z. furfuracea, Ait. ; *Z. latifolia*, Lodd. ; *Z. Fischeri*, Miq., ♀ : the four bundles have no centripetal xylem. A small bundle, either *concentric* or collateral in structure, occurs on ventral side of row as a branch from one of normal bundles.

Z. Leiboldii, Miq., ♀ : abnormal, bearing *three* sporangia ; in consequence, vascular system of stalk is concentrated on side on which two sporangia are borne.

Ceratozamia latifolia, Miq., ♂ : *medullary* bundles, either *concentric* or collateral in structure, in axis of cone ; three bundles in stalk of sporophyll ; no centripetal xylem.

C. mexicana, Brongn., ♂ : of three bundles in stalk, median one is much smaller than other two.

————— ♀ : ring or double row of bundles in stalk, whose xylem is in all cases directed inwards ; these arise from division of two original bundles arising from cylinder of axis. Owing to young state of organ no difference in respective development exists.

C. Miqueliana, H. Wendl., ♀ : row of three to four bundles in stalk, of which two lateral are of great size compared with the others ; along with largely developed centrifugal, few small centripetal tracheides usually present, as is also the case with smaller bundles ; other smaller bundles, quite apart from normal row, with either normal or inverted orientation.

The more general characters of the sporophyll are the following :—

Male. A single bundle leaves the cylinder of the axis of the cone, which, on entering the stalk of the sporophyll, divides into three. The bundles supplying the sporangia are much smaller in size than the similar ones on the female side, owing to the comparatively brief period of attachment to the sporophyll of the microsporangia and the short functional activity of the latter. They also diverge less from the mesarch structure of those of the foliage-leaf than do the bundles of the female sporophyll.

Female. Two bundles leave the cylinder of the axis of the cone, usually dividing up in the cortex into a larger number, so that, as a rule, four bundles occur in the stalk of the sporophyll, of which the two lateral ones are much larger than the rest, this being correlated with their function of supplying the megasporangia during the long period of development and attachment of the latter to the sporophyll. The divergence from the ordinary mesarch structure of the foliage-leaf is much more marked here.

In the *sterile* portion of the sporophyll of both sexes, i. e. the part above the insertion of the sporangia, the mesarch structure of the bundles prevails, showing how, the sporangial element being eliminated, the ordinary and typical structure of foliar bundles reappears. As compared with the bundles of the stalk, the centripetal is as a rule much more developed than the centrifugal xylem, while the phloem, which shares the development of the centrifugal xylem in the stalk, becomes reduced and insignificant.

As a general theory resulting from the preceding investigations, it appears to me a quite probable view that the sporophyll in Cycadaceae is a more primitive foliar organ than the foliage-leaf, and for the following reasons:—

a. The theory of Bower with regard to the development and morphology of spore-producing members in the Lycopodineous series of plant-forms and the phylogenetically late appearance of assimilating foliar appendages, which arise by progressive sterilization of the tissues of the former, appears to me to be a highly natural hypothesis and one containing a large element of truth.

Now, it seems to me highly probable that the Fern-sporophyte had a very similar origin, that it also arose from a fertilized oospore which, instead of producing motile reproductive organs, gradually replaced these latter by asexual, non-motile spores contained in sporangia which eventually became raised into an aerial position by progressive sterilization of the tissues of the young developing sporophyte: a theory which will not be accepted by those who incline to the view that the Fern-sporophyte had an entirely different origin from that of the Bryophytes¹, with which group it is here my purpose to emphasize its similarity of origin. There is, in fact, no reason to think that the order of development of the two kinds of foliar appendages, sporophyll and foliage-leaf, should, in the Fern-series, have been fundamentally different from that in the Lycopodineous series: the ontogenetic developmental history of the two types is to-day so similar as to point to the probability of their phylogenetic developmental history having been also similar.

This being so, we may assume that evolution may have proceeded as follows. First in order of time, sporophytes which bore sporophylls only would exist; next to these would succeed those in which both sporophylls and assimilating foliar organs were present. But it is quite conceivable that subsequent modification of all the sporophylls might

¹ Scott, Address to Botanical Section of Brit. Assoc. Meeting, Liverpool, 1896, pp. 9-10.

have taken place in certain forms, producing types like the Marattiaceae at an early period, so that the sporangia came to be borne on assimilating fronds, as in the case of most modern Leptosporangiate Ferns. On the other hand, the original type, viz., that in which the sporangiferous organs were distinct from the assimilating leaves, probably persisted right through, even down to the present day. From such forms as these latter I imagine it to be quite conceivable, and even probable, that modern Cycads took their origin.

b. From the investigations of Solms-Laubach, Scott, and myself, it appears that the *peduncle* of these plants has in several ways, notably in the simplified vascular bundle-system, the presence of a mesarch structure in the bundles of the central cylinder, and of concentric strands in various parts of the organ, a more primitive structure than the vegetative stem, and probably therefore more nearly represents the original typical stem-structure. This being the case, it might naturally be expected that the foliar appendages of the peduncle would possess a more primitive structure than the foliar appendages of the vegetative stem.

c. This primitive structure is represented by the *concentric* bundles which occur in both the fertile and barren sporophylls of several genera, especially in the latter organs, where the special physiological function of the former has not interfered with the original structure. These concentric bundles are absent from the foliage-leaves, the structure, number, and orientation of whose bundles are extremely regular, constant, and well-defined, whereas in the sporophylls the reverse is the case, a fact which probably points to their possessing a more primitive structure, viz., one not so perfectly adapted and stereotyped to subserve a special physiological function, as is the case with the foliage-leaves.

In conclusion, the special point upon which I desire to lay stress in this paper is this: that though the sporophyll, according to my view, is a more primitive organ than the foliage-leaf, for the reasons above adduced, the main and, physiologically, most important part of its vascular structure

has become, as a result of the sporangiferous function, much more highly modified from the primitive type than that of the foliage-leaves, this special function influencing more or less all parts of the vascular system. But though this modification in structure has taken place, it has not obscured, to such an extent as in the foliage-leaves, the primitive character of the organ which, either in the form of concentric or partially concentric strands, of irregular orientation and arrangement of the bundles, of great variability in size of the latter, or of a tendency to abortion of certain of the more primitive parts of the vascular system, appears over and over again, in one place or another, throughout all the genera investigated.

I desire to express my obligation to Dr. D. H. Scott for all the assistance and the numerous criticisms which he has, as usual, so kindly afforded me.

EXPLANATION OF FIGURES IN PLATES XVII AND XVIII.

Illustrating Mr. Worsdell's paper on the Cycadaceae.

The following are the abbreviations used:—*ph.* phloem; *ph*¹. ventral phloem; *x*². centrifugal xylem; *x*¹. centripetal xylem; *px.* protoxylem; *tf.* transfusion-tissue; *pb.* bundle from peduncle; *fb.* foliar bundle; *ped.* peduncle; *bs.* barren sporophyll; *sph.* sporophyll (fertile); *sp.* sporangium; *lm.* lamina; *st.* stalk.

Fig. 1. *Cycas circinalis*, L. Diagrammatic transverse view of the arrangement of the vascular bundles in the stalk of the ♀ sporophyll. × 35.

Fig. 2. *Cycas circinalis*, L. Transverse section of a strand from the stalk of the ♀ sporophyll. × 65.

Fig. 3. *Cycas circinalis*, L. Transverse section of a bundle from the lamina of the ♀ sporophyll. × 100.

Fig. 4. *Cycas revoluta*, Thunb. Transverse section of a concentric strand about to enter the megasporangium. × 65.

Fig. 5. *Stangeria paradoxa*, Th. Moore. Diagram of the vascular bundle-system of the ♀ sporophyll.

Fig. 6. *Stangeria paradoxa*, Th. Moore. Diagrammatic transverse view of the arrangement of the vascular bundles in the stalk of the ♀ sporophyll. × 35.

Fig. 7. *Stangeria paradoxa*, Th. Moore. Transverse section of one of the bundles in the stalk of the ♀ sporophyll which supply the megasporangia. $\times 145$.

Fig. 8. *Stangeria paradoxa*, Th. Moore. Transverse section of a bundle from the lamina of the ♀ sporophyll. $\times 145$.

Fig. 9. *Stangeria paradoxa*, Th. Moore. Diagram of the vascular bundle-system of a barren sporophyll at base of ♂ cone.

Fig. 10. *Stangeria paradoxa*, Th. Moore. Transverse section of a concentric bundle in a barren sporophyll. $\times 300$.

Fig. 11. *Bowenia spectabilis*, Hook. Diagrammatic transverse view of the arrangement of the vascular bundles in the stalk of the ♀ sporophyll. $\times 35$.

Fig. 12. *Bowenia spectabilis*, Hook. Transverse section of a concentric bundle from stalk of the ♀ sporophyll. $\times 450$.

Fig. 13. *Bowenia spectabilis*, Hook. Basal part of young ♂ cone, showing the barren sporophylls. Nat. size.

Fig. 14. *Bowenia spectabilis*, Hook. Transverse section of a concentric bundle in a barren sporophyll. $\times 450$.

Fig. 15. *Dioon edule*, Lindl. Transverse section of one of the bundles which supply the megasporangia in the stalk of the ♀ sporophyll. $\times 100$.

Fig. 16. *Dioon edule*, Lindl. Transverse section of a bundle in the lamina of the ♀ sporophyll. $\times 225$.

Fig. 17. *Dioon edule*, Lindl. Diagram of the vascular bundle-system supplying the megasporangium.

Fig. 18. *Encephalartos horridus*, Lehm. Transverse section of a partially concentric bundle in the stalk of the ♀ sporophyll. $\times 110$.

Fig. 19. *Encephalartos horridus*, Lehm. Transverse section of a bundle in the stalk of the ♀ sporophyll. $\times 110$.

Fig. 20. *Encephalartos horridus*, Lehm. Transverse section of a concentric bundle entering the megasporangium (semi-diagrammatic). $\times 100$.

Fig. 21. *Zamia Lindenii*, Regel. Diagrammatic transverse view of the arrangement of the bundles in the stalk of the ♂ sporophyll. $\times 50$.

Fig. 22. *Zamia Lindenii*, Regel. Diagrammatic transverse view of the arrangement of the bundles in the stalk of the barren sporophyll. $\times 50$.

Fig. 23. *Zamia Loddigesii*, Miq. Transverse section of a bundle in the lamina of the ♀ sporophyll. $\times 145$.

Fig. 24. *Zamia Loddigesii*, Miq. Transverse section of a bundle supplying a barren sporophyll from the peduncle of the ♀ plant. $\times 100$.

Fig. 25. *Zamia Leiboldii*, Miq. Dorsal and lateral views of an anomalous ♀ sporophyll, bearing three sporangia. Nat. size.

Fig. 26. *Ceratozamia mexicana*, Brongn. Diagrammatic transverse view of the arrangement of the bundles in the stalk of the ♂ sporophyll. $\times 35$.

Fig. 27. *Ceratozamia Miqueliana*, H. Wendl. Diagrammatic transverse view of the arrangement of the bundles in the stalk of the ♀ sporophyll. $\times 20$.

Fig. 28. *Ceratozamia Miqueliana*, H. Wendl. Transverse section of a bundle in the lamina of a young ♀ sporophyll. $\times 450$.

Fig. 1
n.s.

Fig. 2
x 15

Fig. 3
x 15

Fig. 4
x 15

Fig. 11
x 600

Fig. 12
x 300

Fig. 16
x 350

Fig. 15
x 30

R.W.P. del.

Fig. 5
X 15

Fig. 7
X 15

Fig. 8
X 75

Fig. 9
X 75

Fig. 13
X 500

Fig 10
X 10

Fig. 14
X 300

Fig. 1
n.s.

Fig. 2
x 15

Fig. 3
x 15

Fig. 4
x 15

Fig. 5
x 15

Fig. 7
x 15

Fig. 8
x 75

Fig. 9
x 75

Fig. 11
x 600

Fig. 12
x 900

Fig. 13
x 500

Fig. 16
x 350

Fig. 15
x 300

Fig. 14
x 300

Fig. 10
x 10

Fig. 17
x 600

Fig. 18
x 400

Fig. 21
x 1200

Fig. 22
x 300

Fig. 23
x 750

Fig. 27
x 180

Fig. 28
x 500

R.W.P. del.

Fig. 19
x 400

Fig. 20
x 750

Fig. 24
x 750

Fig. 29
x 800

Fig. 25
x 750

Fig. 31.

Fig. 32.

Fig. 17
X 600 Fig. 18
X 400 Fig. 23
X 750 Fig. 19
X 400 Fig. 20
X 750Fig. 21
X 1200 Fig. 22
X 300 Fig. 27
X 180 Fig. 28
X 500 Fig. 26
X 600

Fig. 30.

Fig. 31.

Fig. 24
X 750Fig. 29
X 800

Fig. 32.

Fig. 25
X 750

Worsdell, Wilson Crosfield. 1898. "The vascular structure of the sporophylls of the Cycadaceae." *Annals of botany* 12, 203–241.

<https://doi.org/10.1093/oxfordjournals.aob.a088691>.

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