On the Fertile Shoots of Mesoxylon and an Allied Genus.

BY

D. H. SCOTT, F.R.S.

With Plates I–III and three Figures in the Text.

CONTENTS.

THE FERTILE SHOOTS OF *MESOXYLON MULTIRAME*.

IN a recent paper on the structure of this species of *Mesoxylon* (Scott, 1918, p. 453) it was pointed out that the axillary shoots are branch-systems of a special kind, entirely different from the relatively main axis which bears them. They are characterized by the bilaterally symmetrical organization of the shoot, with a much flattened stele, and by the distichous branches, which bear reduced leaves or bracts, as well as other appendages which may be either prophylls or secondary branchlets. The shoots are closely associated with seeds (*Mitrospermum compressum*, A. Arber) and may have been the organs which bore them. They are termed 'fertile shoots', as there is little doubt that they were connected with reproduction. In the present communication it is proposed to describe these organs fully, and to discuss the evidence available as to their function.

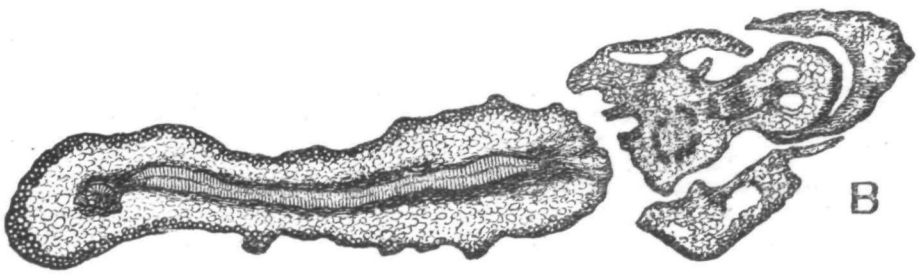
Description of the Specimens.

In some ways the most important specimen is one shown in immediate association with a stem of *M. multirame*[1] bearing axillary shoots, for here we have direct evidence for the fertile shoot belonging to the plant. This

[1] Sections Scott Collection 2564–70.

specimen will be considered later, but in the first instance it will be most satisfactory to describe a much better preserved example from another series;[1] though not actually associated with a stem, many leaves of the *Mesoxylon* type are present, and the structure of the shoot itself leaves no doubt as to its nature.

The first section of this series is an important one and is fully illustrated (Text-fig. 1; Pl. III, Figs. 17–19). The main part of the specimen is a much flattened, apparently naked axis, in approximately transverse section, measuring about 6·5 × 1·5 mm. (Text-fig. 1). It has an extremely long and narrow stele, just as in the well-known axillary shoots of *M. multirame* (Scott, 1918, Pl. XIII, Fig. 22). The secondary wood is 3–5 elements thick; where the stele is least collapsed, groups of irregularly arranged elements with somewhat thick walls are seen at the inner edge of the



TEXT-FIG. 1. Transverse section of fertile shoot, A, and its branch, B. For details see Plate III, Figs. 17–19. × 12. S. 2781. From a drawing by Mr. G. T. Gwilliam.

secondary zone, and may possibly represent the centripetal xylem of the stele, though the other sections lend little support to this interpretation (Pl. III, Fig. 18). The stele is branching; at one end a small round stele with little or no pith is passing out, and immediately beyond it a small distal bundle is seen (Pl. III, Fig. 19). These features are very constant wherever this phase of branching is observed.

At the opposite end of the section (B) there is a large branch detached, but obviously broken off from the main shoot (Text-fig. 1; Pl. III, Fig. 17). It bears bracts, seen both in connexion with the branch and just free; each bract has a single vascular bundle. The branch itself has a rounded stele, with its bundles somewhat widely spaced, and a considerable pith.

The branch is also giving off a distal appendage (cut obliquely), clearly subtended by one of the bracts, which ensheathes it (Pl. III, Fig. 17). This appendage therefore seems to be a secondary branchlet. The presence of

[1] Sections S. 2781–95. All the specimens described in this paper are from Shore, Littleborough.

an appendage has been observed in several cases, but its nature is open to question (see p. 7).

The main shoot has a certain amount of hypodermal sclerenchyma which extends into the branch, and is especially well developed on the abaxial side of the bracts.

The next section (2782) is not so complete, but at the end (A) where the little round stele was given off in 2781, we now see the base of a branch attached, with a round medullate stele just like that of the former branch. It thus appears that the relatively large stele of the branch, with its pith and distinct bundles, is an expansion of the little pithless stele first given off from the main stele of the shoot. The relative dimensions are—for the branch-stele when first given off, about 0·25 mm.; for the stele when it has passed into the branch, about 0·7 mm.; measuring to the outside of the wood only in each case. The branch seen in the previous section (at the end marked B) is in this case (2782) only represented by bracts.

In the third section (2783) (Pl. I, Fig. 1) the branch of which we saw the base before (at the A end) is here quite free. The bracts and their bases are well shown, but the stele has perished. At the opposite end of the section (B) another little stele is being given off; it is cut obliquely enough to show that tracheides extend to the centre. There are some irregularities in the wood of the main stele here which may be pathological. Off this end a branch or bud is present in oblique section—perhaps the upper part of the first branch.

In the fourth section (2784) a little branch-stele is again detached (at the A end). It shows the small distal bundle, which here seems to have just separated from the branch-stele.

In the fifth section (2785) the branch-stele (at the A end) has moved farther out; it has expanded slightly and acquired a pith. The little distal bundle has moved far out into the cortex. Beyond the opposite end there are some bracts, cut longitudinally, and at a greater distance are two buds in transverse section, each showing both the bracts and a stout appendage lying outside the bract-cycles (Pl. I, Fig. 2). The presence of these buds is explained by the next sections, which show that the axillary shoot curved, so as to be cut in a more longitudinal direction in the later sections; the buds evidently belong to the part of the shoot which runs almost longitudinally. It is not necessary to follow the series farther in detail; enough has been said to show that the axillary shoot gives off distichous leafy branches alternately, the plane of branching being that of the flattened stele of the shoot. The branch, besides the small leaves or bracts, bears a further appendage, the nature of which is discussed below (p. 7).

Anatomically each branch receives a stele from the main shoot; it is small when first given off, but rapidly expands and becomes medullated. Each bract contains a single vascular bundle, while the appendage has

a minute stele or mesarch bundle. In the later sections of the series another axillary shoot (in 2793) and two or three more branches or buds are met with. In two of these (in slide 2789) there is an appendage in addition to the bracts, like that shown in Pl. I, Fig. 2. In one case it is possible that a second appendage is present in the same bud.

The fertile shoot is associated, though not very closely in this case, with a number of seeds. In the series of fifteen sections twelve distinct specimens of *Mitrospermum compressum*, A. Arber, occur. They present all the characters of the species, and there is no doubt as to their identification (see p. 18). None of them, however, show any special relation to the fertile shoots, so the evidence is simply that of association, and such force as it has depends on the high number of the associated seeds. One of the *Mitrospermum* seeds (shown in sections 2792–4) appears to be young, judging from the comparative thinness of the cell-walls of the sclerotesta, but though this seed is in the neighbourhood of the second axillary shoot there is no indication of any connexion.

Some of the sections of the *Mitrospermum* are interesting in themselves; in one (section 2781) the prothallus is preserved; another (2787) shows four pollen-grains in the pollen-chamber, and a third (2791) passes through the chalaza. Though these details are irrelevant to our immediate question, it has been thought worth while to figure the two former (Pl. II, Figs. 15, 16).

It is fair to mention that other seeds, *Physostoma elegans* and *Conostoma oblongum*, occur in the series, but only a couple of specimens of the former and one of the latter.

We have next to consider the specimen of a fertile shoot associated with a vegetative stem of *M. multirame*.[1] The stem is of the ordinary type, about 2 cm. in diameter, with a pith varying from about 7 to 9 mm. in diameter in different parts of the specimen, and wood from 2 to 2·5 mm. in thickness. It is thus a rather small and young stem (Pl. I, Fig. 4).

All the distinctive characters of the species, especially the very gradual convergence of the twin-bundles of the leaf-trace at the margin of the pith, are shown, though the preservation is not specially good. The stem, particularly in its lower part, bears a number of axillary shoots, of which the characteristic steles are conspicuous (Pl. I, Fig. 4); they have the usual tangentially elongated or flattened form, and their secondary wood is thicker on the inner than on the outer face.

The fertile shoot lies quite close to the stem (Pl. I, Fig. 4); it is not much flattened, though the outline is irregular and distorted. The transverse dimensions are roughly 2·9 × 2 mm. In the section in which the shoot first appears (2564) the main stele is badly preserved, but at one end (A) a small, round, pithless stele has been given off, and there are traces of a minute distal

[1] The vegetative stem runs through the series 2563 to 2574, from below upwards; slides 2984 and 2985 appear to be of the same stem, as are also the longitudinal sections 2575–8.

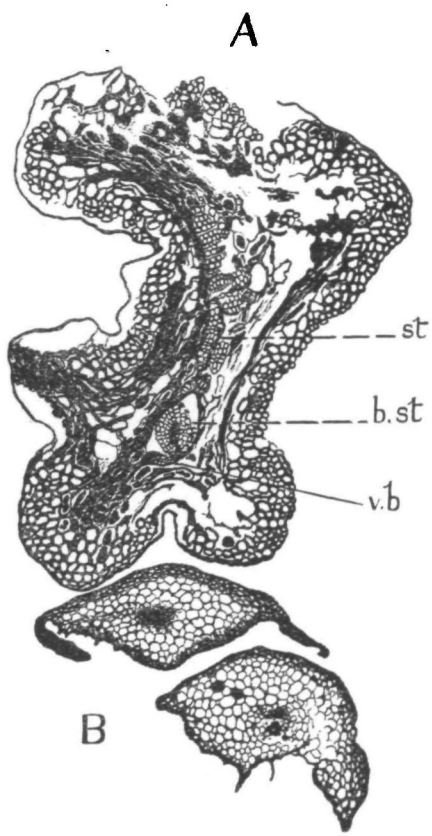
strand. The hypodermal sclerenchyma of the shoot is strongly developed. At the opposite end (B) the shoot bears a large hastate branch, not much smaller than itself, measuring, in the oblique section, about 2·4 × 2 mm. in diameter (Pl. I, Fig. 4, *b*). The three projections appear to be the bases of bracts; no other appendage is distinguishable. The middle is occupied by a large medullate stele, with bundles well separated, just as in the former specimen. The pith has almost perished. The distal arc of the vascular ring projects outwards, but this may be due to accidental causes.

In the next section (2565) the little round stele (at the A end) has enlarged and acquired a small pith; at the opposite end the branch is detached, but the preservation is bad.

The third section (2566) (Text-fig. 2) is favourable for the axillary shoot, in which the very narrow stele is fairly preserved; at one end (B) the usual round branch-stele, with its distal bundle, is passing out. Branches at either end are represented by bracts (shown at B).

The next section (2567) shows little change; the same round branch-stele and distal bundle are present, as before.

In the fifth section (2568) the shoot has diminished somewhat in size (to about 2·5 × 1·75 mm.); it is badly preserved, but bears a large hastate branch, much like that in the first section, but so cut as to appear attached by a narrower base (Pl. I, Fig. 5). At a distance of only 0·8 mm. from the shoot, at the opposite end to the branch, is a seed of *Mitrospermum compressum*, in transverse section. There is, however, no indication of any connexion with the fertile shoot.



TEXT-FIG. 2. Transverse section of fertile shoot, A, and bracts, B. *st.*, main stele of shoot; *b.st.*, stele of a branch; *v.b.*, distal bundle. At B, two bracts, belonging to a branch of the shoot. × 40. S. 2566. From a drawing by Mr. G. T. Gwilliam.

In the following section (2569) little remains of the shoot. A second seed is present, close to the former; it is a rather young *Mitrospermum*, judging from the comparatively thin-walled sclerotesta; again there is no evidence of connexion with the shoot or its branches.

Nothing more of interest is shown in the series. In another section, apparently from the same specimen (2985), a detached axillary shoot is present close to the stem, but it does not show branching, for it is no doubt cut near the base.

I have found no other specimens of *Mitrospermum* in this series besides the two mentioned above. In this case, therefore, their significance depends, not on their number, but on their close association with the fertile shoot. Whether the two seeds were originally attached to the shoot cannot be determined, but it is not improbable that this was the case.

The specimen is inferior to that in the previous series; in particular the organ which we have called the appendage of the branch is nowhere clearly shown, though it was almost certainly present, as the other characters agree so closely with those of the former specimen. The special interest of the shoot just described lies in its close association, on the one hand, with *Mitrospermum compressum*, and on the other with a stem of *Mesoxylon multirame* bearing axillary shoots. From the structure of the fertile shoot, especially its narrow, flattened stele, there can be no doubt that it is of the same nature as the axillary shoots borne on the stem; it evidently constitutes the upper part of a shoot, of which the base may have been still attached to the main stem.

There is another example of a fertile branch shown in a single section (3040); the specimen is associated with leaves of the *Mesoxylon* type, but not with a stem or with seeds. It is the best specimen for the general habit, as it is so little distorted. The shoot is seen in somewhat oblique transverse section, and measures about 5×2 mm. (Pl. I, Fig. 6). The identity with the axillary shoots of *Mesoxylon multirame* is manifest (cf. Scott, 1918, Pl. XIII, Fig. 22). The constriction near one end of the section seems to be accidental. The stele is about 2 mm. long by only 0·37 mm. broad, and is thus a good deal flattened, though the whole shoot is not. As pointed out in a previous paper (Scott, 1918, p. 443), the narrow form of the stele in these shoots is no doubt in the main the natural one. The secondary wood is three or four elements thick; no centripetal xylem is preserved. The *Dictyoxylon* outer cortex is well developed; dark elements (secretory sacs?) are, as usual, present in the inner cortex.

At one end of the section the shoot bears a large branch or bud, nearly 3 mm. in diameter (Pl. I, Fig. 6, *b*). It consists of an axis, continuous with that of the shoot, and a number of bracts, several of which are in connexion with the axis, while one is free. The large medullate stele of the branch (0·8 mm. in diameter) is cut obliquely. On its distal side several leaf-trace bundles are seen on their way out to bracts. The dorsal bands of fibres in the bracts are well shown.

The specimen thus exhibits the general characters of the fertile shoot clearly, but affords no new data. No distal appendage is shown, but the plane of section would probably have missed it.

Nature of the 'Appendage'.

The nature of the appendage of the branch seen in several sections of the first series described (from 2781 onwards) remains doubtful. From the evidence of the section represented in Text-fig. 1 and Pl. III, Fig. 17, it would appear that the appendage is a secondary branchlet, for it is clearly subtended by a bract. The other four cases observed (a typical example is shown in Pl. I, Fig. 2) are all from detached buds or branches. In all of these the appendage lies outside the regular cycles of bracts, and is of relatively large size; in the case figured, for example, it measures quite 1 mm. in diameter, while all the rest of the bud is only about 1·7 × 1·3 mm. The appendage is not subtended by a bract in any of these examples, though in that figured there appear to be one or two on one side of it. The structure of the appendage does not suggest a branchlet; it rather resembles a somewhat large bract cut through its basal part; it is flattened or grooved towards the axis of the branch. The slender vascular strand in the case figured has a square xylem-group with the smallest elements almost central (Pl. I, Fig. 3); it thus appears to be mesarch, and does not differ essentially from the bundle of a bract. The distribution of the fibrous tissue is also similar in the appendage and the bracts; in both, at a little distance above the base, it is chiefly concentrated on the abaxial surface, where it forms three or more bands, one being median.

On the whole, therefore, the evidence, apart from the case of the section 2781 (Text-fig. 1), appears to be in favour of the appendage being itself of the nature of a bract. It is possible that the appearance of a branchlet subtended by a bract in the case cited may be deceptive, for here also one might interpret the appendage as a bract, cut very obliquely and still in connexion with the branch, the apparently subtending bract being merely one of an overlapping series.

In the other cases, where the appendage lies to the exterior of the bract-cycles, one might interpret it as the prophyll of the branch, probably supplied by the little bundle given off from the branch-stele near its base (see Pl. III, Fig. 19 and Text-fig. 2). In any case it cannot be said that there is any sufficient evidence for the appendage representing the pedicel of a seed, as at first seemed probable.

Anatomical Details.

A few points in the anatomical structure of the fertile shoot and its branches remain to be considered.

The wood generally has been found to consist of spiral and scalariform elements, thus resembling the inner zone of the wood in the vegetative stem. Considering the thinness of the wood in the shoot and branch, this is not surprising.

As already mentioned, there is in one case (Pl. III, Fig. 18) some evidence for the presence of centripetal xylem in the stele of the main shoot. There is, however, no indication of the protoxylem between the centrifugal and the apparently centripetal elements; neither do the other sections confirm the presence of the latter. Most probably such appearances are merely due to displacement and compression of portions of the centrifugal wood. One would not, in fact, expect centripetal xylem to be represented in the main shoot; in the vegetative stem it is always associated with the leaf-traces, and, as the axillary shoot is leafless, there are no leaf-traces here.

In the branch the case is different, for here the stele receives the traces of the numerous bracts, so that we may expect to find centripetal xylem. But, unfortunately, the preservation is never good enough to show the structure clearly. In the best section for the branch-stele (2781) (Pl. III, Fig. 17) one can see that the greater part of the xylem of the bundles is centrifugal and in radial series; a few irregularly arranged elements on the inner margin may probably represent the centripetal part of the xylem. This applies to the branch-stele after it has expanded and acquired a pith; where it is first given off from the main stele it has a purely centric structure, with neither centripetal xylem nor pith (Pl. III, Fig. 19 and Text-fig. 2).

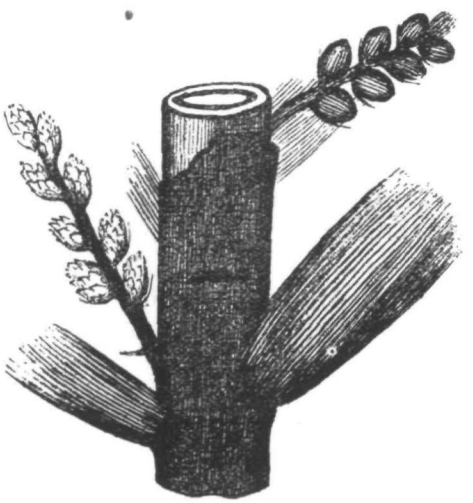
There is no doubt that the bundles of the bracts themselves are mesarch, with a fair amount of centripetal xylem. The case figured with the protoxylem nearly central (Pl. I, Fig. 3) is from an 'appendage', but, as explained above (p. 7), the structure does not differ from that of an ordinary bract.

The distribution of the sclerenchyma in the axillary shoot is in the usual form of a *Dictyoxylon* hypoderma, sometimes nearly continuous (Text-figs. 1 and 2; Pl. I, Figs. 1, 5, and 6). The branch has little free surface, but on the bracts themselves the fibrous tissue is often well developed, occurring on both surfaces but chiefly on the distal side, where it forms several often more or less confluent bands (Text-fig. 2, Pl. I; Figs. 2 and 6; Pl. III, Fig. 17). The parenchyma of the cortex contains sacs with dark contents, similar to those occurring in the vegetative stem (Scott, 1918, p. 452).

Discussion.

The very peculiar characters of the shoots under consideration, and in particular their bilateral symmetry and distichous branching, at once distinguish them from the vegetative axis and indicate a special function. As Grand'Eury said, in speaking of one of his species of *Cordaianthus*: 'La disposition distique des bourgeons est le signe d'une nouvelle destination' (Grand'Eury, 1877, p. 229). On general grounds there could be no

reasonable doubt that the function of such highly modified shoots was connected with reproduction; as a matter of fact there are the closest analogies with various well-known Cordaitean fructifications, and *Mesoxylon*, as we know, was a near ally of *Cordaites*. Grand'Eury says of *Cordaianthus*, 'Les bourgeons floraux plus ou moins nombreux ont une disposition généralement distique' (l. c., p. 227). Our axillary shoot of course corresponds to the main axis of the inflorescence, which Grand'Eury describes as 'fleshy', and the distichously arranged branches to the floral buds. Some of Grand'Eury's figures of *Cordaianthus* agree remarkably well with our specimens, and might almost serve as restorations of them. Attention may be especially directed to *Cordaianthus baccifer* (l. c., Pl. XXVI, Figs. 10, 12, 13) and to the illustrations in Pl. XXV, which show the inflorescences as borne on the stem; one of them is reproduced in our Text-fig. 3. The 'naked peduncle' (e.g. *C. glomeratus*, l.c., p. 230; cf. *C. gemmifer*, Pl. XXVI, Fig. 5) is clearly comparable to the leafless main axis of our axillary shoot. Grand'Eury lays stress on the absence of bracts, flowers, and leaves on the peduncle (l. c., p. 228).



TEXT-FIG. 3. Part of a branch of *Cordaites laevis* (restored). It bears several leaves and two inflorescences, the upper ♀, the lower ♂, with distichous floral buds. From Grand'Eury. About natural size.

The dimensions of the smaller specimens of *Cordaianthus* are quite comparable to those of our specimens. It may be further pointed out that in Grand'Eury's figures showing the inflorescences *in situ* (l.c., Pl. XXV) their insertion lies some little distance above the subtending leaf. This agrees with the position of our axillary shoots (Scott, 1918, p. 448). In position, form, size, and general morphology our fertile shoots thus agree with the inflorescences known as *Cordaianthus*. One point of difference may be mentioned. Grand'Eury (l.c., p. 228) describes the floral buds as borne in the axils of bracts, which are shown in many of his figures, though they are sometimes abortive. There appears to be no subtending bract to the bud or branch in our specimens, for the distal bundle, which might have been interpreted as the trace of such a bract, springs from the branch-stele, and not from the stele of the main shoot (see Pl. III, Fig. 19, and Text-fig. 2). It would thus seem to have supplied a prophyll of the branch, rather than

a subtending bract. The distinction between the two would, however, be scarcely recognizable in specimens preserved as impressions, and the difference is of little significance.

We now come to the comparison of the actual floral buds or branches with those of *Cordaianthus*, and here there is more opportunity for detailed correlation, for fairly full data are supplied by the work of Renault and especially by the later investigations of Bertrand, while, so far as I know, no previous observer has described the structure of the main axis of the inflorescence. Renault (1879, Pl. XVII, Fig. 1) shows a transverse section of the axis of *Cordaianthus subglomeratus*, with some indication of the vascular ring, but here there is little analogy with our specimens, as the floral buds are not distichously arranged.

Renault (1879) has little to say about the structure of the axis and bracts of the floral buds; his attention was concentrated on the stamens and ovules. His figures, however, show the bracts arranged spirally in numerous cycles, each bract having a single vascular strand (l. c., Pl. XVI, Figs. 12–15; Pl. XVII, Figs. 1–3, 11, 13, 14). The bracts of the female catkin are described as thicker and more coriaceous than those of the male (l.c., p. 312).

Much fuller details are given by the late Professor C. E. Bertrand in his paper on the Female Bud of *Cordaites* (Bertrand, 1911). His observations are confined to the detached floral bud or catkin (which he sometimes calls the 'inflorescence'), and there is no reference to the main axis, which appears not to be represented among Renault's preparations on which the account is based.

The axis of the young bud, he says, has no free surface; it is covered by the bases of the bracts (l. c., p. 25). The vascular ring consists of about ten isolated strands surrounding a pith. Each strand includes on the inner side an irregular group of spiral elements, with 2–4 groups of radially arranged secondary elements on the exterior. The illustration (l. c., Pl. V, Fig. 37) shows that the structure of the stele of the bud essentially agrees with that in our specimens (cf. Pl. III, Fig. 17). A detailed comparison of the other tissues is superfluous, as the preservation is poor both in his material and ours.

The bracts in Renault's specimens are remarkably like ours. Those figured by Bertrand (l. c., Pl. V, Fig. 43) are almost identical with the bracts of the bud shown in Pl. I, Fig. 2 (see also Text-fig. 2); the form of those cut near the base is the same, and that of the more distal bracts very nearly so. The bracts, however, are much less numerous in our specimens, perhaps because some are lost. The structure of the bracts in the French specimens is described by Bertrand in great detail (l. c., pp. 30–7). Here it may suffice to mention that in the free, middle part, the bract has two bands of fibres on the distal face, and a less developed fibrous layer

on the inner side. In ours the distal bands, where they are distinct, are more numerous. The parenchyma is large-celled, especially towards the middle, just as in ours. The vascular bundle is described as identical with a single nerve of the vegetative leaf of *Cordaites* (l. c., p. 34); in our specimens it is mesarch, which comes to the same thing. Bertrand's Fig. 41 shows a bundle exactly like that of an imperfectly preserved bract in one of our specimens. In the basal part of the bract the fibrous bands disappear just as in ours. Bertrand speaks of hairs on the bracts, which have not been detected in our specimens.

Considering that there is no question of specific identity, the agreement between the branches in our specimens and the floral buds of the French fructifications is remarkably close. Taking both general morphology and detailed structure into consideration, we may conclude with confidence that our fertile shoots with their branches are of the same nature as the inflorescences of *Cordaites*; they constitute, in fact, the *Cordaianthus* of *Mesoxylon multirame*.

The question remains, Of what sex was this *Cordaianthus*? The detailed comparison has been with a female fructification, but there was little difference in general morphology and structure between the two sexes. Male catkins, however, are short-lived organs, and it is hardly likely that we should find the accessory parts mature and fairly preserved without some trace of the stamens themselves. Also any force that association may have tells in favour of the fertile shoots having been seed-bearing organs. Supposing that this was their nature, it is probable that some of the Mitrospermums which we find in the neighbourhood of the fertile shoots, especially the younger seeds, may have been borne on them and become detached. In the best known female specimens of *Cordaianthus* the seeds are borne laterally on the catkin, each terminating a short pedicel, probably in the axil of a bract (Bertrand, 1911, p. 37). The ovules are surrounded by the bracts of the catkin, from among which the ripening seed may emerge. We have found no satisfactory evidence of the presence of seed-pedicels, for the 'appendage' appears to have been of the nature of a bract, except perhaps in the one case shown in Text-fig. 1 and Pl. III, Fig. 17, and even here, as we have seen, the interpretation of the appendage as a branchlet or pedicel is open to some doubt. Unfortunately, then, we are at present unable to explain how the seeds were borne, and the solution of the question must await the discovery of more perfect specimens. Possibly the seed may have been terminal on the branch.

In any case the nature of the fertile shoot of *Mesoxylon multirame* as a *Cordaianthus* has been sufficiently demonstrated.

Other Shoots associated with Seeds.

We have now to consider two examples of shoots which show in their structure no relation to *Cordaianthus*, and indeed resemble vegetative buds rather than inflorescences, but are more or less closely associated with seeds of the *Mitrospermum* type. As we shall see, they show an unmistakable relation to *Mesoxylon*, though there are reasons for doubting whether they can properly be included in that genus.

The specimen to be first described is represented by seven transverse sections, the series running from below upwards.[1] The axis, with the leaf-bases, has a diameter of about 8 mm. The whole surface is clothed with the massive leaf-bases, the true cortex being comparatively narrow (Pl. I, Figs. 7, 8). At some places the leaf-base is seen expanding into the lamina, and imperfectly preserved laminae of other leaves surround the specimen.

There is a somewhat narrow zone of wood, about 10–20 elements in thickness; in places the centripetal xylem of the leaf-traces can be recognized, most clearly in the second section (2599). The most interesting point is that the leaf-traces are single where they pass through the wood. They run out horizontally, so that they can be traced far out into the leaf-base, forking once or twice after reaching the cortex. Farther out in their course they become more vertical, and undergo repeated divisions, for in the outer part of a leaf-base as many as nine little bundles, cut very obliquely, have been observed (Pl. I, Fig. 7, *l.b.*). The structure of the wood and also the *Dictyoxylon* cortex are like those of a *Mesoxylon*, and the pith, so far as can be judged from transverse sections, appears to have been discoid, for the displaced diaphragms are shown (Pl. I, Figs. 7, 8). Periderm was formed, cutting off the leaf-bases.

The leaves in connexion with or surrounding the axis have many bundles, and are of the ordinary *Cordaites* or *Mesoxylon* type. The xylem of the foliar bundles appears to be mainly centripetal. In the upper sections (e.g. 2603) periderm had formed in the leaves, usually on both surfaces—an interesting point, which strongly suggests a resting, vegetative bud. In the upper part of the specimen the wood diminishes in thickness.

There is nothing in the structure of this specimen to indicate that it was a fertile shoot. It is, however, associated with seeds, apparently of *Mitrospermum compressum*, of which five specimens occur in the series, two of them lying near the bud. One of the seeds shows signs of youth.

[1] The numbers of the sections in my collection are 2598 to 2604. They were received in August, 1910, from Mr. Lomax, who described the specimen as 'a small apical shoot', and called attention to the association with the seeds of *Cardiocarpon* (now *Mitrospermum*) *compressum*.

The other specimen, represented by six sections, is more remarkable, for the axis increases rapidly in diameter from below upwards, and appears to approach the growing point at the upper end.[1] At the base (section 3017) the shoot measures altogether about 4·5 mm. in diameter; the stele is about 1·7 mm., with a minute pith, only about 0·4 mm. in diameter; the wood is of unequal thickness, from 0·37 to 0·9 mm. (Pl. I, Fig. 9). Two single leaf-traces are passing out. The cortex and leaf-bases are obscure in this section, but the axis is surrounded by broad, ill-preserved leaves. In the next section (3018) the diameter of the shoot has increased to 7–8 mm. The stele is incomplete, but evidently larger than before, with the wood 0·53 mm. thick in the part preserved; numerous bundles are seen entering a leaf-base, as in the previous specimen. The third section (3019) (Pl. II, Fig. 10) is a much better one and shows a marked change. The diameter of the whole shoot is here about 8 × 10 mm. The stele measures 3 × 2·5 mm. and the pith, which is pentagonal in form with gaps at the angles, about 1·5 mm. The wood reaches 0·57 mm. (24–30 elements) in thickness. A large single leaf-trace is passing out. The pith here, as in all the sections which show it, seems continuous; there is nowhere any indication of a discoid structure. Centripetal xylem is distinctly shown at certain points around the pith.

In the fourth section (3020) the dimensions have further increased, the whole diameter being about 10 × 15 mm. The stele has a diameter of 3 × 2·8 mm. and the pentagonal pith of 1·8 mm.; the wood has a fairly uniform thickness of 0·4 mm. There is a forking leaf-trace in the cortex, opposite one of the gaps in the ring of wood.

In the two sections last mentioned the large leaf-bases and the encircling leaves are better preserved, though still imperfect; they seem to agree essentially with those of the former specimen; certainly the leaf-bases are relatively more strongly developed than on the vegetative stems of *Mesoxylon*, and the leaves themselves are polydesmic and probably of the Cordaitean type.

In the next section of the series (3021) the axis is destroyed, but the uppermost section (3022) is interesting, for it shows the stele in a very young condition. The preservation is bad on the whole, but a ring of quite isolated, vascular bundles is shown. There appear to be nine of these bundles, though some are obscure, surrounding a large pith and separated by broad principal rays. The secondary wood of each bundle is only four or five cells thick; in some cases a few centripetal elements can be recognized. At one place a leaf-trace is passing out, almost horizontally.

[1] The series is 3017–22, from below upwards. The sections were received from Mr. Lomax in October, 1910. He rightly regarded this specimen also as an apical shoot (possibly, as he then thought, of *Mesoxylon multirame*) and attached great importance to its intimate association with the seeds.

The diameter of the vascular ring is about 2·5 mm.; allowing for the small development of the wood, this is about the full size of the stele in the preceding sections. Evidently we are here approaching the apical region of the bud; it is interesting to find that the vascular bundles are at first widely separated, and that it is only at a later stage that they become united into a more or less continuous vascular zone.

About nine seeds of *Mitrospermum* occur in the series, some of which are evidently young. In section 3019 three of the seeds closely surround the shoot and all appear young, the cell-walls of the sclerotesta being but little thickened. In one of them the indications of youth are especially marked; all the cell-walls are remarkably thin, the megaspore is relatively small, and there appears to be a thick layer of nucellar tissue persisting between the megaspore and the integument.

Discussion.

There can, I think, be no doubt that the two specimens just described are of the same kind. Both are of the nature of buds or apical shoots, as is proved by the leaves wrapped closely round the axis. They agree in the structure of the wood, in the single leaf-traces dividing in the cortex, and in the massive leaf-bases. The chief differences are, first, in the structure of the pith, which seems to have been discoid in the first specimen and continuous in the second. There is a slight difference also in the form of the pith, which is markedly pentagonal, at least where it attains its full size, in the second specimen, and only faintly angular in the first. This, however, is a small point.

Another conspicuous difference is the striking contraction of the whole shoot and its stele towards the base in the second specimen, while the diameter is fairly uniform throughout in the first. This distinction suggests that the second specimen may have been a lateral bud, and the first a terminal one. This suggestion might perhaps also throw some light on the difference in the structure of the pith.

The anatomical habit of both shoots is distinctly that of a *Mesoxylon*; the presence of centripetal wood and the polydesmic structure of the encircling leaves show that the affinity is a real one. But in the important character of the single leaf-trace there is a marked distinction from *Mesoxylon*, for in all the species referred to this genus the trace is double where it passes through the wood. This, in fact, has been made a character of the genus (Scott and Maslen, 1910, p. 237). It is true that in the buds of the fertile shoot of *M. multirame* the leaf-trace is single, but here the reason is obvious, for it supplies a monodesmic bract. In the shoots now under consideration the leaf-base and leaf have many bundles, and yet the trace is single at its origin, only dividing as it passes through the cortex. This peculiar feature might no doubt be due to the shoots being of a special

morphological nature, differing from vegetative branches. They might then belong to some species of *Mesoxylon*. But specimens of ordinary vegetative stems of the *Mesoxylon* type have now come to light which agree with these shoots in having single leaf-traces, and it is suggested that the shoots belonged to a plant of this kind. The stems in question will be described immediately; in the meantime the attribution of the bud-like shoots must be left an open question (see p. 17).

There is nothing to show that these shoots were connected with reproduction; they have all the character of vegetative buds, and bear no resemblance to any form of *Cordaianthus*. If they bore branches of the nature of fructifications, no trace of any such organs is to be found in the specimens. Yet the association with *Mitrospermum* seeds, and especially with young seeds, is striking. Probably it is accidental, for if all the seeds are of the same species they could not have been borne both on these shoots and on the *Cordaianthus* of *Mesoxylon multirame*.

I shall return to the subject of association at the conclusion of the paper.

Stems of the *Mesoxylon* Type with a Single Leaf-trace—a New Genus.

The stems in question are represented only by two isolated transverse sections in my collection.[1] The smaller of the two specimens (2983) is about 11 mm. in diameter in its present condition, but the cortex is incomplete (Pl. II, Fig. 11). The stele (to the outer edge of the wood) measures about 9×8 mm. and the pith about $5 \times 3{\cdot}5$ mm. The pith is almost destroyed by Stigmarian rootlets, and it is impossible to determine whether it was discoid or not. The small-celled wood is from 1·3 to 2·5 mm. thick. The medullary rays are narrow and uniseriate, and the general structure of the wood, so far as can be judged from a transverse section, is similar to that of a *Mesoxylon*, such as *M. multirame* or *M. poroxyloides*. It also agrees essentially with that of the bud-like shoots described in the preceding paragraphs.

Three leaf-traces, each manifestly a single bundle, are seen on their course through the wood; they pass out obliquely but not horizontally. In two of them the centripetal xylem can be clearly seen, and in one, at any rate, the intermediate position of the protoxylem is evident (Pl. II, Fig. 12). A fourth bundle is just leaving the pith, and this also shows the same mesarch structure. The inner edge of the wood is not well preserved, and though there are indications of centripetal wood at some points, it is nowhere very clear, apart from the outgoing traces. The phloem and

[1] The numbers are 2983 and 2993, both received from Mr. Lomax early in 1916; they were found at Shore, Littleborough.

pericycle are poorly preserved, and the inner cortex, which alone is present, shows a not very distinctive parenchymatous structure.

On the data available it appears that this specimen is a stem allied to *Mesoxylon*; the size, and especially the considerable development of the wood, indicate that it was an ordinary vegetative shoot.

The second specimen (section 2993) is of a much larger stem (Pl. II, Fig. 13). Only the pith and wood are preserved, and the latter is incomplete. The maximum radius, to the outer edge of the wood, is almost 2 cm. The pith is about 6 mm. in diameter; it is nearly complete, but it is quite likely that the plane of section may happen to coincide with a diaphragm. Its contour is obscurely angular. The structure is very uniform, the cells merely becoming smaller towards the outside; many of them have dark contents. The appearance is very similar to that of a diaphragm of *Mesoxylon multirame* when seen in horizontal section.

The structure of the wood is the same as in the former specimen, except that the rays sometimes appear to be biseriate, a feature often met with in species of *Mesoxylon*. It shows a more definite appearance of 'annual rings' than is usual in carboniferous woods; examined with a lens the rings look quite like concentric bands of autumn wood (Pl. II, Fig. 13). But they prove, on closer investigation, not to be really continuous, and though some of the cells are flattened this is not at all generally the case. The distinction appears to depend mainly on a somewhat greater thickness of the cell-walls in these bands.

Two single leaf-traces are seen passing out obliquely through the inner part of the wood (Pl. II, Fig. 13).

At several points of the inner edge of the wood a prominent group of primary xylem is seen, which is evidently centripetal in development, and comparable to the primary xylem of a *Mesoxylon* (Pl. II, Fig. 14). In all cases such groups occur singly, never in pairs; they clearly represent the downward continuation of single leaf-traces which have passed in at a higher level.

Discussion.

These two specimens differ practically in nothing except size, and may safely be referred to the same species. The characters open to investigation are somewhat meagre; in the general structure of the wood and pith (when shown) and in the presence of centripetal xylem, both in the outgoing leaf-traces and in strands at the inner edge of the wood, the stems agree with *Mesoxylon*. They differ from that genus in the important point that the leaf-trace, as it traverses the wood, is single and not double. At the same time it is evident that the specimens are ordinary vegetative stems, and thus directly comparable with those on which the genus *Mesoxylon* was founded. It will be noticed that the pith is smaller than is usual in *Mesoxylon*.

Without altering the generic characters of *Mesoxylon* it is impossible to include the stems in question in that genus, for the generic diagnosis contains the statement: 'Leaf-traces double where they leave the pith, the two strands uniting at a lower level' (Scott and Maslen, 1910, p. 237). There is no question of dropping this character, on which great stress has been laid in all descriptions of the species of *Mesoxylon*. It must, however, be understood that it applies essentially to the vegetative stems only.

It thus becomes necessary to establish a new genus for the specimens just described, and the name I propose to adopt is *Mesoxylopsis*. I think we are logically compelled to include in the new genus the two bud-like shoots (of the 2598 and 3017 series) previously described. They too have single leaf-traces, and the evidence goes to show that the shoots were vegetative organs. The fact that they bore polydesmic leaves shows that the singleness of the leaf-trace was not simply an adaptation to a reduced foliar structure. The case for separation from *Mesoxylon* is in fact just about as strong for these buds as it is for the larger stems just described. Although, therefore, we cannot absolutely prove that the bud-like shoots may not have been peculiar specialized branches of a *Mesoxylon*, the presumption on present evidence is that they belonged to *Mesoxylopsis*, and I have taken account of their characters in drawing up the following diagnosis of the new genus:

MESOXYLOPSIS, gen. nov.

Pith probably discoid in the mature stem.

Wood dense, with narrow, usually uniseriate medullary rays.

Leaf-traces single where they leave the pith and pass through the wood, forking repeatedly in the cortex and leaf-base.

Centripetal xylem present in the leaf-traces at the margin of the pith and throughout their outward course into the leaves.

Leaf-bases massive, crowded.

Leaves polydesmic, of the type of *Cordaites* and *Mesoxylon*.

All the specimens may be referred to a single species which I have pleasure in naming *Mesoxylopsis Arberae*, sp. nov., after Dr. Agnes Arber, F.L.S., who has so kindly aided in the determination of seeds associated with the shoots described in the present paper.[1] The characters of the species are those of the genus. In the specimens observed the pith is relatively small, not exceeding 6 mm. in diameter.

CONCLUSION.

In the first part of the paper the structure of the fertile shoots of *Mesoxylon multirame* is described. They are found to be identical with the axillary shoots, which have been known since the first discovery of the species.

[1] See below, p. 18.

The fertile shoot is bilaterally symmetrical; it consists of a naked main axis, containing a flattened stele, and bearing distichously arranged bud-like branches, lying in the plane of the major axis of the main shoot. Each branch has a cylindrical, medullated stele, and bears numerous spirally arranged bracts, with a single vascular bundle of mesarch structure. A large bract, lying outside the others, may probably be the prophyll of the branch. In one case an appendage, apparently of a different kind, was observed, which might possibly be the pedicel of a seed.

In general morphology, and in the detailed organization of the lateral buds, the fertile shoots show a close agreement with the distichous forms of *Cordaianthus*, described by Grand'Eury, Renault, and Bertrand, and are clearly of the same nature. The sex of the inflorescence has not been determined, as no reproductive organs are attached, but the probability is in favour of its having been a seed-bearing organ. It is associated with the seeds named *Mitrospermum compressum* by Dr. Agnes Arber.

Two shoots of a different kind are then described, which appear to have been of the nature of vegetative buds, for their structure is that of a stem, and they bear closely packed polydesmic leaves, of a Cordaitean type. The leaf-traces of these shoots are single where they traverse the wood, only dividing in the cortex. These shoots also are associated with seeds of *Mitrospermum compressum.*

Lastly, two larger stems of the *Mesoxylon* type are recorded, in which the leaf-traces are likewise single in passing through the wood. These stems and the bud-like shoots are placed together in a new genus, *Mesoxylopsis*, differing essentially from *Mesoxylon* in the leaf-trace being single and not double. The one known species is named *Mesoxylopsis Arberae.*

The equally intimate association of *Mitrospermum compressum* with the *Cordaianthus* of *Mesoxylon multirame* on the one hand, and with the bud-like shoots of *Mesoxylopsis Arberae* on the other, raises grave doubts as to the value of the evidence from association, always so uncertain in palaeobotany, and doubly treacherous among the crowded and intermixed fragments of the coal-ball petrifactions. It was, however, clearly desirable to ascertain whether the seeds of the two categories were in fact specifically identical. Dr. Agnes Arber, F.L.S., to whom I have submitted sections showing the seeds associated with both kinds of shoots, kindly allows me to quote her opinion, as follows: 'The sections of the seeds *all* seem to me to be typical *Mitrospermum compressum*, and I see no reason for separating those in the three slides in which they are associated with *Mesoxylon multirame.*' At the same time Dr. A. Arber calls attention to a remark in her preliminary note on this seed (A. Arber, 1910, p. 393): 'There is sufficient variation among the specimens, both in dimensions and structure, to suggest that *Cardiocarpon* [now *Mitrospermum*] *compressum*, instead of

being a single species, may possibly represent an assemblage of seeds belonging to closely allied plants.'

It is therefore not impossible that seeds of the *Mitrospermum compressum* type, at present indistinguishable from one another, may have been borne both by *Mesoxylon multirame* and *Mesoxylopsis Arberae*. But, in the existing state of our knowledge, we are not justified in making any such assumption, and the significance of the evidence from association in the two cases is at present quite doubtful. Considering, however, that the fertile shoots of *Mesoxylon multirame* have now been shown to agree in morphology and structure with a *Cordaianthus*, it is highly probable that the platyspermic seeds associated with them may have really belonged to the plant.

The genus *Diplotesta*, to which Bertrand referred the ovules of his *Cordaianthus* (Bertrand, 1911), appears to be closely allied to *Mitrospermum* (Brongniart, 1881, Pls. XIII and XIV; Bertrand, 1907), and the latter genus is in every respect a seed of the type which there is good reason for attributing to the Cordaitales (see Seward, 1917, pp. 332–56).

The main result of the present investigation is, however, the proof that *Mesoxylon multirame* bore a *Cordaianthus* in all respects comparable to the inflorescence of *Cordaites*. The close affinity of the two genera and the definite location of *Mesoxylon* in the family Cordaiteae are thus securely established. There is little doubt that the new genus *Mesoxylopsis* is of like affinities, but further evidence is needed before its exact position can be determined.

While the evidence from association with seeds has proved too uncertain to be relied on, great credit is due to Mr. James Lomax for calling attention to the shoots described in the present paper. In the case of the fertile branches of *Mesoxylon multirame* his conviction of their 'fructiferous' nature has been fully confirmed.

The photographic illustrations to the present communication are the work of Mr. W. Tams of Cambridge. The drawings, both the text-figures and those in the plate, are from the pencil of Mr. G. T. Gwilliam, F.R.A.S. To both these gentlemen I desire to return my thanks for their skilful aid.

References.

Arber, Agnes (1910): A Note on *Cardiocarpon compressum*, Will. Proc. Cambridge Philosophical Soc., vol. xv, pt. v, p. 303.

——— (1912): On the Structure of the Palaeozoic Seed *Mitrospermum compressum* (Will.). Ann. Bot., vol. xxiv, p. 491.

Bertrand, C. E. (1907): Les caractéristiques du genre *Diplotesta* de Brongniart. Bull. de la Soc. Bot. de France, 4e série, tome vii, p. 389.

BERTRAND, C. E. (1911): Le Bourgeon femelle des *Cordaites* d'après les préparations de Bernard Renault. Bull. de la Soc. des Sciences de Nancy, p. 1.

BRONGNIART, A. (1881): Recherches sur les Graines fossiles silicifiées. Paris.

GRAND'EURY, C. (1877): Flore carbonifère du Département de la Loire et du Centre de la France. Paris.

MASLEN, A. J. (1911): The Structure of *Mesoxylon Sutcliffii* (Scott). Ann. Bot., vol. xxv, p. 381.

RENAULT, B. (1879): Structure comparée de quelques tiges de la Flore Carbonifère. Nouvelles Archives du Muséum, tome ii, 2e série, p. 215.

SCOTT, D. H. (1912): The Structure of *Mesoxylon Lomaxii* and *M. poroxyloides*. Ann. Bot., vol. xxvi, p. 1011.

——— (1918): The Structure of *Mesoxylon multirame*. Ann. Bot., vol. xxxii, p. 437.

SCOTT, D. H., and MASLEN, A. J. (1910): On *Mesoxylon*, a New Genus of Cordaitales. Preliminary Note. Ann. Bot., vol. xxiv, p. 236.

SEWARD, A. C. (1917): Fossil Plants, vol. iii. Cambridge University Press.

EXPLANATION OF PLATES I–III.

Illustrating Dr. Scott's paper on the Fertile Shoots of *Mesoxylon* and an Allied Genus.

The photographic figures require to be examined with a lens.

PLATE I.

Photographs by Mr. W. Tams.

Figs. 1–6. Fertile shoots of *Mesoxylon multirame*.

Fig. 1. Transverse section of the fertile shoot shown in Text-fig. 1; at A is a detached branch with bracts, and at B the bracts of another branch. × about 7. S. 2783.

Fig. 2. Another detached bud, transverse, with numerous bracts, *br.*, and a large appendage, *ap.* × 22. S. 2785.

Fig. 3. Vascular bundle of the appendage in Fig. 2, showing the central protoxylem, *px.* × about 200. S. 2785.

Fig. 4. Part of transverse section of a stem of *M. multirame*, accompanied by a fertile shoot. x^2., secondary wood of the stem; *ax.*, an axillary stele of the same; *F.S.*, main fertile shoot; *b.*, branch attached to it. × about 8. S. 2564.

Fig. 5. Another transverse section of the same fertile shoot; *F.S.*, main shoot; *b.*, large hastate branch attached to it. × 17. S. 2568.

Fig. 6. Another fertile shoot in obliquely transverse section. *F.S.*, main shoot, with narrow stele; *b.*, large branch attached to it, with bracts. × about 10. S. 3040.

Figs. 7–9. Shoots of *Mesoxylopsis Arberae*.

Fig. 7. Shoot in transverse section. *p.*, pith, apparently discoid. $l.t.^1$, single leaf-trace passing through wood; $l.t.^2$, leaf-trace forking in cortex; *l.b.*, leaf-base with numerous bundles; *l.*, leaves surrounding shoot. × about 8. S. 2598.

Fig. 8. Next section of the same shoot. *p.*, pith, as before; *l.t.*, leaf-trace beginning to fork; *l.b.*, leaf-base expanding into lamina on either side; *l.*, leaves surrounding shoot. × about 8. S. 2599.

Fig. 9. Lower part of another shoot in transverse section. *st.*, centre of stele, with small solid pith and very unequal wood in which two single leaf-traces are seen; *l.b.*, one of the leaf-bases. × 17. S. 3017.

PLATE II.

Photographs by Mr. W. Tams.

Fig. 10. From a higher section of the same shoot as Fig. 9, showing the enlarged stele and surrounding tissues. *p.*, the large, solid pith; *l.t.*, a single leaf-trace passing through the wood. × about 15. S. 3019.

Figs. 11–14. Stem of *Mesoxylopsis Arberae.*

Fig. 11. General transverse section. *l.t.*[1], single leaf-trace starting from the pith; *l.t.*[2], another leaf-trace; *c.*, remains of cortex. × about 7. S. 2983.

Fig. 12. The leaf-trace, *l.t.*[1], from Fig. 11 and neighbouring tissues, more magnified. *x.*[1], centripetal xylem of leaf-trace. × about 50. S. 2983.

Fig. 13. General transverse section of another stem, showing rings of growth. *p.*, more or less solid pith; *l.t.*[1], *l.t.*[2], single leaf-traces passing through wood. × about 4. S. 2993.

Fig. 14. The leaf-trace, *l.t.*[1], from Fig. 13 and neighbouring tissues more magnified; *x.*[1], centripetal xylem of leaf-trace. × about 50. S. 2993.

Figs. 15, 16. *Mitrospermum compressum.*

Fig. 15. Transverse section of seed. *sa.*, sarcotesta; *sc.*, sclerotesta; *pr.*, prothallus, a delicate, imperfectly preserved tissue, filling the megaspore. × about 16. S. 2781.

Fig. 16. Part of obliquely transverse section through upper part of a seed. *sc.*, sclerotesta; *p.c.*, the pollen-chamber, in which four large pollen-grains, *p.g.*, are contained. × 125. S. 2787.

PLATE III.

Mesoxylon multirame.

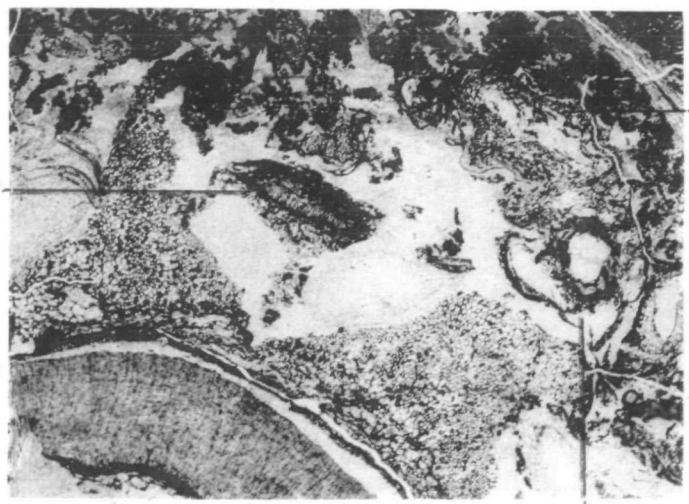
From drawings by Mr. G. T. Gwilliam. All are from the section shown, as a whole, in Text-fig. 1.

Fig. 17. The branch B of the fertile shoot, in approximately transverse section. *st.*, stele of branch; *br.*, a free bract; *ap.*, appendage; *br.s.*, bract, apparently subtending the appendage. × about 30. S. 2781.

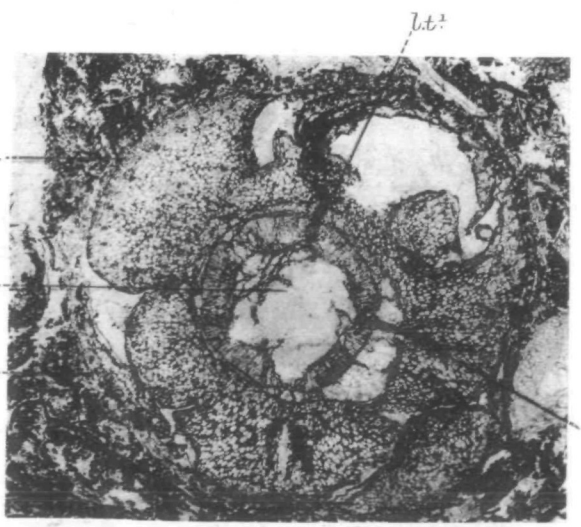
Fig. 18. Part of stele of fertile shoot, transverse. *x.*[1], apparent primary wood; *x.*[2], secondary wood. × about 170. S. 2781.

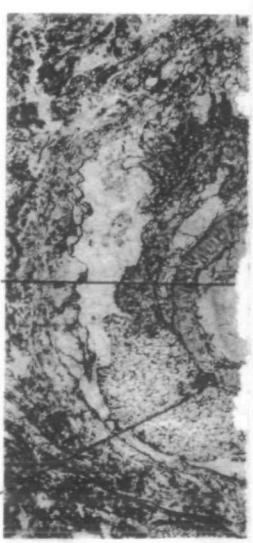
Fig. 19. Part of fertile shoot, at A end, transverse. *st.*, portion of main stele; *st.b.*, stele of a branch; *v.b.*, distal bundle. × about 60. S. 2781.

1.



4.

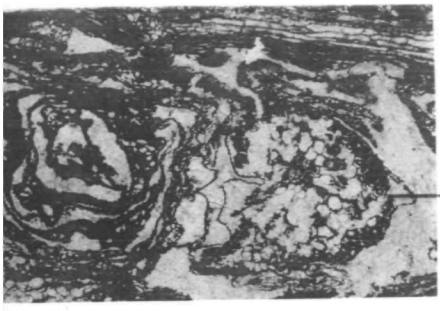




7.

Tams, phot.

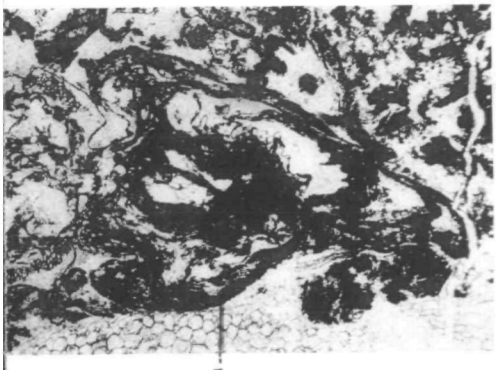
SCOTT — MESOXYLON AND MESOXYLOPSIS.



2.

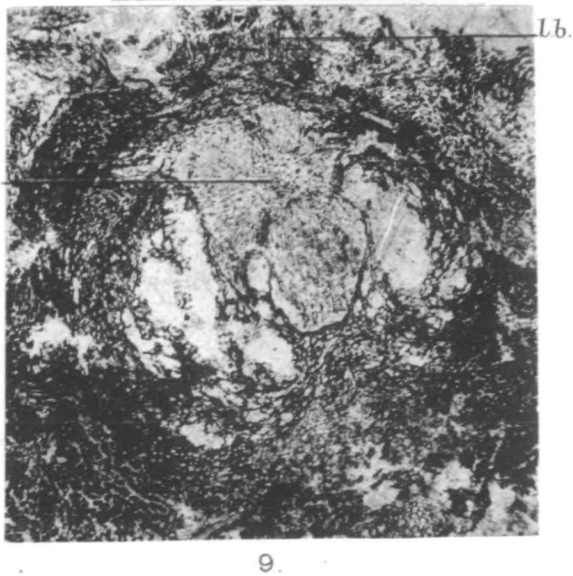
3.

6.



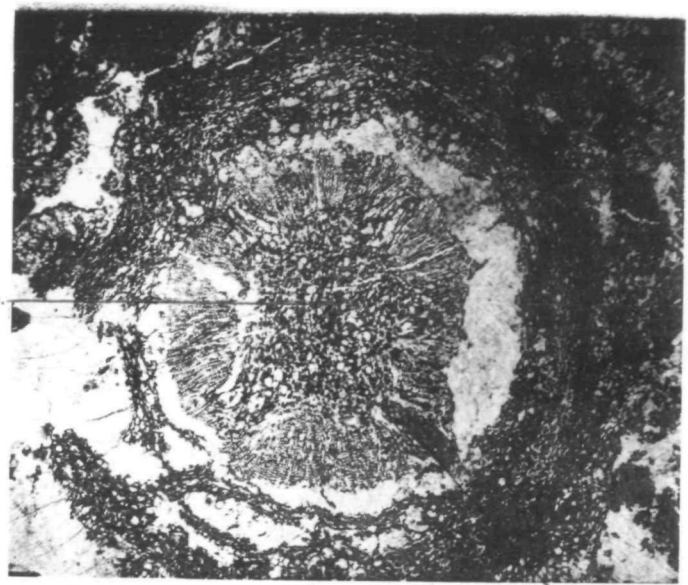
5.

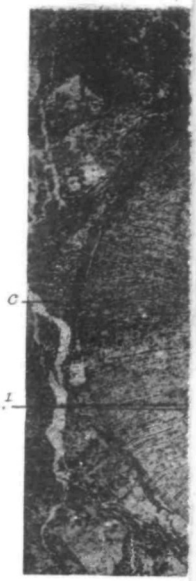
8.



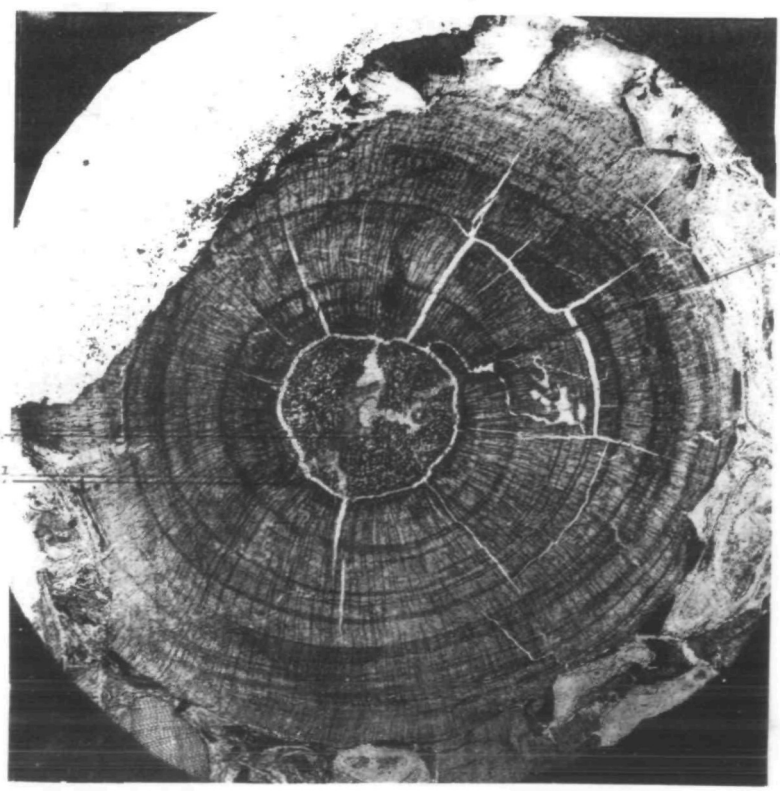
9.

Huth, coll.





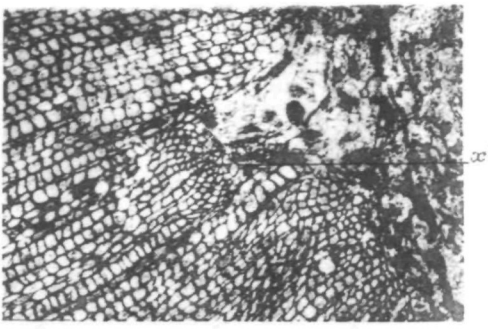
10.



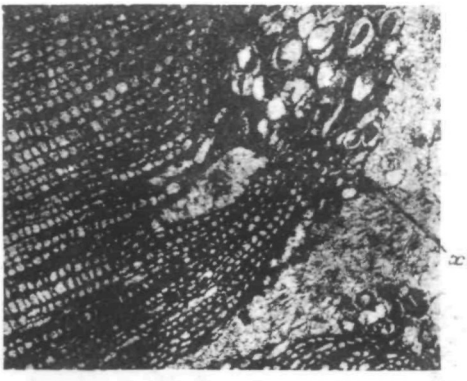
Tams, phot. 13.

SCOTT – MESOXYLOPSIS AND MITROSPERMUM.

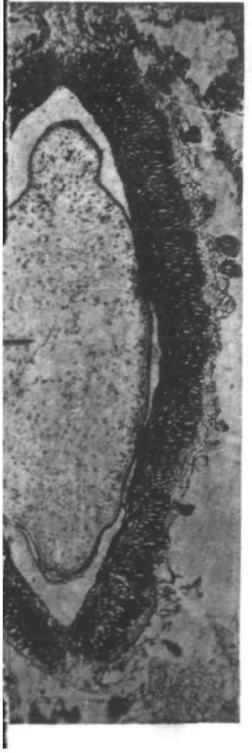
11.



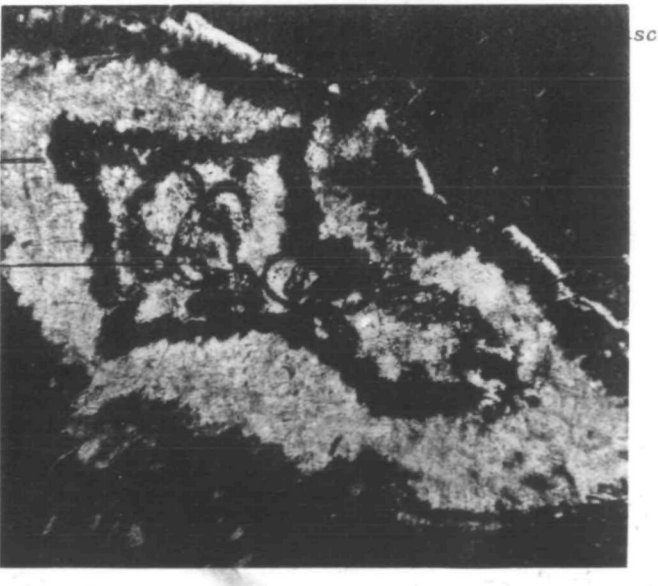
12.



14.

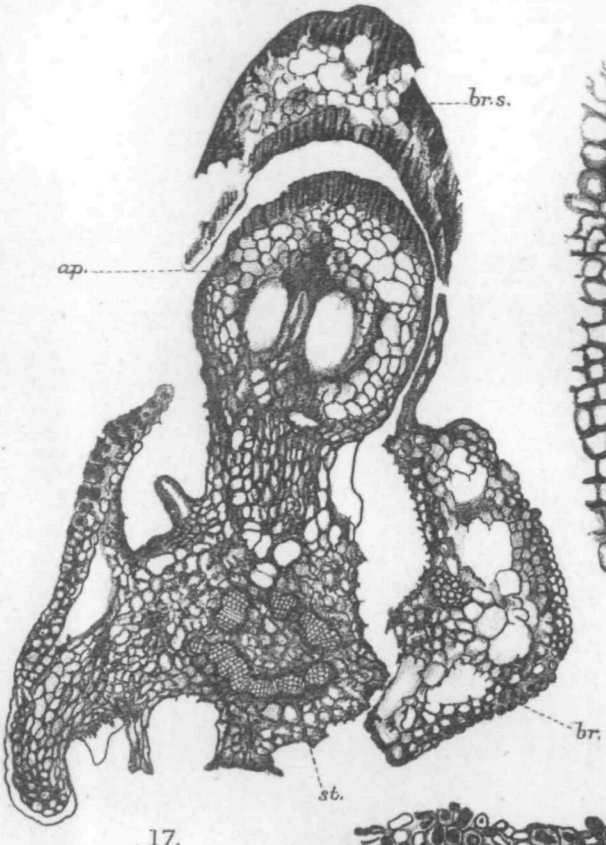


15.

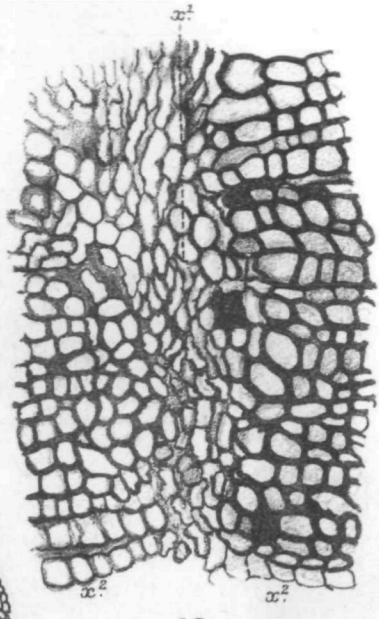


16.

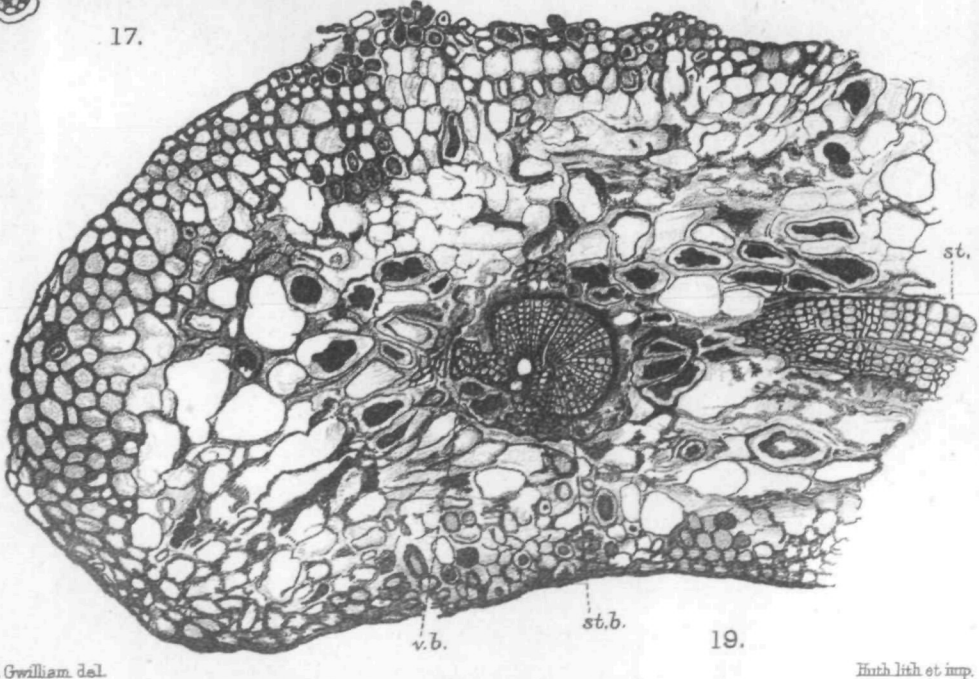
Huth, coll.



17.



18.



19.

G.T. Gwilliam del. Huth lith et imp.

SCOTT — MESOXYLON.