The Anatomy of *Palaeostachya vera*.

BY

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With Plates XXXII and XXXIII, and four Figures in the Text.

MORE than thirty-seven years ago Williamson described before the Manchester Literary and Philosophical Society¹ 'A New Form of Calamitean Strobilus', from a fragmentary calcified specimen which Mr. Butterworth had found in a nodule from the Upper Foot Coal at Roe Buck, in Strinesdale, Saddleworth. The title of that paper is interesting. It was a 'new' Calamitean cone, because another had already been described by Carruthers and Binney, and the latter cone (*Calamostachys*) was admitted by Williamson to be Calamitean. Indeed, he states (p. 261) regarding the two cones that 'the differences which they present' are 'but generic, not ordinal ones', and, further on, he argues that his new cone must be Calamitean 'since no one appears to doubt that such is the character of Mr. Binney's strobilus'. Early in 1887 more specimens of the new cone were found among nodules from the Oldham district, and were described by Williamson in the same year before the Royal Society² as 'The True Fructification of Calamites.' As is well known, the title of this second paper was meant to emphasize Williamson's later conviction, that *Calamostachys* could not be a Calamitean cone. With the true ardour of a man who is sure of his new belief, he tells us 'Mr. Carruthers believed he had found it [the fruit of *Calamites*] in *Calamostachys Binneyana*, and Mr. Binney arrived at a similar conclusion. I have always rejected these conclusions because of the conspicuous differences between the morphology of the Calamitean twig and that of the axis of *Calamostachys*.' As a memorial of this new belief, Seward,³ when he referred the 'True Fructification' to Weiss's genus *Palaeostachya*, chose '*vera*' as the specific designation.

¹ Williamson, '69.

² Ibid., '87.

³ Seward, '98, p. 358.

Latterly, in his joint paper with Dr. Scott,¹ Williamson yielded again to the view, now undoubted, that *Calamostachys* was a true Calamitean fructification, thus admitting it to a closer relationship with *Palaeostachya*.

FIG. 1. Diagrammatic Longitudinal Section of Cone. $\times 14$. Vascular tissue, *black*. Soft parenchyma, *dotted*. Sclerized, *lined*. *Left* side passes through bundle; *right*, between bundles. In each case plane of section would pass *between* adjacent sporangia; on left these are omitted for clearness, on right they are inserted as solid objects in surface view. *D.C.*, 'disc-canal.' The sclerized tissue is here indicated (by broken lines) as seen through the parenchyma, which fills it; *Pt.xy. C.*, protoxylem-canal of main bundle; *S. Pt.xy. C.*, protoxylem-canal of sporangiophore-trace; *Pt.xy.*, plug of protoxylem left in the canal at the node. The only fact of importance indicated in the diagram for which the evidence is not quite satisfactory is the superposition of the sporangiophores over the bracts, and the superposition of the successive whorls.

This view of the relationship I hope to confirm in the present paper with the more ample data for comparison, provided by a complete reinvestigation of all the existing sections of *Palaeostachya* undertaken at the suggestion

¹ Williamson and Scott, '94.

of Dr. Scott. This examination has also brought to light certain new features which I think tend to modify, in some considerable degree, our ideas regarding the position occupied by *Palaeostachya* in the Calamarian series of fructifications.

A slightly revised account of the anatomy of this cone was published in the joint paper just referred to,¹ while Dr. Scott summarized his view regarding it, and gave an excellent figure of a transverse section in his collection, in his 'Studies.'²

Considerable difficulty has been experienced in preparing a complete account of the anatomy of this cone. The state of preservation is only fair, and the sections themselves being old, are badly cut and thick. Consequently strong and carefully controlled illumination is necessary to make out the details. These difficulties, coupled with rapid working, are probably responsible for the numerous mistakes in Williamson's account.

General Features. I have little doubt that the general external appearance of this cone would be fairly represented by Weiss's figure of his *Palaeostachya pedunculata*.³ In diameter our cone was about the same as Weiss's specimen. Its length cannot now be determined, but it does not appear to have been short. It was pedunculate, and from the fact that four successive transverse sections passed through one peduncle, we may fairly conclude that that particular peduncle was not less than half an inch in length. The internodes had a length of about 4.7 mm. Round each of the swollen nodes of the axis were placed usually eighteen oblique sporangiophores, in the axils of about the same number of bracts. The bracts were free, but imbricating except towards the tips, first horizontal, then ascending. They probably hid completely the fertile parts from view. The sporangiophores were peltate, and each bore four sporangia, all the sporangia in a whorl being closely appressed. The axis was typically Calamitean in its anatomy, fistular, without nodal diaphragms, but with a complex system of supporting tissue in the cortex at each node. Text-Fig. 1 shows this sclerized tissue in longitudinal section. It formed a thick plate-like ring as described below, with (usually) nine unsclerized intervals, which now appear as 'canals' owing to the non-preservation of the soft parenchyma which formerly filled them. On the right side, the section passes through these canals. The soft tissue in them is imagined to be transparent, and the sclerized part to be seen through it. The eighteen bundles of the axis were approximated in pairs lying between these 'canals,' as seen in Pl. XXXII, Fig. 7. The diagrammatic section shows clearly the anomalous course of the sporangiophore-trace, which is the most remarkable point now brought to light. It indicates also the swelling of the vascular tissue at the nodes by the addition of secondary tracheids.

¹ Williamson and Scott, '94, p. 916.

² Scott, '00, p. 61.

³ Weiss, '76, Taf. xv.

As mentioned in the description accompanying the section, the evidence that the sporangiophores were superposed on the bracts, and the members of the successive whorls also superposed, is insufficient (see p. 375).

The Axis. The interest of this structure centres mainly in its very typical Calamitean anatomy. It alone causes *Palaeostachya* to be undisputed as the cone of a Calamite. A transverse section of the peduncle is not to be distinguished from a young vegetative shoot, while a similar internodal section through the fertile portion differs only in the slight

FIG. 2. Slightly oblique internodal transverse section. R. $31 \times 9\frac{1}{4}$ dia. Plane of section ascends from right to left. This section has sporangia more complete than any other, and in conjunction with Text-Fig. 1 will give a fairly complete idea of the cone. It should be remembered that the soft cortex is completely removed. Br. = bract; Sp. = sporangiophore; O.S. = outer sporangium; I.S. = inner sporangium; S.ScL. = sub-epidermal sclerenchyma; Ptxy.C. = protoxylem canal.

'pairing' of the bundles. Two further peculiarities distinguish this axis from the vegetative stem; there were no nodal diaphragms across the medullary cavity, while these were functionally replaced by nodal rings of sclerized cortex—the 'nodal discs' of Williamson.

Cortex. No section shows this completely preserved, and only one shows fragments (Fig. 11). In this it appears to extend over about a quarter of the radius of the complete axis. It is a simple, large-celled, parenchymatous cortex, with its largest elements towards the exterior. On the outside of the xylem-bundles, groups of smaller elements may be traced, which no doubt represent the phloem (Fig. 8, *phl.*). The epidermis is preserved only in a section through the insertion of a sporangio-

phore. It has here divided to form four or five layers of periderm cells (Fig. 10, *pd.*). The epidermal layer itself is perfectly normal.

The most interesting feature of the cortex is its elaborate system of sclerized elements. Briefly, the stereome structure consists of a series of thick rings, one at each node, placed like phlanges round the cylinder of xylem strands and sclerized medulla, and braced together externally by vertical sub-epidermal sclerized strands. Such a skeleton must have made the axis extremely rigid, and no doubt points to an erect habit for the cone. The nodal rings (the 'discs' of Williamson) are simply zones of sclerized parenchyma occupying the entire width of the cortex, and having a vertical thickness about equal to their width (Figs. 1, 2, and 7). The junction of the sclerized zone with the soft cortex was not sharply defined, the extent of the sclerization here, as in other parts of the cone, being variable. Since a complete sclerized ring would be a physiological impossibility, large rounded intervals were left, through which the soft tissue was continuous (Figs. 1 and 7, Text-Fig. 1). By the decay of the soft tissue they now appear as 'canals' (the 'cortical lacunae' of Williamson), but in one case (Fig. 8, *par.*) there is sufficient soft tissue left to justify the view here stated. These 'canals' alternate in position with the pairs of bundles, and are usually nine, occasionally eight or ten in number. The 'disc' provided a firm basis for the attachment of both bracts and sporangiophores, the mechanical tissue of each of which joined on to it.

From the edge of the disc, between the bases of the sporangiophores, vertical bands of sub-epidermal sclerization swept upwards. Sometimes the whole band from node to node was sclerized, sometimes the upper portion appears to have remained soft, so that the sclerized part remains as a long, upward-projecting tooth. In some cases these bands joined up laterally just above the disc to form a complete sheath of sclerized hypoderma. It is evident that here, as in the disc itself, the extent of the sclerization is somewhat variable. These variations are indicated in Text-Fig. 1, and in the accompanying Text-Fig. 3.

Medulla. Within the ring of vascular bundles there was a zone of medullary tissue around the pith-cavity some five to ten cells in thickness.

FIG. 3. Oblique-transverse section. Q. 334. $\times$ about 11. Showing irregularity of sub-epidermal strands of cortical sclerenchyma. The plane of the section rises from A to B.

The average size of the cells increases towards the centre, and they are all vertically elongated except at the nodes (Figs. 1, 2, 13). Only two or three layers immediately round the cavity were thin-walled, the remainder sclerized. The medullary rays consisted likewise of regular thick-walled cells. The rays between the bundles of a pair merge insensibly into the medulla internally, and the 'disc' externally. Those between the pairs of bundles stop short at the 'cortical canals.'

Vascular System. The wedge-shaped xylem bundles form a ring round the medulla. Of these bundles there are usually eighteen, occasionally from sixteen to twenty, arranged normally in pairs, which lie alternately with the 'large canals' of the 'nodal discs.' This pairing of the bundles is the most striking feature in the anatomy of the axis. It is perhaps more apparent than real, and seems to be due to the abnormal orientation of the bundles necessitated by the mechanical arrangements at the nodes, where the phloem must be turned so as to lie within the 'canal,' while the xylem must correspondingly rotate in the opposite direction. If the bundles were normally orientated the disc would obviously be much weakened. Thus the pair of bundles lying between two canals have their xylem masses turned towards one another, and so approximated, while the phloem masses are turned away. Each bundle is endarch, and has a 'carinal' canal representing the degenerated protoxylem exactly as in *Calamites* and *Equisetum*. Traces of the broken tracheids may be seen in the longitudinal section of the canal.

At the node the protoxylem remains, obliterating the canal at that point (Fig. 1, *ptxy.*). In a mid-internodal section, each xylem bundle is seen to consist of some twenty to forty very small tracheids. The whole of this wood appears to be primary and centrifugal, though one section shows one tracheid apparently centripetal, but only, I think, because the section does not cut the carinal canal medianly at that point.

The tracheids are all either spiral or annular. On approaching the node the bundles increase rapidly in size by the addition externally of a considerable mass of secondary wood. As in *Calamites* these secondary tracheids were, in the youngest condition, limited to the nodes only, while the later-formed tracheids extended successively further and further into the internodes. It was this characteristically Calamitean development of secondary xylem which first convinced Williamson of the affinities of this cone. These secondary tracheids are larger than the primary ones, and are scalariform or pitted with two to four rows of eye-shaped pits (Fig. 14, *B, C*). Where this secondary wood is thickest, there are about ten to fifteen layers of tracheids (Fig. 3).

The node, using this term to indicate the level at which the vascular bundles give off their branches to the appendages, and at which there is the usual shortening up and disturbance of the course of the

tracheids, was situated just a little below the lower limit of the 'nodal disc.' The secondary wood was here thickest, and gradually died out above and below, extending in the upward direction just about to the upper limit of the 'disc.' I have diligently endeavoured to determine whether or not there is an alternation of bundles in the successive internodes. No tangential section exists sufficiently perfect to determine whether the successive whorls of appendages are superposed or not. From an examination of the numerous sections which cut more or less transversely through the node, I feel little doubt that no regular pectination occurred, while, on the other hand, one or two sections show features which seem explicable only on the assumption that occasional communications (probably irregular) did occur between adjacent bundles.

Vascular Supply of the Appendages. The course of the bundles which supply the bracts can only be traced with great difficulty, but it is evidently quite simple. Several of the bracts themselves show traces of quite a large xylem-bundle, and in the transverse section (Fig. 15) a single median bundle is clearly seen. There is no evidence in any case of more than a single bundle in the bract, though as Fig. 15 represents a section not far from the tip, it cannot be regarded as conclusive. The trace in the cortex is practically always lost, owing to the removal of the surrounding parenchyma, and for the same reason it is generally lost from the bract itself (see below, p. 378). A single section shows very imperfect macerated fragments of this bundle in the cortex, but its origin from the main bundle is fairly well seen in several cases (Fig. 20). It arises from the primary wood of that bundle just where the carinal canal is obliterated, and passes radially outwards and slightly upwards through the nodal secondary wood, which course was no doubt continued through the cortex till it curved downward into the bract. No gap is left in the main bundle, and as all the tracheids throughout the bract-bundle appear to be spiral or annular, it may be concluded that it received no contributions from the secondary wood.

Sporangiophore Bundles. Since the course of these bundles is the main point which fixes the position of this cone in the Calamarian series, it is a fortunate circumstance that they are accompanied through the cortex by sclerized tissue, and so are completely preserved. Yet the totally unexpected nature of the course led to its remaining long undiscovered during the present investigation. The origin of the bundle is *immediately* above that of the bract-bundle; i.e. they originate one above the other at the same node. But the sporangiophore bundle does not separate from the main bundle until it has ascended through almost exactly half the internode. It is then sharply reflexed, descends rapidly to the upper limit of the sclerized 'nodal disc,' and sweeps horizontally across the upper part of this to the base of the sporangiophore. The great

importance of this course, and the interpretation to be placed on it, justifies the further particulars now to be given. The course of the bundle across the upper part of the sclerized disc is clearly seen in radial longitudinal section in Fig. 21. The figure also demonstrates the fact that the bundle approaches the axis in an ascending, not a descending path, and though it is difficult to distinguish tracheids elsewhere, sufficient traces may be found to prove that the bundle followed the outer edge of the triangular patch of sclerenchyma limited internally by the space *S.Ptxy.C*. At the apex of this triangle, traces of reflexed fibres may be seen, as indicated in the drawing. The space *S.Ptxy.C*. I can only interpret as the protoxylem-canal of the ascending limb of the bundle. Any doubt which might be felt as to the bundle really passing round the sclerenchyma is completely removed by the numerous oblique-transverse sections, in which the sclerenchyma is seen forming the angular projections between alternate pairs of the main bundles, and showing the sporangiophore bundles hanging on to the projecting angles (Fig. 7, *Sp. tr.*). It remains to prove that that point where the sporangiophore-trace comes into contact with the main bundle, at the apex of the triangle of sclerenchyma, is not the origin of the trace. The evident reflexion of the accompanying fibres (Fig. 21) and the existence of the canal *S.Ptxy.C*. suggest otherwise. Moreover, were that point a true node, one would expect the ground tissue cells to be 'shortened-up,' and the protoxylem canals of the main bundles to be obliterated as at the ordinary nodes. But no such modifications exist. Finally, the canal I have referred to in Fig. 21 as probably the protoxylem-canal of the trace, is a constant feature in the transverse sections, especially in those through the disc, where it appears as a small lacuna external to the main carinal canal, approaching nearer to the latter canal as the section gets closer to the node, till, immediately above that point, the two spaces become confluent, causing an 8-shaped space (see Figs. 12, 13, and 16). I think this leaves no doubt as to the correctness of the view here taken.

Figs. 6 and 19 show the sporangiophore-trace crossing the 'disc' in transverse section, and give a fair idea of the dimensions of the bundle. In Fig. 6, *M*, a patch of dark tissue is seen at each end of the mass of tracheids. This tissue forms a strand accompanying the bundle, and crossing the 'disc' immediately underneath it, so that in sections at a slightly lower level the separate patches here seen become confluent. These dark patches are very conspicuous features in sections of the 'disc' (Fig. 7, *M*). One such patch is drawn in Fig. 18. The cells are elongated, with square or oblique ends, and are almost completely filled with a dense black material. At first I took this tissue for sclerenchyma, in consequence of its being always well preserved, but it is obviously not ordinary sclerenchyma, and is probably not sclerized at all. The 'melanotic' cells of the

ordinary calamites possibly represent a similar tissue. The continuation of this tissue in the sporangiophore is referred to below.

The Bracts. The number of these appendages in each whorl appears to have been equal to that of the sporangiophores, or nearly so, *certainly* not double that number as formerly stated. The adjoining Text-Fig. 4 is a camera-lucida outline sketch of a section fairly supporting this statement. The crushing of the bracts towards the left may account for their appearing

FIG. 4. Oblique-transverse section, W. 1568, illustrating the fact that the number of bracts, *Br.*, is about equal to that of the sporangiophores, *Sp.* There were eighteen sporangiophores (= projections on axis $\times 2$). Camera-lucida outline sketch.

rather more numerous on that side than theory requires. Text-Fig. 2 may also be referred to in this connexion.

Williamson¹ describes the surface of his first specimen of this cone as showing 'a series of strongly marked ridges and furrows, the former being apparently about twenty in number'; and then adds that each furrow appeared to be occupied by one bract. In that cone there were twenty sporangiophores.

The bracts were free, or very slightly connate at the base, first horizontal, then ascending. The horizontal bases were in contact laterally, the ascending portions imbricating, except towards the tip. The general form must have been broadly lanceolate, the widest point being near the base of the ascending portion, while the apex was probably acuminate, and overlapped to a small extent the bracts of the whorl above. The only

¹ Williamson, '69, p. 249.

tissue generally preserved is the sclerenchyma, which extended as a broad band under the ventral surface, and occupying about two-thirds of the width of the bract (Fig. 15, *scl.*). The figure just referred to shows the lozenge-shaped form of the complete bract. The section is probably from about the middle of the ascending portion. The epidermis is well marked. Towards the dorsal side palisade-tissue is distinctly indicated. The single median bundle, which is evident projecting from the sclerenchyma into the adjacent soft tissue, retained this relative position throughout the bract. Usually, it has vanished along with the soft tissue. Its vessels were spiral and annular. The general form and extent of the parenchyma in the horizontal part of the bract is indicated in the diagram Text-Fig. 1. The thickness of the entire bract is there under-, rather than over-estimated.

The Sporangiphores. In an external view these organs must have appeared to be practically in the axils of the bracts, though as will be realized from an examination of the oblique nodal section, Fig. 7, they did not become completely free for a short distance above the insertion of the bract.

The sporangiophore itself was very similar to the typical form found in *Calamostachys*. The stalk was straight, and in a transverse section generally showing the form of a square with rounded angles, and with its diagonals placed radially and tangentially—a form obviously due to the pressure of the four sporangia which surrounded it. The structure of the stalk is very imperfectly preserved. Fig. 5 (*sp. tr.*) shows the median vascular bundle fairly well, while a few sections show very imperfect traces of it nearer the distal end. All efforts to determine its orientation have been unavailing. Surrounding the bundle is a regular mass of tissue, of more or less longitudinally elongated elements, bounded by a simple epidermis. In this tissue I have not been able to trace the phloem. A considerable portion of this ground-tissue consists of the elongated dense black elements which have been referred to above (p. 376). Usually, nearly all the cells between the bundle and the sub-epidermal layer on the outer side of the stalk are of this type, while there are commonly some on the inner side as well. They may be symmetrically disposed round the bundle, or even mainly on the inner side.

The peltate head is preserved only in fragments. The most nearly complete example is that of Fig. 4. The mushroom-like form is well shown, and the thick black external covering of long palisade-cells. The space below this was doubtless (from analogy) occupied by soft parenchyma in which the stalk bundle divided into four branches, one for each sporangium. There is evidence that the outline of the head was undulating, as indicated in Text-Fig. 1.

The Sporangia. As already indicated, each of the sporangiophores had four sporangia round it, so that there were normally seventy-two

sporangia in a whorl. The four belonging to one sporangiophore were set so that two were inner and two outer, or, as would perhaps be more accurate, two superior and two inferior. The whole of the sporangia were closely packed so as to fill completely the space enclosed between the bracts and the axis. Consequently as seen in radial longitudinal section they were roughly triangular, the outer ones base downwards, the inner base upwards (Text-Fig. 1). Seen in transverse section they appear as truncated wedges, the radial length of which will obviously vary with the position of the section in relation to the nodes (Text-Fig. 2).

The wall of the sporangium is exactly similar to that found in *Calamostachys*. It consists of a single layer of cells which are characterized by 'buttressed' walls, such as are familiar in the latter genus (Fig. 17). It is difficult to distinguish between buttresses and radial walls, and consequently to make out the real form and size of the cells. As far as can be made out these cells are brick-shaped, or lozenge-shaped in surface view, about 35μ in the shorter and 100μ in the longer diameter.

The thickening was practically confined to the inner and radial walls of the cells. I have seen no indications of a tapetal layer, but this could scarcely be expected in view of the state of preservation and ripeness of the cones.

Williamson,¹ in his description of the cone, makes a point of the partial or entire absence of the sporangial walls in some sections, and regards this as probably due to resorption as a means of liberating the spores in the absence of elaters. This seems to me quite an unnecessary assumption, in view of the fact that decomposition had proceeded to the extent of removing nearly all the soft tissue in the cone.

Attachment of the Sporangia. No details of this can be given, but the main fact is certain, that they were borne on the under surface of the peltate expansion of the sporangiophore, near its periphery.

The Spores. There is no indication of heterospory, no variation in the size of the spores in one or in different sections being noticeable. The spores are normally circular in form, with a diameter of about 80μ . A characteristic feature, in the existing material, is that each spore shows two distinct walls, separated by an interval, besides which there is generally a large rounded or irregular dark mass in the centre.

The outer walls of adjacent spores are closely packed together, and consequently polygonal in section. The inner, which has a diameter about three-quarters that of the outer, is usually round. The most probable interpretation appears to me to be that the two walls merely represent the extine and intine, the latter having shrunk away from the former owing to a process of plasmolysis which would not improbably take place in the peaty mass of material before or during its calcification. In the same way

¹ Williamson, '87, p. 53.

I interpret the dark mass in the centre as the shrunken and carbonized remains of the cell-contents.

Williamson,¹ however, regarded the outer wall as belonging to the spore mother-cell, and stated that each mother-cell contained a single spore. This view would be possible if we regarded the spores as megaspores. Against this we have the fact that they would be rather small—they are just about the same size as the spores of *Calamostachys Binneyana*—and, further, in view of the fact that the ‘mother-cell’ wall is still not degenerated, we might fairly expect to find traces of the remaining spores of the tetrad, such as are found in *C. Casheana*. A careful search has failed to show anything which could possibly be interpreted in this way. I think it would also be rather surprising that all the cones should be macrosporous. Hence in the evidence available I see no ground for the assumption of heterospory, which this view seems to involve.

There are no other points regarding the spores which call for comment.

Affinities of the Cone. It is not intended to enter into any elaborate discussion of this question, since I do not consider that it can profitably be done without a complete reinvestigation of our knowledge of the fructifications of the Calamariaeae. The only point which is really vital to this paper is whether or not the new features of the cone, now brought to light, necessitate such a revision of our ideas as to its affinities as would cause us to take it out of the genus it is supposed to belong. The Equisetales and Sphenophyllales, which groups I regard as more closely associated than generally suggested, all agree in having cone-like fructifications, in which the sporangia are borne on stalked sporangiophores; rarely directly on leaf-like organs. The cones of the two phyla broadly differ, those of the former having sporangiophores attached to the *axis* of the cone, while in the latter the sporangiophores are attached to the leaf-like bracts. Further, the Calamariaeae have typically four, the Sphenophylleae one or two sporangia on each sporangiophore. Of course the former, too, are generally without the centripetal wood possessed by the latter. The fact that the two cones more recently described by Dr. Scott, *Cheirostrobis*² and *Sphenophyllum fertile*,³ between them reduce the separation of Calamarian and Sphenophyllaceous cones to a matter of the type of primary wood, does not affect the present question. *Palaeostachya* has only one character in which it in any way even appears to approach the *Sphenophyllum* group: its axillary sporangiophores. This feature we have seen to be totally deceptive, and hence we may confidently assert that our cone is not to be placed on the Sphenophyllaceous side of the Calamarian series. Among the Calamarian cones themselves, two other types are known from petrified material—*Calamostachys* and *Bornia*—while *Cingularia* must be made the type of a fourth group still unknown among our petrified remains. Since

¹ Williamson, '87, p. 53.

² Scott, '97.

³ Scott, '05.

the only feature of importance which distinguishes the *Bornia* cones from *Calamostachys* is the entire absence of bracts, and as this feature is not constant in *Bornia* itself, the relations of that genus need not be separately considered. *Cingularia* offers no ground for detailed comparison, as its internal anatomy is entirely unknown. Only *Calamostachys* remains. Here there seems to be a fundamental difference. Nodes surrounded by bracts alternate with nodes surrounded by sporangiophores. So we have said. But I think there is already sufficient evidence to throw serious doubt on that statement. Renault¹ describes the vascular supply of his *Calamodendrostachys Zeilleri* in these words:—‘ Dans l’espèce que nous avons figurée on compte quatorze coins ligneux, chacun muni d’une lacune, i (Figs. 5 et 6); de chaque côté se trouvent de petits faisceaux ligneux, muni ou non de lacunes, i’, qui après s’être élevés dans l’entre-nœud, au-dessus des points d’insertion des sporangiophores, *sp.*, *redescendent* pour y pénétrer en restant à la partie supérieure de la portion horizontale de ces organes. Les petits faisceaux dont nous venons de parler sont au nombre de quatorze, et forment, dans une grande portion de l’entre-nœud, une couronne très grêle discontinue en dehors du cercle des faisceaux principaux; ils séparent de ces derniers au-dessus du verticille de bractées stériles immédiatement placé au-dessous du verticille fertile que l’on considère, s’élèvent verticalement dans l’entre-nœud, puis redescendent pour pénétrer dans les pédicelles des bractées fertiles.’ It seems scarcely possible to doubt that the ‘petits faisceaux’ are the strict homologues of our sporangiophore-traces. As in *Palaeostachya*, they are equal in number to the principal bundles, they separate from them ‘au-dessus du verticille de bractées stériles,’ they ascend vertically in the internode, and are then reflexed to pass into the sporangiophores. The reflexed portion of the trace is not carried so far down as in *Palaeostachya*, and the traces are not radially opposite the principal bundles, but alternate with them. These appear to me to be the only two structural differences of classificatory importance between *C. Zeilleri* and *Palaeostachya*.

In our English *Calamostachys* it was commonly assumed that the sporangiophores represent independent fertile whorls. The influence of the ventral-segment theory of the sporangiophore has thrown doubt on this. Williamson and Scott² noticed that the principal bundles passed the fertile ‘nodes’ without interruption of their protoxylem canals, and state that ‘the fertile nodes . . . show scarcely any modification of structure as compared with the internodes.’ In a fine longitudinal section of a *Calamostachys* with the pith preserved (Manchester Museum Coll. Q. 295), it is a striking feature that the pith cells are ‘shortened-up’ at the level of the bracts, while they pass by the sporangiophores unchanged. These facts appear to me to raise the strongest doubt against the view that the

¹ Renault, '96, p. 130, Pl. LX, Figs. 3-8.

² Williamson and Scott, '94, pp. 905-6.

sporangiophores represent independent whorls. I feel convinced that it will be found that the sporangiophore traces really arise just above the bract-traces, and then rise in contact with their parent-bundles till they turn out into the appendages to which they belong. If this view is correct, then the only important differences between *Calamostachys* and *Palaeostachya* are the absence of any considerable reflection of the sporangiophore-trace in the former, and the possession of (approximately) two bracts to each sporangiophore. I do not think that much stress should be laid on either of these differences. Among various Calamite cones the sporangiophore may be found attached to almost every part of the internode. The number of bracts in the whorl appears to have been anything from that of the sporangiophores up to three or more times as great as the latter.¹ It is noteworthy that although the specimens of *Calamostachys* with structure preserved have *approximately* two bracts to each sporangiophore, the relation is seldom exactly two to one, while in *Palaeostachya* it is possible that the number of bracts somewhat exceeded that of the sporangiophores. A tendency to multiply the number of appendages in each whorl seems to have been a characteristic Calamarian feature. Hence I would conclude that *Calamostachys* and *Palaeostachya* need not be remotely separated.

An interesting suggestion as to a possible explanation of the course of the sporangiophore trace in *Palaeostachya* was made to me by Mr. Boodle, to the effect that the triangle of sclerenchyma which is seen in longitudinal section between the ascending and descending limbs of the trace may be an upgrowth of the sclerized tissue of the disc, which has carried the trace with it. Against this view, however, I would urge the following considerations: Firstly, in *Calamodendrostachys* there is already a real, though small, reflection of the trace, while no sclerized tissue is present. Then the tissue referred to appears to me to be associated with the trace itself more intimately than with the disc. I have pointed out (p. 378) that in the sporangiophore-stalk there is a mass of dense resistant tissue which completely or partially surrounds the bundle, and that is a continuation of the strand of similar tissue which lies under the bundle in the 'disc.' No section exists good enough to show clearly the nature of the triangle of 'sclerenchyma' referred to above, but I strongly suspect that it consists, in part at least, of that same strand of tissue following the bundle and reflected with it. I think Fig. 21 accords with this view as well as can be expected. Finally, the only explanation of such an upgrowth would be a mechanical one, and I should doubt if any appreciable gain in rigidity is obtained in this way, though I would not profess to understand the remarkable mechanical adaptations of this cone. In view of all the facts at present available, the phylogenetic explanation seems to me much more probable, though even if the alternative view should prove correct, the

¹ Weiss, '76, Taf. xvi, Fig. 3 B, *Calamostachys germanica*.

close relationship of *Calamostachys* and *Palaeostachya* would not be seriously diminished.

Lignier¹ has already ably advocated the view that the 'fertile whorl' of *Calamostachys* is merely a displaced series of fertile segments of the sterile leaves, and has pointed out the significance of the course of the traces of the appendages in these fructifications. In the same paper he interprets the tetrasporangiate sporangiophore as the result of the fusion of adjacent sporangiophores in pairs, so that the compound organ now lies superposed to the interval between the pair of leaves to which its component sporangiophores belonged, while the total number of sporangiophores is reduced to half that of the bracts. This ingenious interpretation affords an admirable explanation of the structure of *Calamodendrostachys* and of some specimens of *Calamostachys*. In the numerous specimens of the latter genus in which the sporangiophores are more than half as numerous as the bracts, it will be more difficult to apply, while in *Palaeostachya vera* it cannot be applied. It does not appear to me that the relationship between the number of bracts and of sporangiophores in Calamitean cones is as definite as would appear to be commonly supposed. The only rule which seems to hold generally is that the sporangiophores are always equal in number to the primary bundles of the axis, or practically so, while the bracts are equally or more numerous. Thus, while agreeing with Lignier as to the probable origin of the sporangiophore and the mode of multiplication of the appendages, I think it must be allowed that the sporangiophores and bracts, having become separated, might be multiplied independently and sometimes irregularly. I should therefore regard it as more probable that the double number of bracts as compared with sporangiophores in *Calamostachys* is due to the bracts having undergone more division than the sporangiophores, rather than as due to a process of refusion among the latter.

Regarding the propriety of retaining our cone in the genus *Palaeostachya*, we may note that there is nothing in Weiss's² definition to exclude it: 'Stem and branches with asterophyllitiform leaves. Cones attached at the nodes in pairs (or singly?), cylindrical, articulated. Bracts free, arcuate; sporangia attached to a straight columella or sporangiophore arising out of the axils of the bracts, elliptic, verrucose. Sporangiophore with peltoid apex, four inwardly-directed sporangia (secundum Renault).' In two respects the specimen now described does not fit in with the conception of *Palaeostachya* which up to now has been prevalent. The axillary position of the sporangiophore appears to be a secondary one, and consequently the cone does not provide a link between the Sphenophyll cones and *Calamostachys*, but represents a further modification of the latter type; while the number of bracts is certainly not double that of the sporangiophores. But

¹ Lignier, '03.

² Weiss, '76, p. 103.

neither of these features belongs to Weiss's original conception. The latter arose as an error of observation, the former was an assumption to satisfy a theory. Our own specimen and Weiss's type of *Palaeostachya elongata* seem to agree in all points of generic importance observable in both, and therefore I see no reason why they should not share the same genus until some vital distinction can be proved.

Solms Laubach¹ has placed Renault's *Volkmannia gracilis* in this genus, and it undoubtedly has (approximately) two bracts to each sporangiophore, but I do not think that reference makes that character an essential feature of the genus. Weiss's 'genera' can only be regarded as types, not as genera in the true sense. It will be rather surprising if all Calamitean cones with axillary sporangiophores are ultimately found to come within the limits of a single biological genus.

At least, so long as Weiss's classification is adopted there can be no doubt that this cone must be placed in his genus *Palaeostachya*, which he makes for cones with sporangia attached in fours to peltate sporangiophores which arise in or near the axils of the bracts. The course of the sporangiophore-traces may be added as a further generic character. Finally, it is of interest to note that Weiss himself suggests that both *Cingularia* and *Palaeostachya* arose from *Calamostachys*, by the movement of the sporangiophores upward in the former, downward in the latter case.

SUMMARY.

Palaeostachya vera is a Calamarian fructification characterized by axillary sporangiophores.

Cones cylindrical, pedunculate. Diameter about 14 mm., length unknown.

Axis with external diameter of 4 mm., the vascular cylinder being about 2.7 mm. Primary vascular bundles generally eighteen, in pairs, probably not alternating at nodes, each with a protoxylem (carinal) canal on inner side, which is obliterated at the nodes. Secondary wood present at nodes only. Bract traces leaving bundles nearly at right angles, not divided. Sporangophore-traces arising immediately above bract-traces, passing outwards very obliquely through the secondary wood of the parent-bundle, ascending in contact with bundle through half-internode, then redescending obliquely to enter the base of the sporangiophore.

Cortex mainly parenchymatous, with a sclerized ring above each node (the 'disc') perforated by nine unsclerized patches (the 'disc-canals').

Bracts approximately equal in number to the sporangiophores (generally eighteen), with a single bundle, sclerized ventral and parenchymatous dorsal portion. Lanceolate. Free. Sporangophores peltate,

¹ Solms Laubach, '91, p. 332.

bearing four sporangia each. Sporangia flattened in transverse, triangular in vertical section. Walls consisting of a single layer of buttressed cells as in *Calamostachys*. Spores about .08 mm., all of one kind.

In concluding this paper I desire to express the thanks I owe to Dr. D. H. Scott, F.R.S., for valuable suggestions, the loan of his own slides, and facilities for the examination of those in the Williamson Collection, and to Prof. F. E. Weiss, D.Sc., for the loan of the slides in the collection of the Manchester Museum, Owens College.

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EXPLANATION OF PLATES XXXII AND XXXIII.

Illustrating Mr. Hickling's paper on *Palaeostachya vera*.

The letters attached to the catalogue-numbers of the slides are as follows: Q. = 'Cash' Collection (Manchester Museum); R. = Manchester Museum (general) Collection; S. = Scott Collection; W. = Williamson Collection (British Museum).

PLATE XXXII.

Fig. 1. Oblique transverse section. On left, in 'disc'; on right, below. *Br.* = bract, sclerized tissue of ventral surface; *Br'* = soft tissue of ventral portion of bract; *C* = portion of cortex, immediately below bract; *Ptxy.* = protoxylem mass obliterating canal at node; *2ny.xy.* = secondary wood: note how this decreases rapidly as section ascends. S. 474. × 16.

Fig. 2. Longitudinal (slightly oblique) section through node showing 'arching' of secondary tracheids over node. Section is not quite median through node. It shows the relation of 'disc' to node. *D.* = 'disc'; *n.* = node; *Pt.xy.C.* = protoxylem canal of bundle. W. 1573. $\times$ about 38.

Fig. 3. Transverse section of axis at node. Note large amount of secondary wood; absence of protoxylem canals. R. 143. $\times$ about 38.

Fig. 4. Peltate expansion of sporangiophore. R. 31. $\times$ about 38.

Fig. 5. Sporangiphore cut longitudinally, showing its bundle, *Sp.tr.*, in lower portion, where it adjoins cells of disc. R. 30. $\times$ about 38.

Fig. 6. Oblique transverse section of part of disc showing curved sporangiophore-trace crossing it. *Sp.tr.* = sporangiophore-trace; *M.* = tissue described at p. 376. Q. 336. $\times$ about 38.

Fig. 7. Oblique 'disc' section. At right edge, section cuts near lower limit of 'disc'; plane of section rises towards left edge. Note the ring of buttresses formed by the pairs of sporangiophore-traces and their accompanying sclerenchyma. *Br.* = base of bract; '*L.Can.*' = large 'disc canals'; '*Sm.Can.*' = small 'disc canal' (= torn-out sporangiophore-trace); *Sp.* = sporangiophore-stalks cut at various levels; *Sp.tr.* = sporangiophore-trace, descending limb; *Sub-ep.Scler.* = strand of sub-epidermal sclerenchyma. R. 30. $\times$ about 11.

Fig. 8. Oblique transverse section through lower portion of part of disc, showing large 'disc canal' half filled with parenchyma. *Par.* = parenchyma in 'disc canal'; *Phl.* = secondary phloem. R. 140. $\times$ about 38.

Fig. 9. Internodal transverse section. Above level reached by sporangiophore-trace. Shows small amount of wood in bundles as compared with that at nodes. Cf. Figs. 1 and 3. Q. 332. $\times$ about 38.

Fig. 10. Bases of two sporangiophores just emerging from disc. Part of section, Fig. 7. *M.* = tissue described at p. 376; *Pd.* = periderm; '*Sm.can.*' = 'small outer canal' (= torn-out sporangiophore-trace). R. 30. $\times$ about 38.

Fig. 11. Portion of internodal transverse section with cortex preserved. R. 142. $\times$ about 38.

Fig. 12. Portion of transverse 'disc' section. *Px.C.* = protoxylem canal of main bundle; *Sp.Px.C.* = protoxylem canals of sporangiophore-traces (really more distinct than they appear in photo), see drawing, Fig. 16. Q. 336. $\times$ about 38.

Fig. 13. Similar section at slightly lower level. Each of the three protoxylem canals is seen to be elongated. They are dividing into the canals of the main bundles and those of the sporangiophore-traces. R. 34. $\times$ about 38.

PLATE XXXIII.

Fig. 14. Typical tracheids. *A*, annular, from sporangiophore-trace. Q. 337. $\times$ about 200. *B*, scalariform, from secondary nodal wood. S. 474. $\times$ about 280. *C*, pitted, from secondary nodal wood. R. 30. $\times$ about 280.

Fig. 15. Transverse section through vertical portion of bract. *Scl.* = dorsal sclerenchyma. R. 32. $\times$ 66.

Fig. 16. Uppermost bundle shown in Fig. 12. The protoxylem canals of the main bundle and the sporangiophore-trace are here clearly seen. Q. 336. $\times$ about 150.

Fig. 17. Portion of sporangium wall in tangential section showing form of cells and 'buttresses.' R. 31. $\times$ 146.

Fig. 18. Tissue accompanying sporangiophore-trace, in transverse section through 'disc.' R. 144. $\times$ 120.

Fig. 19. The sporangiophore-trace bundle shown in Fig. 6. Q. 336. $\times$ about 136.

Fig. 20. Longitudinal section through node showing origin of bract-trace. *Pt.xy.C.* = protoxylem canal, obliterated at node; *D.* = part of 'disc.' W. 1573. $\times$ 70.

Fig. 21. Longitudinal section showing course of sporangiophore-trace and its accompanying tissue. Slightly oblique. *Pt.xy.C.* = protoxylem canal of main bundle; *S.Pt.xy.C.* = protoxylem canal of sporangiophore-trace; *Sp.* = sporangiophore; *Br.* = bract; *D.* = 'disc'; *D.C.* = 'disc canal.' W. 1577. $\times$ 60.

1.

3.

4.

5.

2.

6.

7.
Sm. Can.

8.

9.

10.

12.

Sp. Px. C.
Px. C.
Sp. Px. C.

11.

13.

el.

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