A *Stigmaria* with Centripetal Wood.

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With Plate XV.

ONE of the most striking features in the structure of the *Stigmarian* axis is the fact that its primary wood shows, as a rule, a centrifugal development, while in the stems of *Lepidodendron* and *Sigillaria*, which formed the aerial continuation of the *Stigmarian* axis, the primary wood was invariably developed in a centripetal direction.

There seems to be a general opinion that this latter course of development of wood is the more primitive one. Its occurrence in the stems of the small number of recent Lycopodiales must perhaps not be taken as an argument in favour of this view; but the existence of this type of wood in the Lower Carboniferous *Calamites pettycurensis*, in *Sphenophyllum*, and in the Pteridospermeae, where the 'old wood' may be taken as a precursor of the 'new wood' of the Cycadales (see Scott, '02), are facts which seem to indicate the course taken in the evolution of the vascular system in the stem of the higher plants.

Whether the centrifugal development of the wood in the *Stigmarian* axis is the primitive condition of that organ, or similarly due to a substitution of 'new wood for old', has, however, remained an open question.

It is true a few specimens of *Stigmaria* have been described with a centripetal development of their primary wood, but this character seems in no way associated with other primitive characters. On the contrary, the *Stigmaria Brardii* described by Renault ('88) in the first instance as *Stigmaria flexuosa*, from Tracy St. Loup, near Autun, which, in its outward appearance, resembled the *Stigmaria rimosa* of Goldenberg ('58) (Pl. XII, Fig. 3), should, according to Solms-Laubach ('94), be correlated with *Stigmariopsis*, which must probably be regarded as more highly specialized than *Stigmaria*. According to Grand'Eury *Stigmariopsis* is the basal portion of *Clatharia* and *Leiodermaria*, forms of *Sigillaria*.

As far as I know, no specimen of *Stigmaria* with centripetal wood has been described from the English Coal Measures, and as some importance is attached to this arrangement, both as regards the primitiveness of its

character and the morphology of the Stigmarian axis, it seems desirable to describe in some detail a specimen which has come into my possession through Mr. James Lomax, of Bolton.

It was found in a calcareous nodule from the well-known Hard Beds of Halifax, and is of small size, the central vascular cylinder measuring only .75 cm. in diameter. Dr. Scott, to whom I showed the specimen, drew my attention to the resemblance of its primary wood to that of the stem of *Lepidodendron mundum*, and particularly of the axis as a whole to that figured by Williamson ('89) as a stem of *Lepidodendron mundum* with secondary thickening. An examination of this specimen in the Williamson collection at the British Museum convinced me that we had to do with the same plant as that described by Williamson, and the account which follows will, I think, suffice to show that in it we have a true Stigmarian axis. Whether or not it is to be associated with the stem showing the structure of *Lepidodendron mundum*¹ will remain for subsequent discussion. It is interesting to note that the specimen described by Williamson (cabinet number 416 b.) comes from the same locality as the one before us, and the agreement with our specimen is so close that I was at first inclined to believe that they must have been cut from the same block, but Mr. Lomax assures me that the nodule from which the second specimen was cut was quite untouched when he commenced to work on it. How many sections the first nodule yielded it is impossible to say, but one preparation in the Cash Collection, now in the University of Manchester, is obviously from the same block, and is also labelled *Lepidodendron mundum*. (Cash Collection, Q. 403 A.)

It should also be mentioned that there are in Dr. Scott's collection several slides of an axis, slightly larger but somewhat compressed, which appear to be sections of a similar plant (Nos. 1815 and 1825).

The vascular axis of the recently discovered specimen is about the same size as Williamson's specimen; and seen in transverse section might well be mistaken for a *Lepidodendron* twig. Of the outer tissues the periderm alone is preserved, and is arranged in wide folds around the vascular cylinder (see Fig. 1, Pl. XV). In its greatest extension it measures 4 cm., but this does not give a real idea of its size, as one of its folds comes right in to the central cylinder. As near as possible the periderm must have had a circumference of not less than 15 cm., while that of the central cylinder is about 2 cm.

The *periderm* consists of 6–8 rows of thin-walled rectangular cells, and is very similar to that of a typical *Stigmaria*, such as *S. ficoides*. It shows a considerable tangential extension of many of the external rows of cells, which has been recognized as a characteristic of the Stigmarian bark. (See Scott,

¹ According to Mr. James Lomax the stem showing internally the structure of *Lepidodendron mundum* had externally the marking of *Bothrodendron*.

'Studies in Fossil Botany,' p. 227.) The layers of cells, which must have clothed the periderm on the outside (outer cortex), whether a Stigmarian or Lepidodendroid axis, have entirely disappeared: only in one or two places does one find remains of small rounded cells of the nature of a primary cortex. They are much compressed, and their very poor preservation points to their having been of soft and yielding character, like the outer cortex of a *Stigmaria*, and not of the hard dense nature one finds in the aerial stem of a *Lepidodendron* or *Sigillaria*, and particularly of *Bothrodendron*. Here and there a somewhat denser group of primary cells has been preserved, and these evidently represent the remains of a rootlet-cushion. The presence of these rootlet-cushions, taken in conjunction with the general absence of a resistant outer cortex, the very extensive circumference of the periderm as contrasted with the small diameter of the vascular axis, and the peculiar structure of the periderm cells, all go to prove the Stigmarian nature of the specimen. Of the rootlets which it bore, nothing definite can be said, as none are found in continuity with the specimen. The numerous rootlets, which surround the axis, are not of any one particular type, and they may, of course, belong to other neighbouring Stigmarian axes. Indeed the very bad preservation of the softer tissues of the specimen before us would seem to indicate that it had been dead long before it became petrified, and was invaded by the rootlets of surrounding plants. As is usual in Stigmarian axes, the tissues lying between the periderm and the vascular cylinder are very defective. One would indeed not expect them to be well preserved in a specimen in which the outer cortical tissues were destroyed. As a matter of fact the space within the periderm has been largely invaded by Stigmarian rootlets, and only here and there are found dense brown masses, consisting probably of the débris of the delicate middle cortex. In certain places there are more or less irregular patches of wide and short reticulate tracheids (see Fig. 7, Pl. XV), which seem to have some connexion with the rootlet bundles, in connexion with which they will be referred to again. It is interesting to note that similar reticulate cells were described by Renault ('93)¹ in the cortical region of *Stigmaria Brardii*. As figured by him, however (Pl. XXXIX, Fig. 14), they appear more fusiform, as he indeed describes them to be, and they were found according to his description among the periderm cells, and not in the inner parenchymatous zone (middle cortex), which seems to be their position in the specimen under consideration. Indeed they are not only found in the outer portion of the middle cortex, but are present in large numbers close up to the vascular cylinder. This position may not be quite a normal one, as these tracheids have no doubt been displaced owing to the decay of the softer tissues, but there can be no doubt that they were associated with the vascular bundles within the soft, middle-cortex region.

¹ p. 195.

This region was, of course, traversed by the rootlet bundles on their outward passage; but, owing to the defective condition of the parenchymatous tissue, the direction taken by the rootlet bundles cannot be determined with any degree of certainty. They appear in this specimen as irregular in position as those figured by Williamson ('87) in *Stigmaria ficoides* (Plate XII, Figs. 39-41). In all probability they ran somewhat obliquely in this zone, while close to the vascular cylinder their course, as is usual in *Stigmaria*, was almost parallel to the Stigmarian axis. In this region, therefore, the rootlet bundles are cut almost transversely (see Fig. 5, Pl. XV), and they will be seen to consist of a group of medium-sized tracheids radiating very regularly from a centre of smaller elements. The very regular arrangement of the tracheids is suggestive of secondary growth having taken place in these rootlet bundles, a condition which is common in *Stigmaria*, and the fact that the bundles have attained different dimensions (see Fig. 5, Pl. XV) is in favour of this view. But, while in *Stigmaria ficoides* the secondary growth is only on the outside of the monarch rootlet bundle, here the secondary growth has taken place evenly all round the primary elements. Vascular bundles showing similar centric arrangement have been described and figured by Renault ('93) (Pl. XXXIX, Fig. 11) in the case of *Stigmaria Brardii*, with which our *Stigmaria* agrees also in the possession of the above-described reticulate tracheids. In *Stigmaria Brardii*, however, these centrically arranged bundles were the exception rather than the rule, and were taken by him to be arrested branches of the Stigmarian axis rather than the rootlet bundles, which he considered to have secondary wood, arranged in fan-shaped manner only on the outside of the primary wood. In our *Stigmaria*, on the other hand, the cyclic arrangement is the normal one and is evidently that of the rootlet bundles. The primary elements are so small and so few in number that it is impossible to distinguish proto- and metaxylem, but the general impression gained is that of a mesarch bundle, which view is supported by the appearance of the rootlet bundles in their course through the secondary wood (see Fig. 4, Pl. XV).

Owing to the state of preservation there is very little remaining of the phloem and cambium regions. In radial longitudinal sections a few rows of elongated parenchymatous cells are found on the outer boundary of the secondary wood, but they afford very little clue as to the nature of these tissues.

The *secondary wood* (see Fig. 2, Pl. XV), on the other hand, is fairly well preserved, and of normal type. Its nature and extent agree with that of the specimen described by Williamson ('89) as *Lepidodendron mundum* (see his Fig. 15, Pl. V). It consists of medium-sized tracheids, .04 to .05 mm. in diameter, arranged in regular radiating rows, and showing only slight irregularity, where new rays of wood elements become added as secondary growth proceeds. The tracheids are square in transverse section, and are of

the scalariform type, the strong horizontal bars of the lignification being connected by fine vertical striae, as has been noted and figured by Williamson ('89) for *Lepidodendron mundum*, as well as for other *Lepidodendra*.

We come now to the most important feature of this *Stigmara*, and that is to the *primary wood*. As mentioned above, this differs in essence from that of other *Stigmarae* in being centripetal in its development instead of centrifugal. Towards the centre of the axis the secondary tracheids become considerably smaller, without losing anything of the regularity of their arrangement. Then within the cylinder of secondary wood we come to a very definite primary wood, beginning with small protoxylem elements on the outside, and followed on the inside by a metaxylem consisting of about two rows of tracheids, the innermost of which are of very large dimensions. In radial sections the narrow elements at the outside of the wood exhibit often spiral and annular markings, and no doubt this region consists of the protoxylem elements. The metaxylem, on the other hand, consists of scalariform tracheids, some of which are twice the size (.075 to .09 mm.) of the largest elements of the secondary wood. It was no doubt the general arrangement of the metaxylem, as well as the small number and the large size of its tracheids, which influenced Williamson ('89) in his identification of the axis with secondary wood figured by him¹ with *Lepidodendron mundum*, with which the primary wood shows such singular agreement.

Within the metaxylem we come to a pith consisting of parenchymatous cells of rectangular shape when seen in longitudinal section, just as those one finds in *Lepidodendron mundum*.

The secondary wood is traversed by numerous parenchymatous rays, generally one cell thick, though occasionally two cells in thickness. Their thinner tissue has undergone some disorganization, so that they appear on the transverse section more like gaps, but they can readily be seen on the tangential longitudinal section (Fig. 4, Pl. XV). But a feature which distinguishes this type of *Stigmara* from *Stigmara fcooides* and some other forms is the absence of the very broad medullary rays which usually break up the woody cylinder into distinct wedges, and in which the rootlet bundles pass out to the exterior. This is also a character of the *Stigmara* with centripetal wood, figured by Renault. The absence of these broad rays may very well have inclined Williamson to the belief that he was dealing with a *Lepidodendroid* branch. A close examination of the innermost portion of the secondary growth reveals the fact that there is a tendency of the cylinder of secondary wood to break up into segments, as is characteristic of *Stigmara*. This is seen in Fig. 2, Pl. XV, particularly on the upper edge of the primary wood. In radial longitudinal sections, moreover, the rootlet bundles can be seen taking a horizontal course near the middle of the secondary wood, like that figured by Williamson ('87) for

¹ Fig. 15, Pl. V.

Stigmara ficoides. In their origin these rootlet bundles will be seen to agree with those figured by Renault ('93) in a *Stigmara* from the Champs des Borgis, near Autun (see Renault, Pl. XL, Figs. 8 and 9). This *Stigmara*, like the *Stigmara Brardii*, has centripetal wood. The rootlets in coming off did not break the ring of primary wood, but carried with them mainly the protoxylem elements.

Towards the outside the bundles become more oblique, as can be seen from the one included in Fig. 2, Pl. XV of the present communication. This oblique course of the rootlet bundles obviously prevents the cylinder from being split up in the manner usual in *Stigmara ficoides*. Renault's *Stigmara Brardii* seems to agree with our *Stigmara* in this particular too. In tangential longitudinal section the rootlet bundle near the centre will be found to be cut transversely, and then, as stated above, will generally appear to have the smallest elements at the centre, surrounded by larger elements, possibly metaxylems (see Fig. 4, Pl. XV). This mesarch arrangement of the bundle, due, no doubt, to the inclusion of some of the centripetal primary wood of the axis from which the rootlet starts, prevents the bundle from having that tongue-shaped appearance in tangential section which is so generally characteristic of *Stigmara*, where the primary xylem is centrifugal. The rootlet bundle is, however, generally connected with the secondary wood by special tracheids running down to it, as seen in Fig. 4. In these particulars our *Stigmara* agrees with that from the Champs des Borgis, described by Renault ('93). In some cases the appearance is more normal, and the protoxylem seems to have metaxylem developed only on its outer sides (see Fig. 3, Pl. XV). The difference in these two arrangements would, no doubt, depend on the amount of primary wood which takes part in the formation of the rootlet.

On leaving the central woody cylinder, the lateral bundle always shows the centric arrangement so characteristic of this plant, and resembling the condition found occasionally by Renault in *Stigmara Brardii* (see Fig. 5, Pl. XV). Immediately to the outside the bundles show a connexion with the wide reticulate cells which occur in large masses, though whether continuous in the living condition of the plant and forming an interlacing network like those of *Stigmara Brardii* cannot be ascertained, owing to the defective state of preservation of the cortical layer in which these cells lay. By comparison with the similar cells of *Stigmara Brardii* it seems likely that the reticulate cells formed a network in the cortical region. They were evidently connected with the vascular bundles, as can be seen both when these latter are cut transversely (Fig. 6, Pl. XV) or when a longitudinal view of them is obtained (Fig. 7, Pl. XV). In the latter case the vascular bundle is curiously constricted at intervals, not so much by a narrowing of the outer reticulate tracheids as by a constriction of the inner elements. Similar constrictions are shown in the leaf-trace of the *Lepidodendroid* stem

from the calciferous sandstone of Dalmeny, described by Seward and Hill ('99). In Fig. 21, Plate III of their memoir, such a constricted bundle is seen lying, applied there to the secondary wood, which seems almost to take the place of the reticulate cells of our *Stigmaria*. Indeed, the tangential view of the inner portions of the secondary wood in Fig. 23 of Seward and Hill's memoir very closely resembles these tracheids. Whatever the functions of these reticulate tracheids may have been in this case, we may well institute a comparison between them and the transfusion tracheids met with in the leaves of the *Lepidodendraceae* and in the *Coniferae*, where, as in *Torreya* and some other forms, they have, according to Bernard ('04), reticulate markings. But a comparison with a leaf-trace does not upset the conclusion that these are rootlet bundles, for tracheids corresponding with transfusion cells, though differing in function, are found in the rootlets of *Stigmaria*. (See Weiss, '03.)

Traces of the vascular bundles may be seen, though somewhat indistinctly, making their way through the periderm layer to the exterior. Fig. 8, Pl. XV, represents one of these cases from a longitudinal section, showing a vascular bundle (*v. b.*) passing out accompanied by a strand of small parenchymatous cells. This, which undoubtedly represents a parichnos strand, i. e. a portion of the mid-cortex, passing through the periderm, does not preclude the identification of the axis as of Stigmarian nature, for, as I have shown elsewhere (Weiss, '07), parichnos strands are not found exclusively in connexion with the leaf-trace bundles but also with rootlet bundles. And this I am satisfied is the character here, as the parichnos strand narrows down considerably to the outside, where the rootlet cushion would be found. Unfortunately the external tissues are very badly preserved, and it is difficult to identify the external process, though I believe it to be a portion of a rootlet.

It remains for me to sum up the arguments in favour of regarding the specimen under consideration as a Stigmarian axis rather than a stem of *Lepidodendron mundum*, as Williamson had concluded from a more fragmentary and less well-preserved specimen.

In the first place the very wide periderm (see Fig. 1, Pl. XV) and its peculiar structure (Fig. 8, Pl. XV), together with the remains of what must, I think, be taken to be rootlet cushions, speaks in favour of the Stigmarian nature of these tissues; while the absence of primary outer cortex of hard texture distinguishes it from the stem of *Lepidodendron mundum*.

In the curious centrical lateral bundles (Fig. 1, Pl. II) and in the possession of a system of delicate reticulate cells (see Figs. 6 and 7, Pl. XV) this axis agrees more closely with the *Stigmaria Brardii* of Renault ('93) than with any *Lepidodendroid* stem, not excepting the possible *Lepidophloios Harcourtii* from Dalmeny, described by Seward and Hill ('99). It must be remembered, however, that the reticulate cells of the French specimens

appear to be in the periderm and not in the middle cortex as in the *Stigmara* under consideration.

On the other hand, the course of the lateral bundles through the secondary wood is, in some respects, more like that of a leaf-trace than of a rootlet, though its connexion with the secondary tracheids through which it passes is in keeping with the Stigmarian rootlets (see Figs. 3 and 4, Pl. XV). The bundles, in their origin and course, agree, too, very nearly with those of the *Stigmara* from the Champs des Borgis, Autun, described by Renault ('93). There remains to be taken into consideration the arrangement of the protoxylem with its obvious centripetal development. Seeing that Renault has described some undoubted instances of Stigmarian axes with centripetal wood, this arrangement, though more characteristic of Lepidodendroid stems than Stigmarian axes, must not weigh too much against the above-mentioned structure. In fact, its occurrence in conjunction with the peculiar centric lateral bundles and the reticulate tracheids goes far, in my mind, to establish, not an identity but a correspondence, between the axis under consideration and the *Stigmara Brardii* of Renault. I cannot consider them as identical, for the amount of primary centripetal wood and the wavy outline of the latter in *Stigmara Brardii* obviously distinguish it clearly from our specimen. The same may be said of the other *Stigmara* with centripetal wood described by Renault from the Champs des Borgis, and with which our *Stigmara* does not entirely agree.

On the other hand, the very close agreement of the primary wood of our *Stigmara* with that of the *Lepidodendron mundum* (now identified with *Bothrodendron*) suggests the correlation of these two plant-remains.

While believing the specimen to be of Stigmarian character, I would agree so far with Williamson in considering that it might very well belong to the same plant (*Bothrodendron*) to which the leaf-bearing axis described under the name of *Lepidodendron mundum* belongs. This latter is generally of small dimensions, and all specimens, except for the single one described by Williamson, and which I consider identical with the *Stigmara* now under consideration, have been devoid of secondary thickening. This need not, however, be considered an obstacle, for in the first place the fragments so far described may be secondary branches, while, even should they be main shoots, it is quite conceivable that secondary growth may have only taken place in the basal region of the same, and have therefore only been of limited occurrence. Such an occurrence has been described for *Psilotum* by Boodle ('04) and by Miss Ford ('04). Should the same apply to *Bothrodendron*, the secondary growth might occur either at the base of the aerial axis or in the Stigmarian region, or more probably in both.

I incline to the opinion that the axis described in the preceding pages is, as stated above, the Stigmarian portion, both from the very wide nature of the cortex, and from the peculiar lateral bundles, which differ materially

from those known in the upper part of the plant, and which are associated with the system of reticulate tracheids not found in the stem but known to us in other Stigmarian axes. Their function in the extensive cortex of the axis cannot, I think, be that of transfusion tracheids, but rather that of water-storage.

It might be thought that this is not a function likely to be required by a plant rooted, as far as we know, in a marsh; but we know that many plants growing in fresh-water marshes—and still more so in salt marshes—are of xerophytic habit. It must also be remembered that the Lepidodendraceae show certain xerophytic characters, and the Stigmarian rootlets were possibly not very efficient organs for rapid absorption, so that a means of storing water at the base of the stem may have been of some service to the plant in regulating the water supply during certain periods.

That such a tissue occurred in some other forms of *Stigmaria*, as shown by Renault, would, I think, indicate that it is no individual peculiarity of this species, but that it serves some more or less important function of this part of the plant.

In conclusion I should like to mention that, besides the similar *Stigmarias* referred to above as in Dr. Scott's collection, there are one or two other axes, both among Dr. Scott's preparations and among my own, which seem to be of Stigmarian nature, though possessing centripetal wood. The evidence in support of their Stigmarian character is, however, still insufficient, and I have therefore left them out of consideration for the present.

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EXPLANATION OF PLATE XV.

Illustrating Professor Weiss's Paper on *Stigmaria*.

Fig. 1. Transverse section of *Stigmaria*, showing the central cylinder with secondary thickening surrounded by the wide periderm layer (*per.*) which has been much compressed and is thrown into folds. The border of the periderm has been outlined with Indian-ink to render it more distinct. Slide R. 881 *b* magnified. $\times 2\frac{1}{2}$.

Fig. 2. Enlarged view of central cylinder, showing the centripetal primary wood (*p. w.*) surrounded by mantle of secondary wood (*s. w.*); at the upper edge of the central cylinder a rootlet bundle is passing to the exterior. Q. 403 A. $\times 24$.

Fig. 3. Tangential longitudinal section through the secondary wood, showing rootlet bundle (*r. b.*) on its way to exterior. R. 881 *i*. $\times 42$.

Fig. 4. Tangential longitudinal section through the secondary wood, showing the medullary rays (*m. r.*), and a rootlet bundle (mesarch) in the centre of the photograph. *s. r.* = scalariform tracheid. R. 881 *g*. $\times 46$.

Fig. 5. Transverse section at the outer boundary of central cylinder, showing two lateral mesarch bundles (*r. b.*) with centric arrangement of secondary tracheids. The tracheids of the lateral branch are much smaller than those of the secondary wood (*s. w.*) of main axis. R. 881 *c*. $\times 100$.

Fig. 6. Transverse view of lateral bundle (*v. b.*) in the region of middle cortex, showing its connexion with a patch of reticulate tracheids (*r. t.*). R. 881 *h*. $\times 100$.

Fig. 7. Lateral vascular bundle (*v. b.*) in region of middle cortex, showing characteristic constrictions and connected with a large patch of wide reticulate tracheids (*r. t.*). R. 881 *g*. $\times 40$.

Fig. 8. Portion of longitudinal section of periderm (*per.*) through which a vascular bundle (*v. b.*) is passing to rootlet cushion (defective). *par.* = parichnos strand of parenchymatous cell running below the rootlet bundle. R. 881 *i*. $\times 30$.

per. 1.

s.w 2.

3. r.b.

4. m.r. s.tr.

5. s.w.

v.b. 6. r.t. r.t.

7. v.b. r.t.

v.b. par. per. 8.

per. 1.

s.w. 2.

5. *s.w.*

rb. 6. *rt.* *rt.*

3. *rb.*

4. *m.r.* *s.tr.*

7. *v.b.* *rt.*

v.b. *par.* 8. *per.*

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