On the Genus *Myeloxylon* (Brong.).

BY

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With Plates I and II.

IN *Myeloxylon*¹ we have one of those genera of palaeozoic plants with which palaeobotanists have long been familiar, but as to whose botanical affinity the balance of opinion appears to be fairly equally divided. Numerous examples have been figured from English, German, and French localities, but none with tissues sufficiently well-preserved to admit of a complete examination of their anatomical characters. Without claiming for the specimens described in the present paper that they settle the botanical position of the genus, I hope to show that they afford further evidence in support of the view that *Myeloxylon* agrees more closely with recent Cycads than with Ferns. Before considering our new material in detail, it will be well to review the descriptions of previous writers and note the arguments advanced in support of the different opinions as to the relation of *Myeloxylon* to recent plants.

¹ I use this name because it has been adopted by Solms-Laubach in his 'Einleitung in die Paläophytologie,' as better known than the generic name of *Stenzelia*, although the latter has ten years' priority according to Goeppert and Stenzel (*Die Medulloseae*, p. 10 [*Palaeontographica*, vol. XXVIII. 1881]).

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In Corda's great work, *Flora der Vorwelt*¹ (1845), a figure is given of a transverse section of a plant, from Radnitz in Bohemia, under the name of *Palmacites carbonigerus*. As the name implies, this was considered to be a Palm. In his description of the specimen Corda points out that much of the bundle-tissue has been destroyed, and the spaces filled with mineralizing material. In some places (Figs. 4 and 5, Pl. XX.) sclerenchymatous elements are shown in close connection with the vascular bundles. The tracheids are described as scalariform: no mention is made of mucilage-canals, but in Fig. 5 Corda has represented what we may in all probability regard as such. This species of *Palmacites* bears a strong resemblance to *Myeloxylon* (*Myelopteris*) *radiata*.

In 1832 Cotta² instituted three species of *Medullosa*; *M. elegans* is the only one with which we are at present concerned. This species is recorded from Rothliegende (Permian) rocks near Chemnitz and Kohren. In the Robert Brown collection in the British Museum is a specimen which was no doubt cut from the same piece as the section figured by Cotta in Pl. XII. Fig. 2; in this section a number of dark lines of crushed cells are seen in the parenchymatous ground-mass surrounding small 'islands' of mineralized tissue. This mode of fossilization is fairly common in *Myeloxylon* and well marked in some of the examples to be described later.

Brongniart³, in his *Tableau des genres de végétaux fossiles*, changes the name *Medullosa* to *Myeloxylon*, and classes *Myeloxylon elegans* as a doubtful Monocotyledon. Goeppert⁴ describes the hypodermal tissue of *Myeloxylon* as wood; he considers the dark lines in the ground-tissue as part of the natural structure of the plant and not as an accident of

¹ Corda, *Beiträge zur Flora der Vorwelt*, Pl. XIX. Fig. 2.

² Cotta, *Die Dendrolithen*, Pl. XII. Figs. 1 and 2.

³ Brongniart, A., *Tableau des genres de végétaux fossiles, considérés sous le point de vue de leur classification botanique et de leur distribution géologique* (*Dictionnaire universel d'Histoire Naturelle*, vol. XIII. p. 59 [1849]).

⁴ Goeppert, *Die fossile Flora der Permischen Formation*, p. 218 (*Palaeontographica*, XII. 1864–1865).

mineralization. The tracheids are described as scalariform and reticulate. In conclusion Goeppert refers *Myeloxylon elegans* to those plants which must be looked upon as prototypes or synthetic types; he recognises Ferns, Gymnosperms, and Monocotyledons as represented in certain structural details of this palaeozoic species.

Binney¹, in 1872, refers to *Medullosa elegans* of Cotta as the rachis of a Fern or of a nearly-allied plant.

In 1873² Williamson refers the same plant to the Marattiaceae: Schimper, on the other hand, classes *Myeloxylon* with the Cycads.

In 1876³ Renault contributed an important paper in which a number of silicified specimens of *Myeloxylon* (*Myelopteris* of Renault, *Stenzelia* of Goeppert) from Autun and Saint Étienne are figured and described in detail.

Several of the French specimens are much larger than any found in English rocks. The vascular bundles, which, especially in the small petioles, are arranged in fairly concentric lines, Renault describes as consisting of large scalariform vessels with smaller barred and spiral tracheids: the vacant space, which occurs in each bundle next to the group of xylem-elements, is referred to as a gum-cavity. In Plate IV. Fig. 27, one of these spaces is shown containing several cells or 'tubes' with their walls considerably thickened; these are certainly not such elements as one would expect to find forming part of the phloëm which originally occupied the vacant spaces in each bundle. Probably these so-called gum-cells with thick walls have found their way into the cavity left by the decay of the phloëm. In a later work, Renault⁴ makes no mention of the thick-walled cells, and speaks of the bast-part of the bundles as nearly always absent. Certain variations in the arrangement of the hypodermal prosenchyma have

¹ Binney, Proc. Lit. and Phil. Soc. Manchester, vol. XI.

² In a communication to the Brit. Assoc. meeting at Bradford.

³ Renault, *Recherches sur les végétaux silicifiés d'Autun—étude du genre Myelopteris* (Mém. par divers savants; Acad. des Sci., Institut. de France, vol. XXVII [1876]).

⁴ Cours de botanique fossile, vol. III. p. 162 (1883).

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been made use of by Renault as a basis of classification: in one type, *Myelopteris Landriotii*, the fibrous bundles of the hypoderm are circular, elliptical, or reniform; in the second type, *M. radiata*, they are flattened and arranged as radiating bands of sclerenchymatous tissue. Our English specimens agree more closely with the *M. radiata* type. Whilst admitting a few points of difference between *Myelopteris* and recent Ferns, Renault concludes that its true position is with the Marattiaceae. One of the arguments considered by him of great weight in favour of this decision is the common association of *Alethopteris*-leaflets and *Myelopteris*-petioles; and in one case a rachis of *Alethopteris aquilina* is figured showing the same structure as that of *Myelopteris*. The force of this and other arguments will be considered at the conclusion of these notes. Before passing on to Williamson's description of *Myeloxylon*, I may briefly refer to a specimen in the British Museum collection¹ which throws a little more light on the structure of the vascular bundles. This specimen, unfortunately with no record of locality, came in all probability from one of the places from which Renault's silicified specimens were obtained: its general structure and mode of preservation strongly support this view. In Fig. 1, where I have represented one bundle and two canals, a number of thick-walled elements are clearly shown at *s* in contact with the xylem, and at *p* what we may probably consider as one of the protoxylem-tracheids. In the space next to the protoxylem are traces of torn and delicate tissue (*a*), no doubt remnants of phloëm: surrounding the phloëm half of the bundle is a sheath of small parenchymatous cells.

In his seventh memoir² on the Organization of the fossil plants of the Coal-measures, Prof. Williamson gives some account of the history of *Myelopteris* and describes a number of specimens from the English Coal-measures. In these

¹ For access to specimens in the British Museum my thanks are due to Mr. Carruthers.

² Williamson, On the organization of the fossil plants of the Coal-measures, Pt. VII. Phil. Trans. Royal Society, 1876.

fragments there are certain characters which suggest the possibility that they ought not to be included in the same genus as those described by Renault and others, or as the fragments which I have figured. In Williamson's specimens there are peculiarities in the structure of the bundles, and in the arrangement of the hypodermal tissues, which distinguish them from other described examples of *Myeloxylon*: at the same time there are several points of resemblance. The spaces in the bundles, originally described by Williamson as gum-canals and shrinkage-cavities, are now recognised by him as 'true phloëm-portions of the fibro-vascular bundles¹.' *Myeloxylon* is classed by him with the Ferns, and the points of agreement with the Marattiaceae are considered at some length. Some specimens, which Prof. Williamson has generously lent to me for examination, may, I hope, throw further light upon the botanical position of those to which I have briefly alluded.

Grand' Eury² has figured what he considers to be a piece of the epidermis of *Myeloxylon*, showing a number of stomata. He points out a general resemblance between this genus and *Angiopteris* as regards the arrangement of the vascular bundles, but recognises a difference in the shape of the individual bundles; in *Angiopteris* they are elongated concentrically, in *Myeloxylon* they are either circular or elongated radially.

We come next to an important paper by Schenk³, published in 1882. An examination of Cotta's original specimens in Berlin led Schenk to the conclusion that *Myeloxylon* resembles Cycadean petioles more closely than the petioles of Marattiaceae. In this paper we find the collateral nature of the bundles insisted upon as a strong argument in favour of Cycadean affinities: many other characters, whose importance had not been previously recognised, are dealt with in detail.

¹ Letter from Prof. Williamson, June, 1890.

² Flore Carbonifère du département de la Loire et du centre de la France (Mém. prés. par divers savants à l'Acad. des Sci. de l'Institut. de France, vol. XXIV. 1877. Pl. XIII. Fig. 7).

³ Schenk, Ueber *Medullosa elegans* (Engler, Bot. Jahrb., vol. III. p. 156, 1882).

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Felix¹, in a more recent paper, agrees with Schenk as to the close resemblance between *Myeloxylon* and Cycads: he gives a figure of a specimen from Westphalia, and notes the occurrence of certain narrow cells in the parenchyma which he considers may explain those dark lines so often seen running through the ground-mass of *Myeloxylon*-petioles. Schenk and others prefer to regard these dark lines as accidents of preservation. Such specimens as I have examined lend no support to the suggestion of Felix. The question of the true nature of *Myeloxylon* has been fully and impartially discussed by Solms-Laubach² in his *Einleitung in die Paläophytologie*: he figures a single vascular bundle which shows more of the phloëm preserved than in specimens previously described. Solms adds in a footnote an important fact in connection with *Myeloxylon* and recent Cycads: he remarks, 'the latest observations have made it probable that the *Myeloxyla* are the leaf-stalks of *Medullosae*.' 'If this is established,' he adds, 'a new and important weight will be added to the scale on the side of Cycadeae.'

In a discussion on *Myeloxylon*, Schenk³ refers to Williamson's specimens as probably more nearly related to Marattiaceae than are those of Renault. The same author⁴, in a paper on *Medullosa* and *Tubicaulis*, speaks of the *Myeloxylon*-like branch of *Medullosa Leuckarti* referred to by Solms, and admits that the suggestion of Williamson and Renault as to the Fern-like nature of *Myeloxylon* may be correct, but at all events it must be looked upon as belonging to an extinct group.

Mr. Kidston⁵ has figured a bundle of *Myeloxylon* from the

¹ Felix, *Untersuchungen über den inneren Bau Westfälischer Carbon-Pflanzen* (Abhandl. d. K. Preuss. geolog. Landesanstalt, Berlin, 1886).

² Solms-Laubach, *Einleitung in die Paläophytologie*, p. 165, 1857 (Fossil Botany, p. 161, 1891).

³ Schenk, *Die fossilen Pflanzenreste*, p. 45 (Handbuch der Botanik, 1888).

⁴ Schenk, *Ueber Medullosa, Cotta, und Tubicaulis*, Cotta (Abhandl. der Math. phys. Classe der K. Sächs. Gesells. der Wiss., vol. XV. p. 523. Leipzig, 1889).

⁵ Kidston, R., *On the fructification and internal structure of carboniferous Ferns in their relation to those of existing genera, with special reference to British palaeozoic species* (Trans. Geol. Soc. Glasgow, vol. IX. Pt. 1), Pl. IV. Fig. 45.

Coal-measures of Oldham, in which the phloëm is partially preserved: the drawing is hardly sufficiently detailed to admit of a full description, but the specimen appears to agree very closely with that from the Binney collection which is described and figured in the present paper. Kidston compares *Myeloxylon* to *Ophioglossum vulgatum* and to *Osmunda*, and speaks of it as 'a typical marattiaceous fern-stem'¹.

MYELOXYLON FROM THE MILLSTONE GRIT.

It will be convenient to describe such specimens as I have examined under three heads: those to be considered first afford an addition to the short list of Millstone Grit plants². These plant-fragments were found in a block of magnesian limestone, of Millstone Grit age, about five miles N.E. of Lancaster³, by Mr. J. E. Marr. The block is represented in Fig. 2, somewhat less than natural size. In the upper part of the figure a group of rod-like structures is shown, weathered out from the rest of the rock, reminding one to some extent of the structure occasionally seen in limestones and known as 'stylolites.' Dr. Hinde, on seeing the specimen, pointed out the striking resemblance of these rods to the anchoring appendages of *Hyalostelia Smithii* (Young), one of the hexactinellid sponges⁴.

The rods, on microscopical examination, were found to be isolated bundles of tissue weathered out from the rest of the organ of which they form a part. Among fossil plants from the English Coal-measures it is not uncommon to find specimens in which regularly defined areas in a stem or root have been mineralized with their minute structure perfectly preserved, whilst the rest of the tissue has been almost entirely destroyed before the infiltration of the fossilizing

¹ Kidston, loc. cit. p. 50.

² Etheridge, in his Catalogue of Palaeozoic fossils, mentions twenty-eight species of British Millstone Grit plants (Fossils of the British Islands, vol. I. Palaeozoic, 1888).

³ Near Caton, Geol. Surv. Map (inch scale), quarter sheet 91 N. E.

⁴ For description of this sponge, see Palaeontographical Society, vol. XLI. p. 158.

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material¹. Fig. 3 shows this partial mineralization of the tissues as seen in a transverse section cut parallel to the base on which the block rests in Fig. 2. In this section we have a number of isolated islands of tissue, in each of which the xylem-portions of the vascular bundles are well preserved, whilst the phloëm is always absent; and in the immediate neighbourhood of the bundles are a few layers of parenchyma, with here and there distinct canals. At the periphery of the section are seen darker patches which indicate the position of thick-walled hypodermal cells arranged in radiating bands and alternating with radial extensions of the parenchymatous tissue. In many of the groups of tissue seen in Fig. 3, the parenchyma surrounding the vascular bundles is limited by a distinct dark line; this is due to the brown walls of the compressed parenchyma which represent the extent of the mineralization of the tissues. Similar dark lines, cutting up the parenchyma into a kind of network, are shown in Cotta's figure of *Medullosa elegans*, and also in a figure of *Myelopteris* given by Renault: I have already alluded to such lines as probably accidents of fossilization in speaking of Felix's note on *Myeloxylon*. In Fig. 3 a second fragment is represented, smaller than the first and cut longitudinally. To describe in detail the larger transverse section, which measures 2.5 cm. by 2.2 cm.: in looking at the peripheral bundles, where the ground-tissue has not been destroyed, and their original position has therefore been retained, we notice that they are regularly arranged concentrically with the circumference of the section; towards the centre this concentric disposition is much less obvious. The individual bundles, when examined in detail, appear under various forms. In some cases we have a group of xylem almost in the centre of a space bordered by parenchymatous cells: this type is shown in Fig. 4, in which case the position of the xylem suggests a partially preserved concentric bundle, the space having been originally occupied by the more delicate tissue of the phloëm. In Fig. 5, we

¹ There is a striking example of this in a large stem of *Araucaroxylon* in the British Museum (Geological Department).

have another type of bundle, where the xylem-group, which is triangular in form, is still more or less central in position ; at the apex of the triangle some smaller tracheids are seen which suggest protoxylem. In all the vascular bundles of this specimen the parenchymatous cells immediately surrounding the xylem and the phloëm-space are smaller than the ordinary cells of the ground-tissue.

In Fig. 6, a third bundle is represented in which the xylem has been very slightly displaced, and here again smaller elements indicate that the probable position of the protoxylem is on the side of the xylem opposite to the phloëm-space. Close to this bundle we have one of the fairly abundant canals (*c*) which are scattered through the parenchyma ; bordering the canal-cavity are some tangentially elongated cells, such as we find in mucilage-canals of recent Cycads.

Another kind of bundle is shown in Fig. 7 ; the xylem is still attached to the parenchyma at one or two points, and, as usual, on the side next to the vacant space are seen tracheids of smaller diameter.

The *Parenchyma of the ground-mass* appears to be made up of cells fairly uniform in size, except in the immediate neighbourhood of the vascular bundles, where the cells are marked off from the rest by their smaller size, and form a kind of indistinct sheath. Traversing the parenchyma are several canals : these are especially abundant towards the periphery of the section, but this may be due to the fact that the parenchyma towards the centre is much less perfectly preserved.

In Fig. 8, a patch of *hypodermal tissue* is shown ; the preservation is by no means perfect, but sufficiently good to enable us to recognise in the alternating groups of parenchyma and sclerenchyma the same type of structure so clearly seen in Renault's figures of *Myeloxylon radiata*.

In this transverse section (Fig. 3) I have not made out with certainty any groups of thick-walled elements, either in close proximity to the xylem-groups or in the ground-tissue, but there are indications that such elements were here and there

present close to the bundles. The longitudinal sections of the same specimen throw little light upon structural details: the tracheids appear to be scalariform, reticulate, and spiral.

The smaller fragment seen in longitudinal section in Fig. 3 shows, in transverse section, certain characters which are apparently absent in the larger section. In Fig. 9 one of the best bundles is figured; the structure is clearly collateral, and the xylem has not been displaced as in the bundles of the larger fragment. Here also we find smaller tracheids on the side of the phloëm-space, which I am inclined to regard as protoxylem. Surrounding the bundles are smaller parenchymatous cells, with here and there thick-walled mechanical elements. In the same figure is shown a canal with a dark-coloured substance in its cavity, probably the remains of the original secretion. Several of these canals are represented in Fig. 10, the narrow cells surrounding the cavities being well shown; in this section we see indications of the characteristic radial groups of hypodermal tissue. Some of the thick-walled hypodermal cells are seen in longitudinal section in Fig. 11 at *a*; next to these are thin-walled and less elongated parenchymatous cells: at *a'* the tissue is badly preserved, but probably we have here the remains of a group of thick-walled hypodermal cells.

Passing farther along the section, we come to the parenchyma of the ground-tissue, the cells of which are somewhat elongated and arranged in rows. In the canal, cut longitudinally, the contents appear to be divided up into detached pieces by thin transverse septa: an examination of these canals under a higher power led me to doubt the existence of the septa and to attribute the present form of the contents to shrinkage. By comparing the transverse and longitudinal sections of the canals we see how the contents have contracted both transversely and longitudinally.

Part of a canal is represented in Fig. 12 under a higher power; in this figure the darker lines *bb* correspond to the walls *b* next to the canal-cavity in Fig. 10: the limiting lines *cc* of the dark-coloured contents in Fig. 12 are seen at *c* in Fig. 10.

In Fig. 2 at $\frac{1}{x}$ may be traced the elliptical outline of a section, cut obliquely: this is another fragment of *Myeloxylon*, in which the bundles have suffered less displacement than in the larger section, and the state of preservation is on the whole better. Thick-walled cells occur on the xylem-side of some of the bundles; and the tracheids appear to be reticulate and scalariform.

In this fragment we have a connecting link between the larger and smaller specimens, and an additional argument in favour of referring all the pieces preserved in the block shown in Fig. 2 to the same plant. From the above descriptions it is clear that there are a few points of difference between the large and small specimens. In the smaller fragment the bundles are more distinctly collateral; there are thick-walled cells, sometimes in a continuous row, on the xylem-side¹; the canals are more numerous and larger than in the section figured in Fig. 3: but, in spite of these differences, we may include both specimens in the genus *Myeloxylon* and in the type *radiata* as instituted by Renault. Although many of the xylem-groups of the larger specimen occupy a position suggestive of concentric bundles, there are others, whose preservation is more perfect, which point with equal force to collateral bundles; and, on the whole, it seems reasonable to conclude that the apparently concentric structure is the result of the xylem-tracheids becoming detached from the surrounding parenchyma: originally, we may assume, the bundles were collateral. We shall find in nearly all specimens of *Myeloxylon* there are certain peculiarities; but, in dealing with such broken fragments of petioles, it is better to err on the side of including too many varieties under one general type than to attempt to define new species upon insufficient data. We are ignorant as to how far the structures of a *Myeloxylon*-axis of higher order differs from that of a lower

¹ As already remarked, similar mechanical elements are indicated in the large fragment: no doubt the worse state of preservation of this specimen is to some extent responsible for apparent differences between its structure and that of the smaller and more perfectly preserved fragment.

order; that branching does occur we know from the figures and descriptions of Renault¹. Slight differences in structure may in some cases be the result of differences in fossilization; and further, as Thomae² has pointed out, in speaking of fern-petioles, it is hopeless to attempt to determine species by trusting to the anatomical details of detached fragments. The various specimens, therefore, described in these notes are referred to *Myeloxylon radiata* because of the possession of important characters in common. It is quite possible that further additions to our knowledge will render advisable the creation of additional species.

SPECIMENS FROM PROF. WILLIAMSON'S COLLECTION.

One of the slides³ lent to me by Prof. Williamson shows very clearly the essential characters of *Myeloxylon*: these characters are much more clearly defined in this specimen than in the other examples described by Williamson to which I have previously referred. In this section, prepared from an Oldham specimen, the collateral bundles are very distinct, but, as generally happens, the phloëm has not been preserved: thick-walled mechanical elements form an almost continuous ring round the xylem-groups. Another specimen of *Myeloxylon* from Oldham, in the Binney collection, agrees closely with Prof. Williamson's, but surpasses it in preservation; this will therefore be described at greater length.

SPECIMEN FROM THE BINNEY COLLECTION.

In this collection, now in the Woodwardian Museum, Cambridge⁴, I have found two slides of *Myeloxylon*, the one a transverse, the other a longitudinal section, which throw some fresh light on the nature of the vascular bundles.

In the transverse section, which measures 3 cm. in its longest part and 1.7 in its broadest part, the bundles have much the

¹ Renault, Etude du genre *Myelopteris*, Pl. V. Fig. 42.

² Thomae, Die Blattstiele der Farne (Pringsh. Jahrb. XVII. 1886, p. 158).

³ Number 286 in Prof. Williamson's Catalogue.

⁴ For the loan of this specimen I am indebted to Prof. McKenny Hughes.

same disposition as in the large specimen from the Millstone Grit; those near the periphery form a fairly distinct ring, whilst the others appear to have no definite arrangement. The hypoderm is of the normal type of *Myeloxylon radiata*, and need not be further considered. Canals are numerous and possess characters such as have already been described. Many of the bundles are of the type shown in Fig. 13; here we find, for the first time, not only the xylem but also the phloëm intact. In this particular bundle the smaller protoxylem-elements are not quite so clearly marked as in most of the bundles, but the phloëm is preserved with exceptional distinctness. In Fig. 14 a second bundle is figured; here the phloëm is less perfectly preserved, but the small elements of the protoxylem are much more distinct: the sheath of small parenchymatous cells is clearly shown. In Fig. 15 we have another form of bundle, the xylem being in the form of an oblong group of tracheids, and the phloëm in two distinct groups on the same side of the xylem. In all these figures thickened mechanical elements are noticed on the xylem-side, and the presence of these is a constant character in the specimen. The striking resemblance of both these forms of vascular bundle to those of recent Cycadean petioles will be apparent when we sum up the arguments bearing upon the question of botanical affinity. In the longitudinal section of the same specimen we find, in two of the bundles at least, undoubted confirmation of what has previously been assumed but not actually demonstrated, namely, the occurrence of protoxylem or spiral tracheids on the phloëm-side of the xylem. Fig. 16 represents one of the bundles where we have large reticulate and scalariform tracheids in contact, on one side, with the parenchyma of the ground-tissue, and, on the other, separated from the less perfectly preserved phloëm by distinct spiral tracheids of small diameter. The phloëm shown at *P* is not sufficiently well preserved to enable us to describe its structure in detail; it consists of elongated, narrow, and broken elements, whose delicate walls have naturally suffered considerably during fossilization. At *GG* are seen

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some cells of the ground-tissue. In Fig. 17 another bundle is represented in longitudinal section: the phloëm-elements are imperfectly preserved at *P*; next to them is a well-marked spiral tracheid, and following this what appears to be a second spiral element with larger scalariform and reticulate tracheids.

Having described at some length these specimens referred collectively to *Myeloxylon*, it only remains to consider briefly such facts as may help us in attempting to assign this palaeozoic fossil to its natural position in the plant-kingdom.

We may summarise, and briefly discuss, the arguments advanced by those who have referred *Myeloxylon* to the Marattiaceae.

1. *The association of Alethopteris-leaflets with Myeloxylon, and a close agreement in their anatomical characters.*

The figure which Renault gives in support of his statement that *Alethopteris*-pinnules have been found attached to a rachis having the structure of *Myeloxylon* is scarcely conclusive: so far as one can judge from the section represented¹, it is by no means obvious that the structure is the same as that of *Myeloxylon*. If, however, it is found that *Alethopteris* undoubtedly possesses this type of structure, we have no proof that in transferring it from the Ferns to the Cycads we shall be assigning it to a position to which it has no claim².

2. *The branching habit of Myeloxylon.*

Renault has given proof of this in his figures and descriptions of French specimens. Although *Bowenia*, as Solms reminds us, is the only recent Cycad in which the frond is branched, yet this solitary instance in living Cycads is not insufficient when we are dealing with plants of palaeozoic times. In such specimens as I have examined, no signs of branching have been detected.

3. *The vascular bundles, &c.*

It has been pointed out that *Myeloxylon* agrees in its bundles

¹ Renault, Cours de bot. foss. vol. III. Pl. 27, Fig. 12.

² Since this was written I have found some specimens in the Binney collection which, it is hoped, will afford further evidence in reference to *Myeloxylon*-pinnules.

and canals with *Marattia* and *Angiopteris*. The general arrangement of the bundles, as seen in transverse sections of *Angiopteris*-petioles, closely resembles that which we find in *Myeloxylon*; but this agreement ceases when the individual bundles are examined: in the one case we have a typical concentric, in the other a typical collateral bundle. In *Angiopteris* the tracheids do not show any very close resemblance to those of the fossil petiole; the reticulate thickening in the latter is characteristic, and differs from the type of tracheid characteristic of Ferns. As regards the presence of mucilage- or gum-canals in *Marattiaceae* and *Myeloxylon*, we do not find in the former those large canals, bordered by tangentially elongated cells, such as are constantly found in the fossil specimens, and which exactly correspond to the canals of Cycadean petioles.

4. *Hypodermal tissues.*

It is true that we find in *Angiopteris* a subepidermal band of mechanical tissue, but this is usually continuous and not interrupted by radiating groups of parenchyma.

Renault quotes *Angiopteris Brongniartiana*, and *A. Teismanniana* as examples of recent Ferns in which we have a more marked separation of thick- and thin-walled tissues; but, on the other hand, we can point to several species of Cycads where the hypoderm is of the same type as in *Myeloxylon*.

We will next consider the Cycadean affinities of *Myeloxylon*, some of which have been previously dealt with by Schenk.

1. *The collateral nature of the bundles, and the position of the protoxylem.*

This character, so clearly marked in well-preserved specimens, has been passed over by Renault and other writers. It is true, as Solms points out, that this structure is by no means unknown among recent Ferns: in addition to the collateral bundles in the petioles of *Ophioglossum* and *Osmunda*, Haberlandt¹ has shown that this is a common type in the

¹ Haberlandt, Ueber collaterale Gefässbündel im Laube der Farne (Sitzungsberichte der Math.-Naturwiss. Classe der K. Akad. der Wiss. vol. XXXII. p. 121, Abth. I, 1881. Vienna).

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weaker subdivisions of the petioles of many genera. Granting, however, that this arrangement of xylem and phloëm may have been common in palaeozoic fern-petioles, we have still the important fact to remember that in recent Ferns *the protoxylem is not on the side of the xylem next to the phloëm: in Myeloxylon and recent Cycads it is so situated.*

2. *Nature of the tracheids.*

I have referred to the tracheids of *Myeloxylon* as reticulate, scalariform, and spiral. In Fig. 18 is represented part of an oblique section of the xylem of a specimen of *Myeloxylon* from Robert Brown's collection in the botanical department of the British Museum. This shows fairly well the character of some of the tracheids: at *p* we see what may possibly be the remains of spiral thickenings of protoxylem. In no case have I made out true bordered-pits, such as we find in recent Cycads, but it would be rash to attach any great weight to negative evidence in dealing with the minute structure of fossil tracheids. In spite of the absence of bordered-pits in *Myeloxylon*, there are various points of resemblance between its xylem-elements and those of Cycads. In some respects, for example in their reticulate structure, the tracheids of the fossil specimens do not correspond very closely either with Ferns or Cycads.

3. *Arrangement and form of the vascular bundles.*

The disposition of the bundles, as shown in transverse section, is in many recent Cycadean petioles very similar to that in *Myeloxylon*: in Ferns, on the contrary, the bundles are usually arranged in more distinctly concentric lines, such as we find in *Angiopteris*. As we have seen, the common form of the bundle in *Myeloxylon* is that of Fig. 13; this corresponds very closely with the shape of recent Cycadean bundles. In some specimens of *Myeloxylon* there are other bundles than the usual oval type, and these are also repeated in some recent species. If we compare Fig. 15, drawn from Binney's specimen, with the bundle of *Cycas Thouarsii* sketched in outline in Fig. 19, we see at once a close corre-

spondence¹. Other forms of *Myeloxylon*-bundles might be quoted which find striking parallels in *Dioon edule*, *Ceratosamia*, *Cycas*, &c.

The fusion of two or more bundles in living Cycads has been referred to by Vettiers² and also by De Bary³: in the fossil petioles similar instances of fusion are found.

4. *Hypoderm, subepidermal parenchyma, &c.*

In well-preserved examples of *Myeloxylon*, e.g. Fig. 41, Plate V in Renault's paper, there are a few layers of parenchyma immediately below the epidermis. Similar subepidermal parenchyma occurs in *Angiopteris*, as some writers have pointed out; but in petioles of Cycads it is also present. In many specimens of *Myeloxylon* this parenchyma has been destroyed, e.g. in Fig. 8, but in a small section, which occurs on the same slide as the larger Binney specimen, this tissue is clearly shown. The canals of recent Cycads and the fossil petioles are practically identical.

The hypodermal tissue of *Myeloxylon* closely corresponds with that of *Encephalartos horridus*, *Macrozamia Hopei*, and other species. In some of Renault's specimens we see groups of thick-walled fibres in the ground-tissue; Schenk refers to the absence of such in recent Cycads, but, as De Bary has remarked, groups of thick-walled fibres occur in various Cycadean petioles.

In the bundles of Cycads we find a few xylem-tracheids among the delicate phloëm-elements ('bois centrifuge'); these have not been detected in the fossil bundles, as Solms has already noted.

These tracheids are always much smaller than the other elements of the xylem, and, even in recent specimens, cannot in all cases be readily seen; it is not improbable that such might fail to be preserved, or, if preserved, to be distinguished from the surrounding phloëm.

¹ Similar bundles occur in *Stangeria paradoxa*, *Zamia muricata*, &c.

² Vettiers, *Die Blattstiele der Cycadeen* (Inaug. Dissert., Leipzig, 1884).

³ De Bary, *Comparative Anatomy of the vegetative organs of the Phanerogams and Ferns*, p. 337 (1884).

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Finally, there is the connection between *Myeloxylon* and *Medullosa* referred to by Solms and Schenk. The former considers it an additional argument in favour of classing *Myeloxylon* with the Cycads; the latter, in his paper on *Medullosa* and *Tubicaulis*, refers to the attachment of *Myeloxylon* to *Medullosa Leuckarti*, but considers the latter more closely related to the Ferns than to Cycads. This fact has as yet been simply recorded without any full description.

I have endeavoured to state the more important arguments which have been made use of by the advocates of the two opinions as to the botanical position of the plant we have been considering. The conclusion to which I have been led by examining several specimens of *Myeloxylon*, and comparing them with numerous Cycadean and Fern petioles, is that they undoubtedly approach more nearly to the Cycadeae than to the Ferns: it has been suggested¹ that we may refer *Myeloxylon* to a position intermediate between Ferns and Cycads. The few points of difference which distinguish the fossil fragments from the petioles of recent Cycads are, in my opinion, far outweighed by the close parallelism in more essential characters, and it seems reasonable to conclude that *Myeloxylon* should be looked upon as an extinct genus, not exactly corresponding to any recent family of plants, but one which comes very near to the Cycadeae in anatomical structure, and probably occupies a position between Cycads and Ferns, but nearer to the former than to the latter.

¹ Solms-Laubach, loc. cit. (Eng. edit. p. 163).

EXPLANATION OF FIGURES IN PLATES I AND II.

Illustrating Mr. Seward's paper on *Myeloxylon*.

(When not otherwise stated the figures are drawn with objective A, Zeiss.)

Fig. 1. Transverse section of a vascular bundle and two canals. *a*=remains of phloëm, *s*=sclerenchymatous cells. *p*=position of protoxylem.

Fig. 2. Block of Limestone (Millstone Grit) with weathered 'petiole' of *Myeloxylon*. On the smooth surface at $\frac{1}{2}$ is faintly indicated an oblique section of a smaller fragment. Actual size of specimen 10 cm. long and 10 cm. wide.

Fig. 3. Transverse section, rather less than natural size, of the larger petiole shown in Fig. 2, and longitudinal section of a smaller fragment. The white patches in the matrix outside the plant are sections of *Goniatites*.

(For the photographs from which Figs. 2 and 3 are taken, I am indebted to Mr. Barber.)

Fig. 4. Section of one of the vascular bundles of the specimen represented in transverse section in Fig. 3. The xylem has been displaced.

Fig. 5. Another bundle from the same specimen. *p*=protoxylem.

Fig. 6. " " " *c*=canal.

Fig. 7. " " " At *a* the xylem is seen still attached to the parenchyma of the ground-tissue.

Fig. 8. Piece of hypodermal tissue; in the large transverse section of Fig. 3 this appears as a black patch.

Fig. 9. Transverse section of a vascular bundle from a smaller fragment of the Millstone Grit *Myeloxylon*. *p*=protoxylem. *s*—*s*=sclerenchymatous cells. *c*=canal.

Fig. 10. A piece of the hypoderm and ground-tissue, with canals, from the same specimen as Fig. 9. *b*=tangentially elongated 'epithelial cells' of the canal. *c*=limiting lines of canal-contents. *h*—*h*=remnants of thick-walled hypodermal tissue.

Fig. 11. Longitudinal section of the same specimen as Fig. 10. *a* and *a'*=thick-walled cells of the hypoderm.

Fig. 12. Longitudinal section of a canal from the same specimen, showing the dark-coloured contents, &c. Letters same as in Fig. 10. (Objective D, Zeiss.)

Fig. 13. A vascular bundle from the Binney specimen, showing well-preserved phloëm.

Fig. 14. Another bundle from the same specimen. *p*=protoxylem. *s*—*s*=indistinct sclerenchymatous cells.

Fig. 15. This bundle shows two patches of phloëm, the result of fusion of two bundles.

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Fig. 16. Longitudinal section of a vascular bundle from the same specimen as Figs. 14 and 15. *G*=ground-tissue. *P*=phloëm. *S*=spiral tracheid (protoxylem). (Objective D, Zeiss.)

Fig. 17. Another bundle from the same specimen. Letters as in Fig. 16. (Objective D, Zeiss.)

Fig. 18. Oblique section of xylem-elements in a specimen in the Botanical Department of the British Museum. *p* ? protoxylem. *a*=reticulate tracheid. (Objective D, Zeiss.)

Fig. 19. Outline of a bundle of *Cycas Thouarsii*, to compare with Fig. 15. *X*=xylem. *P*=phloëm.

Figs. 1 and 18 are from specimens in the British Museum.

Figs. 2-12 are from Millstone Grit specimens in the Woodwardian Museum, Cambridge, and in my own collection.

Figs. 13-17 are from the Binney specimen in the Woodwardian Museum, from the Oldham Coal-measures.