ON A BRANCHED CONE OF EQUISETUM MAXIMUM

BY

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Abnormally branched cones of *Equisetum* have often been recorded. (cf. Allen (1), Kashyap (4), Stiles (7)). The main interest attaches to the presence in these, of vascular strands in the pith of the main cone-axis. Stiles (7) recorded these medullary strands in his material as never exceeding three in any transverse section. More recently Browne (2) found these medullary strands in three of her specimens, but the utmost development she described was the presence of two such medullary strands.

The strobilus of *Equisetum Maximum* kindly given to me by Professor A. C. Seward for investigation was one of the two specimens obtained from the Cambridge Botanic Gardens. In view of the fact that the medullary strands in this specimen were far more extensively developed than hitherto described for any specimen, I hope the following note may serve some useful purpose.

Plate I, Fig. 1 shows the strobilus in question about 2 3 natural size. The length of the fertile region above the annulus was about 5 c.m. Above the middle region of the cone are given off five small lateral branches from the main cone-axis which overtops them. In the other specimen seven such lateral branches were given off. These lateral branches as well as the main cone-axis bore peltate sporangiophores on all sides. Below the branched region of the strobilus the arrangement of these sporangiophores in more or less regular whorls could be easily made out but in the branched region the whorled arrangement is far less conspicuous.

After removal of the sporangiophores from the branched region, a prominent fissure was noticed at the fork between the branches and the main cone-axis. This may have been due to the rapid growth and elongation of the sporangiophores on the branches and the main cone-axis pressing each other away and thereby tearing the tissues at the angle. It is also very likely that the fissure may mark a region of wounded tissue, in the young strobilus, which later growth has considerably accentuated. If so the branching of the cone may have been the result of wounding, which also probably accounts for the one-sided disposition of the branches.

There are no records of such branched cones in fossil forms. It is thus unlikely that the branched cones in the recent genus has any strong claims to be considered phylogenetically as a reversionary character.

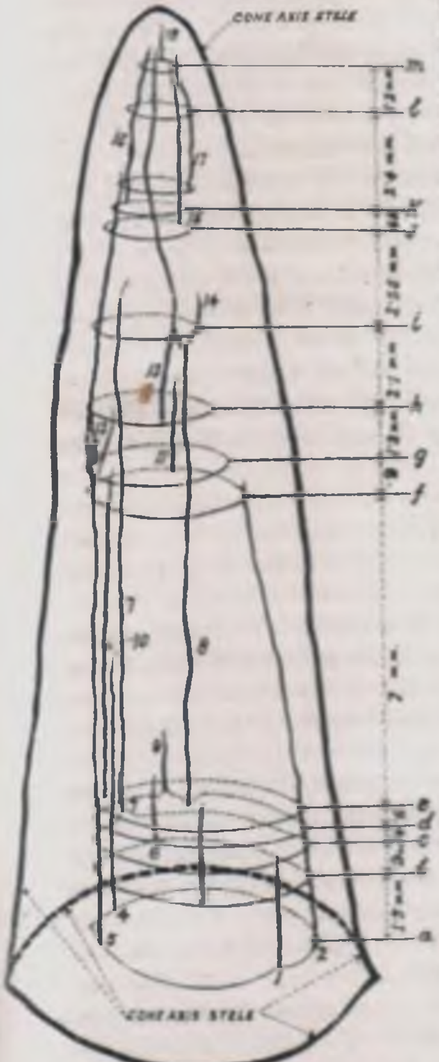
The branches are given off very near each other at slightly different levels. The first branching seems to be due to the cone-axis dividing into two more or less equal parts. The fissure noted above occurs at the angle between these two branches. The stele of the main cone-axis becomes elongate ellipsoidal with a slight constriction at the place where it is going to snap off into two. The resulting steles are about equal in size and roughly U-shaped, with the gaps facing each other. These gaps are soon filled up and two complete independent steles result. One of these, which is slightly the smaller, belongs to the main cone axis which continues unbranched.

The other branch soon forks again in a manner similar to that described above. One of these again divides unequally into two: the stele becomes elongate elliptical and snaps off, giving two unequal U shaped strands with the gaps facing each other. These gaps soon close up. There was no constriction noted in the elongate stelar cylinder marking the line of division. Another interesting feature noted here is that just before these steles have become continuous by the closure of the gap, each gives off a trace from its adaxial side (i.e. the adjacent sides which possessed the gaps). The two traces 'fuse' into one and the resultant double trace goes to supply a single sporangiophore situated at the angle between these two branches.

The other branch behaves in a curiously different manner. Here the steles become much more elongated and flattened and this whole elongate stele divides almost simultaneously into three pieces: one median and two laterals. Constricted necks at the points of division were present.

From what is stated above, it will be seen that the first two cases of branching were of the dichotomous type. In the third case it seems to be a possible case of trichotomy or it may be that one of the branches of the forking soon forks again thus giving three branches from practically the same level. From the single cone at my disposal it is impossible to be certain of the general state of affairs, yet the above brief description of the branching, as it occurs in this cone may be of some use to one having the opportunity and material to carry on a more detailed investigation.

ANATOMY. The anatomy of the upper half of the cone was studied through serial microtome sections. As recorded by Stiles (7) and Browne (2), in my specimen also, only the main cone-axis possessed the medullary vascular strands. Text-fig. 1 represents a magnified (6x) and a semidiagrammatic longitudinal reconstruction of the course of these medullary strands present in my specimen. The broad thick boundary lines of the figure represent the inner periphery of the cone-axis stele. The medullary strands are num-



TEXT FIG 1.

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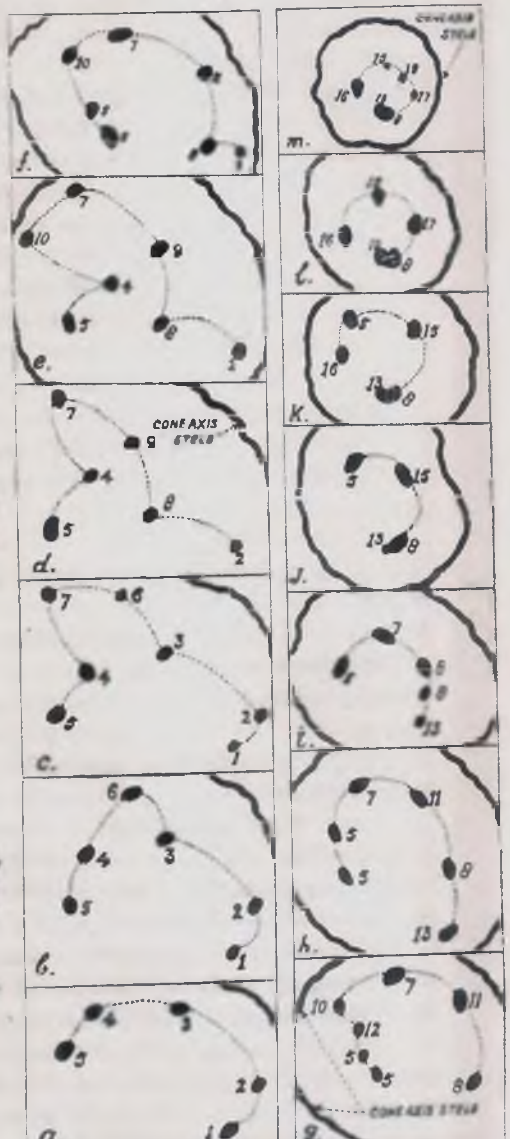

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Fig. 1. Diagrammatic longitudinal reconstruction of the internal system of medullary strands. × *ca* 6.

Fig. 2 (a-m). Camera lucida sketches of transverse sections at the levels indicated in Text-fig. 1. The medullary strands are here shown by the circular shaded areas. The dotted lines are merely to indicate their arrangement in an inner ring. × *ca* 6.

bered in the order in which they appear, except in the case of the first five, all these being present in the last possible section downwards. They are thus numbered indiscriminately without any knowledge as to their exact sequence of appearance. The relative disposition of the medullary strands with reference to one another and the various levels of their origin, are indicated in the figure by the elliptical rings formed of dotted and continuous lines: the portion marked with continuous lines represents the near half while that marked with dotted lines represents the far half of the medullary stele. Thus the position of any medullary strand, whether originating on the proximal or distal half of this internal secondary stele, can be easily ascertained. The actual distance between any two levels indicated by the rings is noted in millimetres on the righthand side of the diagram. Also since these levels have been selected at regions where one or more medullary strands originate, the length and the level of origin of any medullary strand can be easily determined (the diagram being scaled at 6x).

It must be noted that in this longitudinal representation it was found difficult, without introducing further complications, to indicate the variations in the transverse width of these medullary strands at different levels in their upward course. This transverse width on the other hand, is shown much reduced in this longitudinal reconstruction. It was also found difficult to convey from this diagram an exact idea of the position of these strands in the pith. However, for a more exact knowledge in this regard, the reader should refer to text-fig. 2 which represents camera lucida sketches of transverse sections at the various levels indicated in text-fig. 1. The shaded areas represent the medullary strands, while the thick line on the periphery—partly or fully shown—represents the inner periphery of the main vascular cylinder of the cone-axis. The dotted lines in between and joining these strands are put in to show more clearly the position of these strands on an inner ring which is distorted in the lower regions by the presence of extensive cavities in the pith.

It will be seen from the text-fig. 2, a-m, that Stiles' suggestion regarding the arrangement of these medullary strands in an inner ring is fully confirmed. It is also to be seen that there arise in the pith as many as 18 such strands which run for various distances and then die out without any noticeable connection with the strands of the axial stele, neither in the upward nor in the downward direction. In regard to the first five strands my sections do not go down far enough to show the end of even one of them. Below the level of the sections figured the pith was very much hollowed out and the whole cone-axis was completely fistular. It is thus difficult to say anything definitely about their mode of ending downwards but from what was seen for the remaining 13 strands it seems fairly certain that the first five strands were no exceptions and that they also ended blindly. The actual lengths of these vertical medullary strands are as follows :—

No. 1 : 2.5 mm.	No. 8 : 12 mm.	No. 14 : .5 mm.
No. 2 : 11 mm.	No. 9 : 1.6 mm.	No. 15 : 4 mm.
No. 3 : 2.5 mm.	No. 10 : 8 mm.	No. 16 : 4 mm.
No. 4 : 6 mm.	No. 11 : 2.2 mm.	No. 17 : 3 mm.
No. 5 : 18.7 mm.	No. 12 : 1 mm.	No. 18 : 1 mm.
No. 6 : 1.6 mm.	No. 13 : 2.5 mm.	
No. 7 : 13 mm.	No. 13/8 : 7 mm.	

It will be seen that some of the strands have a considerable length. Hitherto the greatest length recorded for these strands is that by Browne (2) who found one of them in her specimen to run a distance of 5 mm. The actual length of these strands in Stiles' specimen is unknown. It will be seen from the above table that the strand numbered 5 runs a distance of 18.7 mm. and that six of these strands exceed 5 mm. in length.

On the whole, these medullary strands follow an approximately straight course in the upward direction. That they are not exactly vertical has already been recorded by Browne (2). These strands being found now on the radius of one axial bundle and now on that of another in successive transverse sections. In this my observations quite agree with hers.

Branching and anastomosing amongst these medullary strands is not uncommon. A case of branching is recorded by Browne (2) where the strand gives off a small branch and continues for some distance before dying out. A similar case is seen in my specimen. In text-fig. 2 e, the bundle marked '5' has in figure 'f' divided into two. One of the two branches soon ends slightly above the level 'h' (text-figs. 1 and 2), while the other continues its course for a much longer distance.

The same division into two is seen for the strand numbered 8 in tex-fig 2. 'i'. One of the branches soon ends and is very likely connected with the short strand numbered '14' which originates at this level. The other branch of strand numbered '8' fuses up with the medullary strand No. 13 (text-fig. 2, 'j') and this compound vascular bundle (13/8 or 8/13) runs to within a short distance of the apex. These are the only definite cases of branching and anastomosing in this medullary stelar system, all the other strands of which run singly for variable distances and end blindly in both upward and downward directions.

The medullary strands wherever well-developed are seen to be very similar in structure to the strands of the axial stele, even the carinal canals being represented in some on their 'centrifugal' periphery. The xylem tracheids are few amongst the thin-walled tissue of small cells, presumably phloem and parenchyma which constitute the major part of the strand. In all the medullary strands, however, the presence of a peculiar tissue of thick-walled parenchymatous phloem-like cells was noted. This tissue, which is the first to appear and the last to die out, has already been recorded by Stiles (7) and Browne (2). My observations generally confirm those of Browne that this tissue occurs centripetally on these medullary strands thus giving the medullary strands an orientation 'inverse' to that of the axial stele bundles.

There is perhaps a mistake in Stiles' observation on these medullary strands that "on the inner side they pass gradually into the ground tissue of the pith but the side towards the periphery of the stem is generally bordered by some thick-walled parenchymatous cells." for in my material and from the observations of Browne (2), exactly the reverse seems to have been constantly true.

Plate I, Fig. 2 shows one such medullary strand inside the main stele of the cone-axis, a portion of which is also seen. The thick-walled tissue of phloem-like cells can be made out both on the medullary and the cone-axis strands. Their position is indicated by the arrows. The same medullary strand is shown highly magnified in Plate I. Fig. 3. The details are fairly clear, specially the thick-walled cells in question.

Plate I, Fig. 4 shows two well-developed medullary strands inside the main cone-axis stele, three of whose bundles are seen. The arrows represent the position of the thickwalled elements on the axial as well as on these medullary strands.

Plate I, Fig. 5 shows one of these medullary strands highly magnified. Some of the thick-walled elements are obliquely cut, thus showing them up as slightly elongated.

There is no doubt that the thick-walled elements occurring on the medullary strands are precisely the same in structure and morphology as those that occur on the main cone-axis strands. From their appearance and situation coupled with definite indications of a seriate arrangement in the constituent cells, it seems very likely that the tissue in question is of secondary origin and identical with the secondary tissue recorded for this species by Cormack (3). The cells of this tissue were seen often to contain large elongate nuclei very suggestive of a phloem tissue. Further considering that the structure in transverse sections of these medullary strands is precisely similar to that of the axial strands, it seems certain that the phloem was not lacking in these medullary strands as Stiles (7) thought probable.

It is also clear as shown in the figures that the thick-walled elements constantly occur on the inside and not on the outside of the medullary strands as was recorded by Stiles (7). It would, however, seem from Browne's observations that they may appear on the outside of these medullary strands occasionally. In my material, however, I have not come across a case like this. Browne also describes that at the inception of a medullary bundle, the thick-walled elements more or less completely surround the bundle and only gradually die out from the outside, persisting on the inner side and thus finally giving rise to an 'inversely' orientated strand. No clear case either of this type has come to my notice although in some of the smaller strands near their point of origin a slight tendency only for these thick-walled elements to surround the rest of the bundle may with difficulty be made out. Even then they never form more than a semi-circular arc as seen in transverse section.

The few tracheids which appear later than the thick-walled tissue are always placed from the beginning on the outside of the medullary strands and face the xylem of the axial stele bundles resulting in the inverse orientation referred to above.

The freedom of this internal system of medullary strands from any connection with the bundles of the main cone-axis stele has been suggestedas strongly reminiscent of the solid central mass of centripetal xylem which was very likely present in the ancestors. Dr. Scott's discovery (5) of centripetal xylem in the stem of *Calamites pettycurensis* [later referred to as *Protocalamites pettycurensis* (6)] makes the suggestion that these medullary strands are really vestigial structures, very attractive indeed. Yet, as has been shown by Browne (2), the cone of *Equisetum maximum* has a much reduced vascular system and the development of these medullary strands may thus easily be a secondary one in response to the need of better conducting facilities in a species with fairly large sized cones. These secondary conducting strands would be perhaps of some advantage, at least in cases where the cone-axis is branched abnormally, and this may possibly explain why these medullary bundles are constantly associated with such abnormally branched specimens or extra large sized cones.

Thus the association of the medullary strands with cases of abnormally branched cones (a condition which probably is not a primitive one), the similarity in their structure to the normal bundles of the cone-axis stele, their inverse orientation and possession of secondary tissue and their arrangement in an inner circle, are all very likely features which are cœnogenetic rather than pallingenetic and are merely to be related to the abnormality obtaining in such cases.

In conclusion I have to offer my sincere thanks to Professo A. C. Seward, Sc.D., F.R.S. and to Dr. H. H. Thomas, Sc.D., for their continued guidance, assistance, and encouragement throughout the investigation which was carried out at the Botany School, Cambridge. I am also indebted to Professor B. Sahni, D.Sc., Sc.D., for his kindly revising the manuscript and for valuable advice and criticisms.

Explanation of Plate Figures.

Fig. 1.—*Equisetum maximum* :—The abnormally branched cone about ½ natural size. The line across indicates the level above which sections were cut.

Fig. 2.—*Equisetum maximum* :—A section microphotographed showing a medullary strand and part of the axial stele. × *ca* 90.

Fig. 3.—*Equisetum maximum* .—The medullary strand from Fig. 2. × *ca* 450.

Fig. 4.—*Equisetum maximum* :—Another microphotograph showing two medullary strands and part of the axial stele. In the medullary bundle marked (1) note the seriation of the elements. × *ca* 90.

Fig. 5.—*Equisetum maximum* :—One of the medullary strands from Fig. 4. × *ca* 450.

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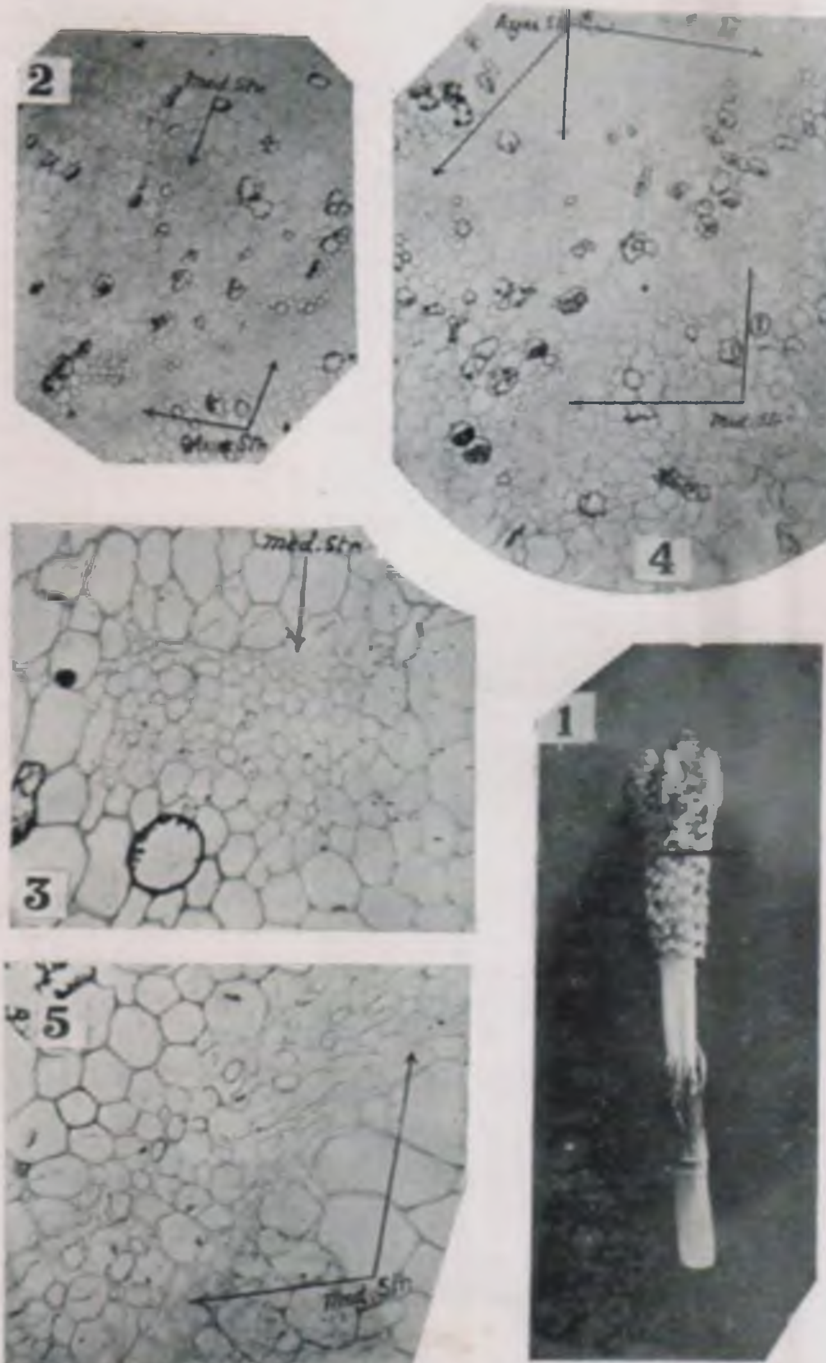

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