Contributions to our Knowledge of the Anatomy of the Cone and Fertile Stem of *Equisetum*.

BY

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With Plates LXIV and LXV and ten Figures in the Text.

HISTORICAL SUMMARY.

IN 1864 appeared Duval Jouve's 'Histoire Naturelle des *Equisetum* de France'; this work contained many new and important researches and also gave an excellent summary of the earlier literature concerning the Equisetaceae. In 1865 Milde published his 'Monographia Equisetorum'; in 1867 appeared Pfitzer's account of the structure and distribution of the endodermis in the German species of *Equisetum*; this paper also contains excellent anatomical observations. In 1876 Famitzin and Janczewski, working independently, published more correct accounts of the branching of *Equisetum*; the following year appeared a short paper by Tomaschek, and in 1878 one by Sadebeck on the embryology of the genus. In 1886 Goebel published a short note on the cones of the Horsetails, and in 1888 Buchtien gave a detailed account of the prothallus and young sporophyte. The same year Müller published an account of the leaf-sheaths of the Equisetaceae, written almost entirely from the point of view of resistance to mechanical strains and tensions. In this year, too, Van Tieghem and Douliot treated of *Equisetum* in their paper on the origin of endogenous members, and in 1890 Van Tieghem published additional observations on the endodermis in the genus. Two years later Leclerc du Sablon described the structure of the tubers, and in the following year Cormack investigated the nodal structure of *Equisetum*, describing what he believed to be secondary xylem. In 1893 Bower, in the first of his papers on the Morphology of the Spore-producing Members, dealt with certain features of the Equisetaceae. Campbell's 'Mosses and Ferns', published in 1895, gave a general account of the group, while in 1899 Jeffrey published a paper dealing in detail with the structure and affinities of the genus. In 1901 Gwynne-Vaughan, in a short communication, suggested a fresh interpreta-

tion of the Equisetaceous bundle; in 1902 a general account of the Equisetaceae was given by Sadebeck in Engler and Prantl's 'Natürliche Pflanzenfamilien'; the same year appeared Chauveaud's account of the anatomy of the root, while the next year the origin and affinities of the Equisetaceae were discussed by Lignier. In 1905 the affinities of the genus were considered by Campbell, and in 1906 Sykes recorded peculiar nodal tracheides in a specimen of *E. maximum*. In 1907 appeared Queva's important paper on the stem and leaf of *Equisetum* and also a short note on the sporangium by Hawkins, while next year was published a second edition of Campbell's 'Mosses and Ferns'. The year 1908 also witnessed the publication of Bower's 'Origin of a Land Flora', in which *Equisetum* is treated at some length, and of Halle's account of the Mesozoic Equisetaceae of Sweden. In the next year Eames published a paper dealing with the anatomy of *Equisetum*, and Jeffrey discussed this subject in a paper entitled 'Are there foliar gaps in the *Lycopsida*?' In this year, 1909, there also appeared a short account of fossil Equisetaceae by Fritel and Viguiier, and a note by Stiles on the anatomy of a branched cone of *Equisetum maximum*. In 1911 Ludwigs published an account, largely biological, of the genus, while in 1912 Vidal dealt with the segmentation of the apical cell and the early stages of anatomical differentiation in *E. palustre*.

MATERIAL.

The present investigations were confined to the cone and the upper part of the fertile stem in three British species of *Equisetum*: *E. arvense*, *E. palustre*, and *E. limosum*. In the case of the first species two complete cones, henceforward termed A and B respectively, were cut into continuous series of transverse sections. Cone A was very young; it was dug up in October and would, therefore, have remained another five months underground. Nevertheless, the xylem of the cone was almost completely differentiated; this series of sections extended downwards below the cone and included four of the vegetative nodes. Cone B was more or less mature, and the series of sections below it only extended to beneath the annulus. Of a larger cone, C, serial transverse sections were made from below the annulus through the lowest seven whorls of sporangiophores. To confirm the phenomena observed in Cones A and B the upper parts of two cones, D and E, were cut serially; the latter cone, though otherwise normal, had two annuli; satisfactory series through this region of the cone could not, however, be obtained. Another cone, F, also had two annuli, and of this specimen a continuous series of sections extending from below the lower annulus through the three basal whorls of the cone was prepared. The transitional region from below the annulus through the basal whorl of the cone was also studied in two cones: in a very large one, G, the diameter of

the stele of which was about $2\frac{1}{4}$ mm., and in a smaller cone, H. Another cone, I, was cut serially into longitudinal sections. As regards *Equisetum palustre*, a cone which I shall term Cone A was cut serially from above the uppermost vegetative whorl into transverse sections; serial sections extending to below the annulus were made of another cone, B. Of another cone, C, serial sections extending from below the annulus to a point just above the second whorl were made. Cone D, a very small and young cone of the variety *polystachion*, was also cut into serial transverse sections, the series including the uppermost whorl of leaves. Serial longitudinal sections through the base of a young cone were also made.

In the case of *E. limosum* a complete young cone, A, was cut into serial transverse sections; these extended downwards to the uppermost vegetative whorl, but did not include quite the whole thickness of the nodal xylem. The whole of a still younger cone, B, with the uppermost vegetative whorl beneath it, was cut up serially into transverse sections. Another series of transverse sections extended from below the uppermost leaf-sheath through the lowest five nodes of an older and much larger cone, C. For all the three species the results obtained were confirmed by numerous longitudinal, transverse, and oblique hand-sections through different cones.

THE CONES OF *E. ARVENSE* AND *E. PALUSTRE*.

The xylem in the cone of *E. arvense* is relatively much developed compared with that of the cone of *E. limosum*; *E. palustre* is intermediate in this respect between these two species. Taking first *E. arvense* we find that below the basal fertile whorl, but some little distance above the insertion of the annulus, the strands of xylem lose the appearance of typical internodal bundles of the vegetative region. The two lateral groups of metaxylem become united by a curved band of tracheides and the carinal canals begin to diminish in size. This curved band of xylem is several cells thick in a radial direction and its concavity at first faces outwards; its ends, continuous downwards with the lateral bands of metaxylem, project like them slightly beyond and externally to the phloem. The latter also forms a slightly curved band, the concavity in this case facing inwards, so that the phloem lines the interior of parts of the pericycle. As we approach the fertile node the band of xylem straightens out and eventually it comes to form a band slightly curved in the reverse direction, so that the xylem assumes the same contour as the phloem and the stele generally. Meanwhile, the xylem of each bundle begins to narrow in a radial direction, though it may still be locally three to five cells thick. As a rule, too, as we approach a node the xylem of a bundle begins to spread laterally towards the xylem of its neighbours. Generally, many of the bundles of the cone of *E. arvense* become united in the nodal regions by the formation of fresh tracheides; usually these develop in continuity

with the xylem-elements of one or both bundles, until these bundles, spreading towards one another, unite a little higher up; but occasionally an island of tracheides first makes its appearance in the parenchyma between two of these widening strands, and the tracheides of the island increasing in number as we pass upwards, the island becomes united higher up to the neighbouring xylem-strands. In this case the island figures, in a longitudinal reconstruction of the xylem, as a small downward projecting tooth. Such 'interfascicular' xylem has at first no phloem outside it; it not infrequently occupies a slightly more peripheral position than the xylem of the internodal strand. But as we pass upwards phloem very soon makes its appearance; and when this has happened, and when the interfascicular tracheides have joined on to those of the internodal strand (from which they are indistinguishable in form), we get perfectly uniform bands, or in some cases a perfectly uniform ring of xylem. These bands or this ring of xylem is in most parts but one or two cells deep, though locally there may be three or even more cells on the same radius; moreover, in a good many places there are internally to the bands or ring isolated tracheides or little groups of tracheides, usually of small size; these may abut on the bands or ring of xylem, especially where these are relatively thick in a radial direction, or they may be separated from them by as many as three or four parenchymatous cells. Such tracheides or groups of tracheides do not as a rule persist for any considerable distance in a vertical direction; in the internode they occur also internally to the separate strands of xylem (cf. Pl. LXIV, Fig. 3). Some little way above the departure of the xylem of the traces these bands or rings of wood found at the nodes break up, portions of the band or ring ceasing to develop as tracheides. The narrow parenchymatous bands thus formed widen rather rapidly and constitute the parenchymatous meshes seen in a longitudinal reconstruction of the xylem (Text-figs. 1 and 2 and Pl. LXIV, Fig. 4). These meshes are usually situated vertically above traces that have departed (in estimating the superposition of meshes to traces in a longitudinal reconstruction allowance must be made for the narrowing or widening of the diameter of the stele, which in the diagram causes a convergence or divergence of lines passing vertically upwards). A change in the number of members in the next whorl also tends to disturb the superposition of parenchymatous meshes to traces, since the xylem here breaks up into a number of strands different from the number of traces. Other irregularities will be considered later. Usually the parenchymatous meshes arise at a small distance above the traces. A glance at the reconstruction of the xylem in Cone A (Text-fig. 1) will show that the vertical height of the xylem persisting above the trace of a sporangiophore is not very different from the height of nodal xylem persisting above a leaf-trace (allowance must be made for the fact that the apical internodes of this very young cone have elongated even less than the

lower ones). But in some cases a parenchymatous mesh only makes its appearance half-way or more than half-way up the internode (e.g. the meshes appearing above the fourth trace of the first whorl, above the fourth and eighth traces of the fourth whorl, and above the third trace of the fifth whorl of Cone A). In other cases the meshes, though not originating so high up in the internode, yet made their appearance at an unusual distance above the node. In a few cases we pass from a trace of one whorl vertically upwards to the trace of the next whorl without meeting any parenchymatous tissue. Thus we get a relatively wide continuous tract of woody tissue connecting part of one whorl with a portion of the succeeding whorl (e.g. the tract of xylem extending above the fifth and sixth traces of the seventh whorl, that above the third trace of the eighth whorl, and that above the first and second traces of the tenth whorl of Cone A). The extent of such sweeps of xylem, though relatively the same, is of course actually much greater in a mature cone than in so young a one as Cone A. Such absence of one or two meshes throughout an internode is not common in any one cone; but I have found it in all specimens of which I made serial sections of any considerable portion of the cone, even in those that contained relatively little xylem. If, instead of involving one or two xylem-strands of the internode below, these sweeps of xylem extended above all the

TEXT-FIG. 1. Longitudinal reconstruction of the xylem of Cone A. The xylem of the stele has been cut in two, spread out flat. Axial xylem black; leaf-traces and parenchyma white. Magnification *circa* 16.

traces of a whorl we should have an internodal ring of wood; occasionally, when all the strands become united at the node—and this of course involves the closure of all the parenchymatous meshes of the internode below—we get a nodal ring of xylem and bast (Pl. LXIV, Fig. 1).¹ Such a local ring is present twice in Cone A, twice in Cone B, and once in Cone E; it was not met with in Cones C, D, F, G, and H, but may have occurred in them, since the series of sections did not include the whole of any of these cones. To judge from isolated hand-sections a ring of xylem occurs locally at the nodes of many cones of *E. arvense*. Milde in 1865 stated that at the level of the fertile whorl the xylem-strands become united into a ring. This is too sweeping a generalization, and curiously enough Milde figures this condition diagrammatically in *E. limosum*, a species in which I have never seen even a near approach to a ring (Milde, i, p. 162, Pl. XVI, Fig. 18).

The cases in which a parenchymatous mesh arises some distance up the internode are clearly intermediate between the forms in which the mesh arises at the usual small distance above the node and those rare cases in which no parenchymatous mesh occurs above a trace. The parenchymatous meshes of *E. arvense* do not, as a rule, attain any considerable width; they are frequently narrower, even in their widest part, which is usually in the middle of the internode, than the strands of xylem between which they pursue their course. As regards their vertical extent, by far the greater number are closed at or before the next node, and these meshes I shall, for convenience' sake, term meshes of the first order. Other parenchymatous meshes that extend into two, three, or more internodes will be termed meshes of the second, third, and higher orders. In Cone A there were 90 meshes originating above fertile whorls and closed before we reach the apex of the cone; of these 81 were of the first, 8 of the second, and 1 of the third order. Within the limits of Cone B 37 meshes originated and were closed: 33 of the first, 3 of the second, and 1 of the third order. As only seven whorls of Cone C were cut serially many of the meshes were still unclosed when the series ended; if the figures of all the meshes closed within the series of sections were given, the proportion of meshes of the first order would appear to be larger than it is in nature; for, of the meshes arising above the upper whorls, more of those of the first order would have space, so to speak, to be closed before the end of the series. But all meshes of all orders that arise above the lowest four whorls are closed before the end of the series of sections; by considering these only we may see the relative proportion of meshes of different orders in this Cone C. On this basis we find that out of 22 meshes 10 are of the first, 9 of the second,

¹ Owing to the fact that the sporangiophores are inserted at slightly different levels, all the meshes may be closed at a node and yet no *single* transverse section will show a complete ring of xylem. This tendency is increased by the fact that occasionally meshes are not closed before, but at, or even just after, the departure of the trace.

and 3 of the third order. It will easily be realized that the persistence of a parenchymatous mesh through a node is the result of a poorer development of xylem. Thus Cone C has relatively less xylem than Cones A and B. For instance, the presence of a very little more xylem between the

TEXT-FIG. 2. Longitudinal reconstruction of the xylem of Cone C of *E. arvense*. Axial xylem black; leaf-traces and parenchyma white. Magnification *circa* 12.

fifth and sixth traces of the second whorl of Cone A would lead to the division of a parenchymatous mesh of the second order into two meshes of the first order. When the xylem developed at a node is less markedly deficient, the mesh that persists appears to be sharply constricted in the nodal region; when, on the other hand, the strands show little or no

increase of xylem at the node, the mesh separating them is little or not at all constricted in this region.

Of none of the other cones were the series of sections sufficiently extensive in a vertical direction to afford useful data as to the height of the meshes; Cone E, however, seemed to have about the same relative amount of xylem as Cone C, and Cone F relatively rather less. The proportion of xylem in Cone G seemed to be about the same as that in Cones A and B. The series of sections of the other cones were too short to allow of such generalizations.

The nature of the meshes originating below the lowest whorl of sporangiophores will be considered in discussing the region transitional from cone to fertile stem.

Even a superficial glance at a reconstruction of the xylem of a cone of *E. arvense* in which the wood is relatively well developed, as it is in Cone A, gives the impression of nodal bands or a nodal ring of xylem, broken up in the internodes by meshes of parenchyma and usually broken too at the nodes by the persistence of one or two of these meshes. The cone of *E. palustre* does not give this impression. Here, too, parenchymatous meshes originate above the sporangiophore traces, but many of them persist upwards through more than one internode. Thus Cone A of this species, which had the largest proportion of xylem, had 19 meshes of the first, 9 of the second, 2 of the third, 4 of the fourth, and 1 of the fifth order; Cone B of the same species had 6 of the first, 7 of the second, 1 of the third, 1 of the fourth, 3 of the fifth, and 1 of the seventh order. Cone D of the reduced variety *polystachion* had only four whorls; it had one mesh of the first, one of the second, and one of the third order. Besides these, other meshes originating below the sporangiophores, and therefore below the cone proper, persist through one or more internodes of the cone; they are relatively more developed in Cones B and D, which have less xylem than in Cone A. Their nature will be considered in connexion with the transitional region. The series of sections of Cone C of *E. palustre* was too short to afford data as to the height of the parenchymatous meshes.

In *E. arvense* the sporangiophore traces are never, except at the extremely reduced apical region of the cone, given off from the edge of a strand or band of xylem, though when a relatively wide parenchymatous mesh persists through a node, the traces of the strands abutting on it may depart from a point very near to the edge of the xylem. In *E. palustre*, however, correlated with the less vigorous development of the axial xylem, traces not infrequently arise from the edge of the strand; i. e. at their point of origin they abut on a mesh persisting through the internode, while many other traces depart from a point very near the edge of a xylem-strand (cf. Text-figs. 3 and 4). These kinds of traces may conveniently be referred to as lateral or slightly internal. Traces that depart from what is more or

less the middle of a xylem-strand may be termed median. When the internodal strands remain isolated the median position of the traces is very obvious, but when the bundles are united into bands or into a ring at the nodes, as they often are in *E. arvense*, the median position of the traces is often not so clear (Pl. LXIV, Fig. 1). Such formation of nodal bands giving off median traces also occurs in *E. palustre*, though it is not so marked a feature of this species (e.g. the band from which the third, fourth, fifth, and sixth traces of the first whorl depart in Cone A, and the band giving rise to the fifth, sixth, seventh, and eighth traces of the fifth whorl of the same cone). In reality we find three sorts of structure above median traces. Firstly, there is the form in which the xylem of the axis is most developed; here there is no mesh, and a relatively wide band of xylem persists through the internode; this type, never common, occurs in *Equisetum arvense*, and apparently in the upper part of some cones of *E. palustre*. Secondly, a parenchymatous mesh may appear above a median trace; this is by far the most widely spread form in *E. arvense*; it is very common too in *E. palustre*, especially in cones with well-developed xylem. The third form of structure is associated with a reduction of axial xylem; here the trace departs from the middle of a relatively narrow strand; this often continues its isolated course upwards, and then of course involves the persistence of meshes on either side of it; above such a trace no mesh is formed. When the meshes on both sides of a strand persist through several internodes the latter pursues an isolated course through several nodes (e.g. the strand arising between the sixth and seventh traces of the fifth whorl of Cone A of *E. palustre*). These conditions are obviously associated with poor development of the xylem. A variation in the behaviour of the strands in the internode above the departure of a median trace of this type occurs when one of its neighbours gives off a median trace of the other type, above which trace there appears a fresh parenchymatous mesh; or in other

TEXT-FIG. 3. Longitudinal reconstruction of the xylem of Cone A of *E. palustre*. Axial xylem black; leaf-traces and parenchyma white. Magnification *circa* 9.

words, when two neighbouring strands give off median traces and one forks a little higher up and the other does not. In this case one of the branches of the forking strand may fuse with the strand in which no mesh appeared. This particular variation, fairly common in *E. limosum*, seems to be very rare in *E. palustre*, where I only observed it twice. Another variation

which may occur, though rarely, in *E. palustre*, associated with a reduction in number of the strands and traces of the next node and internode, consists in the fusion of two strands, from which median traces not subtending meshes have departed, to form a strand giving rise to but one trace at the next node (e. g. the strands giving rise to the sixth and seventh traces of the ninth whorl of Cone A). In all these variations the absence of a mesh is due to poor development of xylem, and is associated with the persistence of meshes of the internode below. In the cases mentioned first the absence of a mesh is due to the unusually strong development of xylem in the upper internode, and is associated with closure of meshes of the internode below.

In *E. palustre* no fresh meshes originate above the departure of a lateral or slightly internal trace ; for though in many cases the xylem-elements superposed to the trace soon die out, the parenchyma which replaces them is laterally in contact with an adjacent parenchymatous mesh originating lower down. The relatively wide band of parenchyma resulting from the congenital fusion of a mesh with one originating lower down may, from a phylogenetic point of view, be considered as biseriate. When the meshes in the cone of *E. palustre* persist through numerous internodes they appear in longitudinal reconstruction to be widened first on one side and then on the other ; this sudden widening usually occurs above a node by the dying out of the xylem superposed to a trace

TEXT-FIG. 4. Longitudinal reconstruction of the xylem of Cone D of *E. palustre* (var. *polystachion*). Axial xylem black ; leaf-traces and parenchyma white. Magnification circa 24.

at or near the edge of one of the strands bordering on the mesh. This gives to the parenchymatous meshes of the higher orders a very sinuous outline. As in *E. arvense*, it is sometimes easy to see that the persistence of a mesh into two or more internodes is due to poor development of xylem at the nodes. For instance, the lignification of a small group of cells between the first and second traces of the third whorl and the

fourth and fifth ones of the fourth whorl of Cone A would have closed the meshes between these traces, and we should in both cases have had two meshes alternating, though somewhat irregularly, with one another. In many cases the amount of xylem present at the node, though not so great as in the two cases mentioned, yet produces a marked constriction of the mesh in the nodal region; where there is no perceptible increase of the xylem in the nodal region the mesh remains of the same width at this level. Another phenomenon, only observed once in *E. palustre*, occurs at the apex of Cone A of this species. Here two meshes originating above the tenth whorl fuse in the upper part of their course by the dying out of the strand between them. The conditions are here complicated by the fact that the strand, by the dying out of which the two meshes come into contact, is unusually wide, and gives off two traces; it is clearly one of those stretches of xylem that extend uninterruptedly through a whole internode. Allowing for the convergence of the lines of superposition of the diagram (Text-fig. 3) owing to decrease in diameter of the stele, we can see that the two convergent meshes originate above the third and sixth traces of the tenth whorl.

Another tendency when the xylem is less developed is for a parenchymatous mesh to be slightly decurrent on one side and below the trace above which it may, phylogenetically, be considered to have originated; in such a case a trace-bearing strand appears to branch just below the departure of a trace. Such a trace would have been median and have subtended a mesh had no premature branching of the strand bearing it occurred; it now appears to be lateral and adnate to one of the branches of the strand. This expression of less lignification is common in *E. limosum*, and an example of it may be noted at the eighth node of Cone A of *E. palustre*, where a mesh, apparently associated with the fourth trace, is decurrent some way below the latter and the third trace. (This mesh might at first sight appear to be between the third and fourth traces, but this appearance is due to the fact that the third trace is very nearly lateral; and as the middle line of the mesh is very nearly directly over the fourth trace the mesh presumably belongs to the latter.)

Only one clear case of the decurrence of a parenchymatous mesh was observed in *E. arvense*, and it was of a different type. The second whorl of Cone B of this species had nine traces, of which two were about half the size of the others and entered one sporangiophore. The smallness of these two traces and the fact that the whorl below and the three succeeding whorls each have eight sporangiophores indicate that we are here dealing, not with two fused sporangiophores, but with one of those cases, to be considered later, in which the first division of the vascular supply of the trace is so premature that the trace is double at its point of departure from the axial stele. Such cases of traces originating as two bundles are not rare, but this

one is exceptional in that the two bundles of the trace are not closely approximated at their point of origin, but are separated by a parenchymatous mesh; the two bundles destined to the sporangiophore do not even depart from the edges of the two strands bordering the mesh, but from points slightly internal to the edges of the axial strands. The middle line of the parenchymatous mesh when followed upwards passes midway between the two xylem-strands entering the sporangiophore; below them it only extends downwards through one-third of the internode, and its origin is clearly quite unconnected with the departure of the traces of the whorl below. The conclusion to be drawn would seem to be that here a single mesh, such as commonly appears above the two halves of a bifascicular trace, has, phylogenetically speaking, slipped down between them for a certain distance.

Quite apart from the diminution in number of the sporangiophores of a whorl, due to the narrowing of a cone at its apex, there is a certain irregularity in the number of members in successive whorls of the cone of *Equisetum* (e. g. the seventh and eighth whorls of Cone A of *E. palustre*). Moreover, traces receiving two bundles are by no means rare. Two forms may usually be distinguished. In the first case the sporangiophore receiving the two bundles is very much larger than the other sporangiophores, and obviously represents two approximated and concrescent primordia. Every stage between a complete concrescence and a merely basal fusion of the stalks can be observed with the naked eye if sufficient material is examined, especially of *E. arvense* and *E. maximum*, in which species concrescence is unusually frequent. In this form the two traces, though they usually arise markedly nearer to one another than to the neighbouring traces, are yet not closely approximated at their point of origin. In the second kind of sporangiophore that receives two traces these arise very close to one another, and the sporangiophore itself is hardly, if at all, larger than the other sporangiophores; generally either of the two traces considered by itself is markedly smaller than the other traces of the whorl. In this case we would seem to be dealing with a case in which the division of the trace is so premature that the latter actually originates as two separate strands. This interpretation is supported by the fact that a certain number of traces, though not completely divided into two bundles at their origin, were more or less deeply constricted in the middle; in this case the division of the trace, though still premature, was less markedly so. Another case intermediate between the traces that originate as two bundles and those that only divide in the sporangiophore was found in the upper part of Cone D of *E. arvense*. Here a trace originated as an already markedly constricted bundle and forked in the axial cortex before entering the sporangiophore. The latter received not only these two bundles, but another whole trace; it was thus a 'double' sporangiophore showing in

one of its two fused constituents a case of premature division of the trace. In some cases, however, it is not easy to decide if we are dealing with a rather large sporangiophore whose trace has divided prematurely, or with an exceptionally small 'double' sporangiophore. The position of the meshes in the internode above and the number of members, when constant, in the whorls above and below may afford the means of judging if we are dealing with a single or a double sporangiophore. In normal cones a bifascicular trace is more often due to premature division.

CONE OF *E. LIMOSUM*.

If we pass to a consideration of the cone of *E. limosum* we see at once that the xylem is much less developed than in *E. palustre*. Though this poorer development of the xylem is very striking it follows the same lines as the reduction of xylem in *E. palustre*. Meshes arising above traces tend to persist through more numerous internodes; they are widened laterally owing to the dying out of the xylem above lateral or slightly internal traces; they tend to 'decur' below and to one side of the traces above which they lie; meshes originating separately also become confluent by the dying out of the strand separating them. This feature, only observed once in *E. palustre* and unknown in *E. arvense*, is very common in Cone B of *E. limosum*. This cone has relatively to its size less xylem than Cone A; in the latter only two pairs of meshes originally separate become thus confluent; in both cases this confluence took place above the seventh whorl. In Cone A 31 meshes arose, and were closed within the cone; of these 13 were of the first, 7 of the second, 7 of the third, 3 of the fourth, and 1 of the fifth order; two meshes persisted unclosed to the apex of the cone, and eventually fuse above the last whorl round the terminal sporangiophore. In Cone B 12 meshes arose and were closed within the cone; 4 of the first, 5 of the second, 2 of the third, 1 of the fourth order. Ten more meshes arose above sporangiophores, but these remained unclosed; of these, one arose above the lowest whorl, and therefore persisted through all the (nine) internodes of the cone; one unclosed mesh persisted through eight internodes, two through seven, one through six, two through five, and three through four internodes. Yet another mesh was unclosed; this originated above the insertion of the annulus (cf. the account of the transitional region), and therefore persisted through the whole of the cone. These unclosed meshes become confluent with one another in a very irregular manner as we approach the apex of the cone; above the tenth and last whorl the number of independent meshes is reduced to three. But if traced downwards these three meshes have a very different history; one of them, that lying between the second and third traces of the tenth whorl of the diagram, consists only of two fused meshes extending a very long way downwards; they become confluent by the dying out of a strand that pursued an isolated course

between them through seven internodes. Each of the other two meshes, if traced downwards, is seen to be built up by numerous confluent meshes of very different lengths. Above the three traces of the uppermost whorl the

TEXT-FIG. 5. Longitudinal reconstruction of the xylem of Cone A of *E. limosum*. Axial xylem black; leaf-traces and parenchyma white. Magnification *circa* 16.

xylem dies out, and in this way the three remaining meshes become confluent round the terminal sporangiophore. The confluence of meshes distinct at their origin is not confined to unclosed meshes; it occurs, though

less commonly, between meshes that are closed before the apex of the cone is reached ; the two cases of confluence of meshes of Cone A are of this type, and another example may be seen above the insertion of the third whorl of Cone B. The reason why the confluence of unclosed meshes is commoner than that of closed meshes is that confluence means the dying out of a strand and thus reduces the number of members of the next whorl. Such reduction is, of course, especially characteristic of the upper part of the cone, and meshes arising above the upper whorls of sporangiophores have less

TEXT-FIG. 6. Longitudinal reconstruction of the xylem of Cone B of *E. limosum*. Axial xylem black ; leaf-traces and parenchyma white. Magnification *circa* 16.

chance of being closed, partly because they reach the apex of the cone if they persist through many internodes, and partly because they are continually widened by confluence with other meshes owing to the dying out of strands. Nor are these facts the only ones that indicate reduction of xylem ; the strands of xylem of *E. limosum* are much narrower, compared with the parenchymatous meshes separating them, than those of the other two species studied.

The series of sections of Cone C of *E. limosum* was too short to afford reliable data as to the height of the meshes.

The meshes originating below the cone and persisting into it will be considered in discussing the region transitional from fertile stem to cone.

It has already been shown that where a strand pursues an isolated course through a node, the absence of a mesh above a median trace—or, in other words, the failure of a strand to branch above a median trace—is an effect of poor development of xylem. This is confirmed by the distribution of this type of median trace. In Cone A of *E. limosum*, the reduction in the number of members in a whorl begins above the seventh node; in the seven lowest whorls, 31 median traces out of 40 subtended parenchymatous meshes. Similarly, the seven lowest whorls of Cone B (in which there was no definite reduction, though the number of the traces varied slightly in different whorls) showed 27 median traces, of which 21 subtended meshes. The five lowest whorls of Cone C, which showed no signs of reduction in the number of members of a whorl, had 34 traces, of which 26 subtended parenchymatous meshes. But when we consider the regions of the cone in which reduction of the number of appendages has set in, we find very few parenchymatous meshes above median traces. This region was not available in Cone C, and in Cone B the region of reduction showed no median traces of either sort; but in Cone A there were in the four uppermost whorls only three median traces subtending meshes, while above six such traces the strand pursued its course upwards without branching. As already pointed out, Cone B has relatively to its size much less xylem than Cone A; in its upper part a large number of traces depart from strands so narrow that the traces are attached to the whole width of the strand. Such traces abutting on both edges of the strand cannot be called median; but they clearly represent a further stage of reduction of the axial xylem to which a median trace not subtending a mesh is attached; in the upper part of Cone B they replace the median trace. They are not, however, confined to the upper part of the cone, and an example may be seen in the eighth trace of the second whorl. No examples of such narrow trace-bearing strands were found in the other species or in Cone A of *E. limosum*. Some parts of the latter had rather more internodal xylem than others; this may cause the closure of the meshes a little way below the node; or the greater development of the xylem may take place above the node; for instance, the third and fourth traces of the fourth whorl of this cone depart from the *edges* of a band which persists upwards through the whole of the next internode; if these two traces were median instead of lateral, the absence of a mesh above them would be due, not to the xylem being poorly developed, but to its being well developed. I have not, however, observed such a case in this species.

Occasionally in *E. limosum*, isolated strands pass through a node without giving off a trace (e. g. two of the strands in the lowest whorl of Cone A, two of the strands in the lowest whorl of Cone B, two of the strands of the third whorl, and a strand of the fourth whorl of the same cone). In such

cases, and a few occur also in Cone C, the strand that does not give off a trace is never wide, but it is no narrower than many trace-bearing strands. Such excess of strands over traces must not be confused with an apparent increase in the number of strands due to the forking of a strand above a median trace occurring a little before the fusion of one or both of its branches with a neighbouring strand or branch of a strand, or to the decurrence of a parenchymatous mesh below and to one side of what would otherwise be a median trace. This apparent increase of the strands at a node may be exaggerated by the fact that the sporangiophores of a whorl are not all inserted at exactly the same level. Thus in one transverse section just above a node of Cone C, there were twenty-five strands and parenchymatous meshes, though the number of sporangiophores in the whorls above and below was but twenty. Such apparent increase of strands is, however, strictly localized to the neighbourhood of the nodes, and the supernumerary strands, if traced upwards or downwards for any distance, soon cease to be independent strands, and may thus be distinguished from those much rarer distinct and separate strands that pass through a node without giving off a trace.

ALTERNATION AND SUPERPOSITION OF WHORLS OF THE CONE.

In *Equisetum* generally, the sporangiophores appear externally to alternate with remarkable regularity; in the young state before the internodes have elongated the shields are closely imbricated. But in internal anatomy there is throughout the three species examined no such regular alternation in the insertion of the vascular traces of successive whorls. It is obvious that when a parenchymatous mesh extends through more than two internodes, all the members of a whorl cannot be accurately superposed to those of the second whorl in a downward direction as they are when succeeding whorls alternate regularly. In fact, the greater or less regularity of alternation of traces of successive whorls depends chiefly on the regularity with which successive meshes are closed at the nodes. In cones of *E. arvense*, especially in those that, like Cones A and B, have their xylem well developed, meshes persisting through a node are in a small minority, and the traces are much more often alternate with those of the node below. Even here the alternation is liable to be disturbed by the occasional occurrence of meshes of the second and third orders; by a change in the number of members of a whorl; by the fact that sometimes, though very rarely, a mesh may originate not vertically above a trace, but at a point above and to one side of it; and by the fact that when two sporangiophores become partially concrescent, their traces tend to become slightly approximated at their point of origin. When a trace has divided prematurely into two closely approximated bundles the mesh is superposed to both, and its position is one of the means of distinguishing a case of premature division of a trace (cf. Text-fig. 2, traces 6 and 7 of the first whorl). When by a close approximation of

neighbouring strands a mesh is very nearly closed at the level of a whorl, and when a trace departs from the edge or very near the edge of one of these strands, it may alternate more or less accurately with the traces of the whorl below, despite the persistence of the mesh through the node. When a strand pursues an isolated course through several nodes (i. e. when the parenchymatous meshes on both sides of it extend upwards through several nodes and internodes) the traces which it gives off, whether lateral or median, are necessarily superposed, though not always accurately so. For when the strand is markedly wider than the traces, successive traces may depart from portions of the strand not in the same vertical line; the traces may, however, be accurately superposed, and when the strand is hardly, if at all, wider than the traces, the superposition is necessarily accurate. The giving off of superposed traces from an isolated strand seems to be an effect of reduction of the xylem, whereby neither of the meshes bordering the strand is closed at the nodes; it is, therefore, natural that this form of superposition of the traces should be commonest in *E. limosum*, especially in Cone B: but it is common, too, in *E. palustre*, and occurs, though rarely, in *E. arvense* (e. g. the ninth and tenth traces of the second whorl of Cone C are given off from isolated strands, and are superposed respectively to the tenth and eleventh traces of the whorl below; and the tenth and eleventh traces of the fifth whorl of Cone C are borne by isolated strands, and are superposed to the tenth and eleventh traces of the whorl below).

In *E. limosum*, though the xylem at the nodes is in excess of that in the internodes, it is only rarely sufficient to close a mesh before the departure of the trace at that node, i. e. to unite two trace-bearing strands, as, for instance, the strands giving off the seventh and eighth traces of the third whorl of Cone A are united. More often the strand, though relatively wide, is not wide enough to come into contact with its neighbours; when a trace departs from the median portion of such a strand a parenchymatous mesh appears a little way above it so that the strand appears to fork just above the node. When two neighbouring strands branch in this way their adjacent branches diverge obliquely and fuse a little higher up to form the trace-bearing strand of the next internode (Text-fig. 7, B); we thus get a regular alternation such as obtains in the vegetative stem. But in the latter, generally in the cone of *E. arvense*, and frequently in the cone of *E. palustre*, there is no need for this fusion to constitute fresh strands alternating with those of the internode below, for the strands are, as a rule, laterally in contact with one another at the nodes at or before the departure of the traces, and by the appearance of parenchymatous meshes above the latter, strands arise alternating regularly with those of the internode below (Text-fig. 7, A). In both these cases, represented respectively by Text-fig. 7, A and B, we get a regular alternation of strands at the nodes; but in the form of alternation illustrated in Text-fig. 7, B, rather less xylem is

in reality developed, and the parenchymatous meshes tend to dovetail into one another at the nodes, since those of the upper internode originate before those of the lower one are closed. In a longitudinal reconstruction of the xylem, the width of the latter at the node is increased by the fact that when the branches of a strand diverge obliquely the vessels are, of course, cut obliquely. A tendency for the parenchymatous meshes of the internode below not to be closed until after the origin of those of the internode above may be noted occasionally in the cone of *E. arvense*, and now and then in

TEXT-FIG. 7. Different forms of course of the strands at the nodes.

the vegetative nodes of the three species that I studied ; but it does not become a marked feature in any of them. According to Pfitzer (Pfitzer, p. 344) this type of alternation, shown in Text-fig. 7, B, is found in the vegetative nodes of *E. variegatum*.

In *E. limosum*, however, it is unusual, except in the fifth and sixth whorls of Cone A, for two or more adjacent strands to give off median traces and fork above their departure. Much more commonly one strand forks and its neighbour does not ; in such cases we get an irregular anatomical alternation between members of successive whorls. Of this irregular

alternation there are three forms : (1) the xylem-strand of the next internode may be formed by the fusion of a branch of a forking strand with a (whole) strand of the internode below (Text-fig. 7, C) ; or (2) by the fusion of two whole strands (Text-fig. 7, D) ; or (3) a strand may fork above the departure of a median trace and one (Text-fig. 7, E) or more, rarely both (Text-fig. 7, F), branches may constitute, independent of any fusions, trace-bearing strands of the internode above. The first form of irregular alternation is by far the commonest in *E. limosum* ; the second leads to reduction in the number of strands, and is therefore more characteristic of the upper part of the cone ; the third naturally leads to an increase in the number of strands in the next whorl unless it is counteracted by the fusion of two whole strands of the internode below. Such irregularities in alternation, when not caused by a change in the number of members of successive whorls, are due to failure to close some of the meshes at the nodes, and therefore to poor development of the xylem in this region ; a further reduction of xylem leads, as already pointed out, to the formation of strands pursuing an isolated course through the nodes, and therefore to the superposition of traces.

A case occurred in Cone C of *E. limosum* in which a xylem-strand appeared to branch without any relation to the departure of a trace. A narrow strand, after giving off a trace, comes temporarily into connexion with one of its neighbours, about three-quarters of the way up the internode (and thus closes a parenchymatous mesh) ; but this connexion only extends for a short distance, and less than half-way up the next internode the strand again detaches itself.

Another exceptional, apparently a unique, irregularity occurs in the lowest whorl of Cone C. Here all the xylem-elements above a xylem-trace do not die out ; but some of them pursue an oblique course and fuse with a neighbouring strand, thus closing a mesh of the internode below and initiating one in the internode above.

The lowest whorl in Cones A and C shows further anomalies ; in both, while certain strands pursued an isolated course through the node and gave off no traces, pairs of strands united to one another at the node gave off three traces.

APEX OF THE CONE.

The structure of the apex of the cone differs in the different species. Externally, the terminal sporangiophore of *E. arvense* is larger than the others, and the outer (in this case upper) surface of the shield of the sporangiophore, instead of being flat or slightly depressed in the middle, is prolonged into a drip point ; this relatively massive terminal structure never has, as the terminal sporangiophores of *E. palustre* and *E. limosum* have, a single more or less circular trace. Cone A was so very young that the terminal internode had not elongated at all, and the apical phenomena

were therefore indistinct ; to ascertain the structure of more mature apices the upper parts of Cones B, D, and E were cut. In all three the last node gave off six traces, but in Cones D and E two of these seem to have entered one sporangiophore. In Cones B and E two unequal bands of xylem, much wider than the ordinary traces, entered the terminal sporangiophore, while in Cone D a similar wide band of xylem and two smaller strands enter the terminal sporangiophore ; before entering the sporangiophore these two smaller strands approach very close to one another, but diverge again without fusing. These two small strands certainly seem to correspond to one of the bands that enter the terminal sporangiophore of Cones B and E.

In the cone of *E. palustre*, of the variety *polystachion* as well as of more typical specimens, the proportion of xylem at the apex seems to be relatively great. Here, indeed, it commonly forms a ring extending upwards from a point below the uppermost whorl of sporangiophores. In Cone A such a ring is only formed a little way above the last whorl, and as the stele has already narrowed considerably, the ring is very narrow ; but even here the amount of xylem relatively to the diameter of the stele is above the average amount in other parts of the cone. In all three apices of cones of *E. palustre* examined the ring narrows rapidly as we pass upwards, and ere long its condensation gives rise to a small solid circular strand (i. e. it no longer encloses any parenchymatous cells) ; in the variety *polystachion* this narrowing of the ring and its condensation into a circular strand are effected partly by the fact that certain tracheides pursue an inward, centripetal course. This small circular strand is the trace of the terminal sporangiophore.

In *E. limosum* the trace of the terminal sporangiophore is formed as the continuation of one of the xylem-strands of the internode below. In Cone B the others seem to die out, while in Cone A they give off, after the departure of the traces, contributions to the strand of xylem that persists ; the latter then narrows very rapidly, becomes circular and concentric, and passes upwards into the terminal sporangiophore as its trace.

As regards the structure of the sporangiophores, Eames has shown that their traces are concentric and mesarch, and I have nothing to add to his remarks (Eames).

THE STRUCTURE OF THE VEGETATIVE NODES.

Before considering the region transitional from fertile stem to cone a few facts as to the structure of the vegetative nodes must be reviewed. As is well known the bundles in an internode of the stem of *Equisetum* consist of three groups of xylem. Of these the carinal or protoxylem group is situated medianly and at the edge of the pith ; its annular or spiral vessels early become disorganized, giving rise to the carinal canal, upon the edge of which abut a few tracheides that have not been torn. The two other groups

are situated at the periphery of the bundle and form bands or groups of elements, the long axis of each group pointing obliquely outwards. They develop some time after the carinal group, and the number of cells in each of these lateral strands varies according to the species from 3 to 15. Quéva states that the lateral xylem is less developed in the rhizome and may even be absent there. According to him, too, the lateral metaxylem is composed entirely of spiral tracheides (Quéva, p. 18); Eames, on the other hand, states that the elements of these lateral strands are in general scalariform, reticulate, or pitted, but that occasionally they contain annular or even spiral tracheides (Eames, p. 589). Bower (Bower (2), p. 389) quotes observations of Gwynne-Vaughan on *E. giganteum*, the details of which have not been published, but which were accessible to him; according to these the lateral strands of this species contain 10–15 tracheides; the smallest of these are at the outside, and they gradually increase in size inwards. The larger elements are coarsely reticulate, the reticulation becoming finer and more regular in the smaller elements until in the smallest it closely resembles spiral thickening.

Gwynne-Vaughan maintained, too, that the lateral metaxylem-strands show indications of centripetal development, especially in the larger species in which the lateral groups are better developed; but he admits he was unable to prove this centripetal development as he had no incompletely developed portions of the stem (Gwynne-Vaughan). Bower endorses Gwynne-Vaughan's opinion with a similar reservation (Bower (2), p. 309). Quéva, however, expressly states that the whole of the lateral metaxylem is centrifugal (Quéva, pp. 25 and 35). Eames also regards the lateral xylem as centrifugal, though he records examples of a certain irregularity in the direction of lignification; I have met with a few cases of similar irregularity in the fertile stem of *E. arvense* (Eames, pp. 591–3). My observations, which were not at all extensive, confirm Eames's view that the prevailing direction of lignification in the lateral strands is from within outwards, but that it is subject to occasional irregularities. In any case the lateral strands seem phylogenetically to represent centrifugal xylem. In the region of the annulus there is no reticulate nodal wood, and as we pass upwards towards the lowest whorl of sporangiophores the lateral groups of xylem become united by elements of a similar nature. Thus in the cone, both in the node and the internode, the xylem of the bundle consists not of three groups, but of a continuous band of tracheides. It seems very probable that in the vegetative internodes the lateral groups of xylem represent the free ends of a more deeply curved band of xylem. In that case the position of the tracheides of the lateral groups of metaxylem in a more or less radial series is due to the more or less marked curvature of a band of which only the carinal tracheides and the free ends are lignified. The primitive form of internodal bundle would then be that of the cone, an interpretation

in accordance with modern ideas as to the conservatism of reproductive axes. Quéva has figured and described a curved band of xylem in the vegetative bundles of the upper end of the internode of *E. littorale* (Quéva, p. 23, Fig. 21). The xylem of the internode of the cone, where the latter contains a circle of more or less equidistant strands, often forms curved bands with the concavity facing outwards, though the curvature is less than we should have to assume for the vegetative node if the lateral strands are supposed to mark the ends of such a band. When wide tracts of xylem involving more than one strand of the internode below persist through an internode of the cone, the curvature of the band of xylem is slightly in the inverse direction, so that the xylem forms segments of a circle concentric with the outline of the stele. Traced downwards the terminal tracheides of the curved xylem-strands of the cone are continuous with the tracheides of the lateral metaxylem of the internode below the cone. We may add here that according to Leclerc du Sablon the xylem in the bundles of the tubers of *Equisetum* is not broken up into a carinal and two lateral groups, but vessels and parenchyma are mixed irregularly (Leclerc du Sablon).¹ Milde has figured a similar bundle of a tuber (Milde, Pl. I, Fig. 22). In the tubers of the fossil Equisetaceae recently described by Fritel and Viguiier, the xylem of each bundle appears to consist of an oval mass of parenchyma mixed with tracheides. Quéva has shown that the elements of the nodal wood are lignified after those of the carinal group, but before the lateral metaxylem of the internode. In 1901 Gwynne-Vaughan, from a study of *E. giganteum* and *E. hiemale*, concluded that the lateral strands may be traced through the node and across the upper surface of the ring of nodal xylem; that after passing above and across the latter they fuse with the similar adjacent strand of a neighbouring bundle to form the alternating strands of the internode above (Gwynne-Vaughan). Quéva, however, writing six years later, seems to be unaware of Gwynne-Vaughan's remarks; he states that the nodal reticulate tracheides are 'in direct relation to the metaxylem, the elements of which show above the node transitional markings' (Quéva, pp. 18-19). According to this botanist, therefore, the tracheides of the lateral strands are gradually replaced by reticulate nodal elements as we pass upwards; higher up this xylem dies out, except at the points where the wood persists as the lateral metaxylem-strands of the internode above, and at these points the reticulate thickening of the elements is gradually replaced by spiral. Ludwigs in a recent paper seems to be of this opinion, though he expresses himself somewhat differently, saying that metaxylem-elements are initiated on both sides of the bundle, and are especially numerous at the level of the nodal diaphragms; that after the departure of the protoxylem into the leaf the two groups of metaxylem

¹ This author also states that throughout the tuber the bundles form an irregular network, a point which would repay further investigation.

fuse and fill up the carinal canal (Ludwigs, pp. 401-2). Quite recently, Vidal has recorded all forms of thickening intermediate between reticulate and annular in the stem of *E. palustre* (Vidal, p. 24). My observations, so far as they go, are in complete agreement with those of Quéva on this point and in contradiction to those of Gwynne-Vaughan; but they were not extensive, and were moreover limited to the fertile stem of three relatively small species in which the lateral metaxylem groups are not particularly well developed.

In 1893 Cormack suggested that there were traces of secondary xylem in the nodal region of *E. maximum* (Cormack). Quéva, after a careful study of the ontogeny, pointed out that though the 'zone génératrice' of the bundle persists later in the nodal region its activity is strictly limited, the divisions of its cells being merely the continuation of the earlier procambial division of the bundle; thus its secondary nature is not proved (Quéva, pp. 33 and 36). Ludwigs is of the same opinion (Ludwigs, pp. 400-1). Nevertheless, Eames states that a few of the living species of *Equisetum* have been shown by Cormack to possess the remains of secondary xylem, and that Quéva confirms the presence of such wood in *E. maximum* and records its occurrence in *E. arvense*. Eames further remarks that he has seen evidence for this ancestral character in both these species, in *E. hyemale* and in *E. hyemale*, var. *robustum*, A. A. Eaton. Finally, Ludwigs, speaking of the reticulate nodal tracheides, says: 'These vessels are supposed to be formed ("sollen sich . . . bilden") from without inwards by the activity of a cambium and represent that which Eames would have us regard as centripetal wood' (Ludwigs, p. 400). It is hard to see how xylem-elements formed internally by a cambium could be anything but centrifugal; nor does Eames regard the nodal xylem as centripetal. On the contrary, he expressly states that so far as he knows no question has arisen as to the centrifugal development of the nodal or supranodal wood, as he, in agreement with Jeffrey, calls it. He adds that it is clear that the innermost elements are protoxylem (Eames, p. 590). It seems clear that Ludwigs' statement that Eames regards the nodal wood as centripetal is incorrect; nor does Ludwigs himself express any agreement with this view. Whether the nodal wood is secondary or not is less clear; on the whole its secondary character seems not to be proved; though from the size of the Mesozoic Equisetales we should *a priori* regard secondary growth as an ancestral character, traces of which might well remain in certain species.

At the level of the uppermost vegetative whorl of the fertile stem of *E. limosum* a diaphragm of the usual type was not found. At the node, owing to the junction of the xylem of the separate bundles into a continuous ring, the separate endodermes of the internodal bundles are replaced by common inner and outer endodermes, this change being brought about

in the manner already described by Pfitzer (Pfitzer, pp. 336-7). The same author has noted that in the nodal region the cells of the outer endodermis have for a little distance thicker walls (l. c., p. 332). I have observed the same phenomenon in *E. limosum*. A little above the departure of the leaf-traces, where the ring of nodal xylem breaks up, the endodermis consists of relatively thick-walled cells that stain very deeply with Bismarck brown; as the breaking up of the ring proceeds these dark brown cells become involuted round the bundles through the parenchymatous

TEXT-FIG. 8. Reconstruction of uppermost part of fertile stem of *E. limosum*. *n.x.* = nodal wood, breaking up into the bundles (*b*) of the internode above; *l.t.* = leaf-trace; *i.b.* = bundle in the internode below; *p.* = parenchyma between the bundles; *p.*¹ = torn parenchyma on the inner side of the bundles; *end.* = endodermis; *sc.co.* = inverted hollow cone of sclerenchyma.

meshes of the upper internode; thus we get a ring, three to four cells deep, of these dark brown cells lying inside the circle of strands; traced upwards this ring communicates through the parenchymatous meshes with the dark brown cells of the outer endodermis. Traced downwards into the lower internode the ring of thickened cells narrows rather rapidly; at first it is connected with the narrow band of parenchyma that persist on the inner side of the vascular bundles; but as we pass downwards it narrows so rapidly that in the mature stem is soon ceases to be in contact with this parenchyma, and in a transverse section lies free in the middle of the central cavity (Text-figs. 8 and 10). The thin-walled elements internal to this ring

TEXT-FIG. 9. Lettering as in Fig. 8.

TEXT-FIG. 10. Lettering as in Fig. 8.

also become torn as the stem increases in width, though not infrequently the torn remains of such thin-walled cells may be seen adhering to the inner side of the thickened ring. As the latter narrows, passing down the internode the cavity which it encloses becomes smaller, until we get a solid core of thickened cells lying free in the central cavity (Text-fig. 9). These phenomena were observed in Cones A and C, in which they were closely similar; the series of sections below Cone B was not sufficiently extensive to show the form of the mass of dark brown cells, but the presence of such cells was ascertained.

Pfitzer has described dark brown cells in the interior of the branch at its insertion on the stem, but he does not seem to have noticed similar phenomena in the main shoots. His description, which, *mutatis mutandis*, agrees with the description given above, runs thus: 'In a radial longitudinal section through the origin of the branch the brown internal mass of the cylinder is seen to widen out laterally . . . in such a way that it comes into connexion with the outer endodermis of the cylinder.' The cylinder ('Röhre') mentioned here is, of course, the ring of xylem found in the lower part of the branch; upwards this cylinder of xylem only breaks up into separate strands above the insertion of the first leaf-sheath of the branch, while below it is attached to two of the cauline bundles; its insertion here is also oblique with regard to the main axis.

E. palustre has in the internode only an external endodermis, but Pfitzer has shown that throughout the node there is also a common internal endodermis, which traced upwards and downwards passes over gradually into the typical pith without coming into contact with the external endodermis. He remarks that in the old stems of *E. palustre* all the cells within the inner endodermis are thickened and dark brown, and says that they constitute the brown diaphragm. In my young specimens the diaphragm was not at all brown. Pfitzer also gives a curious description of the brown cells within the base of the cylinder of the branch of this species. The branch has an inner endodermis, the inner longitudinal walls of which are thick and dark brown; the cylinder also contains thickened dark brown cells; these appear first in the middle of the cylinder, and their development is continued upwards and downwards; when it reaches its highest grade 'the whole interior of the cylinder is filled with a dark brown mass of cells which either shows a dilation ("Anschwellung") above or below or below only, and is surrounded by the unthickened external longitudinal walls of the (inner) endodermis'. If this description is accurate the form of the brown mass of cells would be that of a solid dumb-bell or of a solid normally oriented cone. Pfitzer also describes dark brown cells in the branch of *E. littorale* and in the stem of *E. variegatum*. In the latter species, when the nodal wood breaks up above the departure of the traces, the outer and inner endodermes are replaced by special endodermes round the bundles,

and the endodermal cells lying on the inside of the bundles are thickened, and the thickenings are dark brown. This thickening and colouring of the layers of thickening spreads a little higher up to the pith cells, so that we get a polygon of which the blunt ends project between the special endodermes. Thin-walled cells are often found inside this polygon (Pfitzer).

Jeffrey, working on *E. hiemale*, also records sclerized brown cells. He writes of his Fig. 2, Pl. XXIX, representing a tangential section of the nodal region of *E. hiemale*: 'The magnification is sufficient to show that the medulla of the branch is composed of brown sclerenchymatous cells' (Jeffrey, 1). As the photograph is of an obliquely oriented organ it is not easy to make out the exact form of the sclerenchymatous mass; from the above quotation it might be thought that the whole medulla is sclerized, but it is hardly safe to conclude this from a passing reference like that quoted above. Jeffrey states, too, that the diaphragm of the first node of the branch is very deep, and somewhat sclerified at the ends; this diaphragm does not appear to be connected at the origin of the branch with the above-mentioned mass of sclerenchyma. He also found that in the main stem of *E. hiemale* and *E. limosum* the diaphragm was partially sclerified; this he regarded as sclerified periderm and compared it to the non-sclerified periderm in the diaphragm of certain *Calamites*.¹

THE TRANSITION FROM FERTILE STEM TO CONE.

The annulus seems to mark the position of a reduced node, and the reasons for this must be examined. We have seen from the anatomy of the cone and stem that fresh parenchymatous meshes arise above the nodes; usually they arise at a relatively small distance above a trace that has departed; we have also seen that the closure of meshes of the internode below is effected in the region of the node. This closure of parenchymatous meshes and the formation of fresh ones in the region of the node causes a branching of the vascular strands at this level. We have seen also that when the xylem is much reduced at a node certain of the strands pursue an isolated course upwards into the next internode because sufficient xylem to close the meshes of the internode below is not present, and because the trace-bearing strand remains too narrow to give rise to an independent parenchymatous mesh above the node. We may generalize as to the fluctuating conditions obtaining in the fertile nodes by saying the greater the reduction of *nodal* xylem the larger the proportion of strands that pass through a node without branching. In the vegetative axis in which the nodal xylem is well developed and forms a complete ring (though the internodal xylem is less developed than in the cone), all the meshes are

¹ Since writing the above I have come across H. H. Thomas's record of a nodal diaphragm, hollow in the middle, in a Jurassic species of *Equisetites*. Cf. Mémoires du Comité Géologique de Saint-Petersbourg, N. S. 71, 1911.

closed at and fresh ones originate above the node. A branching of strands independent of the formation of a parenchymatous mesh above a trace that has departed is very rare. It is true that in cones with relatively little xylem, or in parts of cones with little xylem, a mesh may arise below and to one side of a trace ; but in such cases its form and position seem to show that it has, phylogenetically speaking, 'decurved' downwards below the trace to which it corresponds (cf. p. 673). True branching of strands, independent of the formation of meshes above traces, does occur, though rarely, both in cones and stems where the number of members in the next whorl is increased, and still more rarely owing to inexplicable irregularities. But even in cases in which an increase in the number of members causes branching of the strands the area of disturbance of superposition of meshes to traces is narrowly restricted. Branching of some of the strands above the annulus is common, and strongly suggests that we are dealing with a reduced node ; in *E. arvense*, however, the number of sporangiophores in a whorl often considerably exceeds the number of leaves in the fertile stem, and the formation of fresh meshes above the insertion of the annulus might be regarded as the expression of the increase in the number of appendicular members. In this species, too, the number of strands that pass uninterruptedly through the annular node is relatively large. The transitional region was studied in Cones A, B, C, F, G, and H of this species. In Cone A four out of nine strands forked, giving rise to fresh meshes above the annulus. Below the annulus of Cone B there were seven strands, and all passed through the annular region without branching ; in Cone C one only of the eleven strands branched above the insertion of the annulus. Cone F was exceptional and will be considered later ; in Cone G three out of nine strands forked above the insertion of the annulus, while in Cone H one of eleven strands forked. The forking observed in this last cone was the more significant as there were only ten sporangiophores in the lowest whorl of the cone ; thus the branching of the strand was not correlated with an increase of appendicular members, and seems clearly to be a vestigial nodal character. In Cones A, B, and D of *E. palustre*, too, the number of members in the uppermost vegetative whorl was equal to the number in the lowest whorl of the cone ; yet in all these cases a certain number of meshes were closed, and others originated in the neighbourhood of the annulus. In the four cones of *E. palustre* examined, after the closure of certain of the parenchymatous meshes in the region of insertion of the annulus, a band of xylem which effected this closure persisted upwards through the 'internode' lying between the annulus and the sporangiophores ; in this region the absence of meshes was due, as it appears occasionally to be due in the cone (cf. p. 671), not to poor development of nodal wood, but to unusual development of internodal wood.

Cases of closure of meshes of the internode below in the neighbourhood

of the annulus are difficult to observe in *E. arvense*. In Cone A of this species the meshes below the first and second traces of the lowest whorl of sporangiophores are closed, and a fresh mesh of the first order originates between them (cf. Text-fig. 1). In this restricted region the branching gives rise to the formation of a mesh alternating with that of the internode below, and the nodal appearance is most clearly marked in a longitudinal reconstruction, though, of course, the fresh meshes are not subtended by traces. In other cases a mesh is closed in the neighbourhood of the insertion of the annulus, but no fresh mesh originates higher up alternating with it; this may, perhaps, be due, as in *E. palustre*, to the persistence of a band of xylem through the internode above the annulus. This seems to be the case with certain of the strands of Cone C of *E. arvense*. Here the first, the second, the third, the fourth traces, the two bundles composing the prematurely divided sixth trace, and the eleventh trace, are all inserted not vertically above the middle of the strands of the uppermost vegetative internode, but lie more or less above the point of junction of two strands. Thus the meshes above these traces do not alternate with those of the uppermost vegetative internode, but lie more or less above them; on this assumption the meshes corresponding to the third and fourth traces have 'decurved' a little below the traces to which they phylogenetically belong. If parenchymatous meshes had appeared in this band of xylem above the annulus and had been closed again at the insertion of the sporangiophores they would be about half the height of the meshes of the first order of the cone. In Cone A, where two meshes actually arise above the annulus and are closed before the insertion of the basal whorl of the cone, their height is about half that of the meshes of the first order found in the lower and less immature region of the cone. The absence of branching in the region of the annulus in Cone B may perhaps be due, at any rate in part, to this same relatively great development of xylem in the internode above the annulus. The xylem is much more developed in this cone relatively to its size than in Cone C, and at the level of the basal whorl all the strands are united into a ring of xylem. But the fusion of the xylem of the bundles forming a ring takes place at very different levels, and some of the strands fuse as far down as 0.9 mm. below the sporangiophores; if meshes originated just above this lowest fusion and were closed at the height of the sporangiophores they would be, like the meshes of the first order arising above the annulus of Cone A, about half the average height of the meshes of the first order of the cone of the specimen in which they occur. In Cone B, however, it was difficult to be sure if the meshes above the sporangiophores were superposed to those of the internode below, for the diameter of the stele narrowed abruptly at and above the insertion of the basal whorl of the cone, and this narrowing confused the relations of alternation and superposition of the meshes. It is quite possible, therefore,

that in Cone B we are dealing merely with a case of early closure of certain meshes, and parallel cases of early closure are by no means rare in the cone of this species. But in Cone C such an explanation would not account for the fact that the traces of the first whorl seem in some cases to lie above and between the strands of the internode rather than above and in the middle of them; in this cone, too, one fresh mesh originates above the annulus and very much at the level at which some of the other meshes are closed.

To return to *E. palustre*, in which the percentage of closure and of origin of meshes in the annular region is highest and in which the nodal appearance of this region in longitudinal reconstruction is therefore most striking, we find that in Cone A six out of seven, in Cone B four out of eight, and in Cone D four out of six meshes are closed in the neighbourhood of the insertion of the annulus. Notwithstanding the persistence of bands of xylem into the internode above the annulus, four fresh meshes originated above the annulus in Cone A, three in Cone B, and three in Cone D. Cone C was exceptional; though there were eight strands below the annulus and nine sporangiophores in the second fertile whorl, the basal whorl of the cone consisted of but three sporangiophores. The increase in number of trace-bearing strands to nine in the second fertile whorl is due to the fact that above the lowest whorl of the cone a band consisting of three strands (that with two other single strands gave off no traces at this node) breaks up into four strands; thus the increase in the number of strands takes place between the first and second whorls of the cone and not between the annulus and the lowest whorl. Nevertheless, six out of eight meshes were closed and four originated in the neighbourhood of the annulus. It is curious that none of the fourteen meshes originating above the annuli of the cones of *E. palustre* examined were of the first order. It must, however, be remembered that meshes of the first order are much rarer in the cones of *E. palustre* than in those of *E. arvense*.

In *E. limosum* the indications of the nodal structure of the axis at the insertion of the annulus are less marked; in Cone A we notice one case of the origin of a mesh above the annulus. In Cone B there are four meshes which I interpret as arising above the annulus; like the mesh in Cone A they are of the second and higher orders. The mesh below the second trace of the lowest whorl of this cone appears to be closed in the region of insertion of the annulus and markedly below the level of the basal whorl; this is true, too, of the meshes above the twelfth and thirteenth leaf-traces; but this cone is still so young and has elongated so little that it is exceedingly doubtful if we are dealing with bands of xylem persisting through an unelongated supra-annular internode or with early closure of a mesh before the first fertile node. Cone C of this species showed two clear cases of meshes originating above the annulus. This tendency of meshes to be closed slightly above a node was noticed also in various cones (cf. pp. 680-1);

and seems to be one result of a lesser development of xylem. The latter being insufficient to bring the strands laterally into contact at the node, their connexion is effected higher up by the oblique course of the tracheides present.

Strong confirmation of the view that the annulus marks the position of a reduced node was afforded by the region transitional from the fertile stem to the cone in Cone F of *E. arvense*. This specimen had two annuli; the upper one was normal in appearance, the lower one was rather more developed than is usual in this species, especially on one side where the edge was slightly lobed. The insertion of this lower annulus on the axis was remarkably oblique, a phenomenon which may occasionally be observed in normal annuli. According to Duval Jouve the possession of more than one annulus and irregularities of the annulus are very common in *E. arvense*, *E. maximum*, *E. littorale*, and common in *E. sylvaticum*, *E. limosum*, and *E. ramosissimum* (Duval Jouve, pp. 150 and 154). Milde goes so far as to describe the cone of *Equisetum* as having one to two annuli (Milde, p. 161). But I know of no account of the anatomical relations of such abnormal forms. A little distance below the lower annulus of Cone F the anatomy of the stem was that of a typical internode of the vegetative region. There were seven more or less equivalent bundles, each with a large carinal canal and two small lateral groups of metaxylem. A little higher up reticulate tracheides, resembling those of a vegetative node, make their appearance in the adjacent halves of two bundles; these two groups of tracheides and the phloem external to them pursue a course so oblique that about 30 to 40 μ higher up they come into contact. The reticulate wood thus formed is of the same radial extent as that of an ordinary vegetative node; but in the direction of the circumference of the stele it at first occupies only the portion of the stele lying between the carinal canals of two adjacent bundles. The lateral groups of metaxylem at the free ends of these bundles persist for a little distance in the condition of typical internodal lateral metaxylem; but a little higher up they and the cells beyond them become connected with and assume the character of nodal wood. There results a band of reticulate tracheides extending over rather more than a quarter of the circumference of the stele. This band of xylem, however, very soon breaks up into three bundles by the dying out of portions of the woody band. About 320 μ above the first appearance of the reticulate tracheides the band of xylem has broken up into three normal sized bundles; the middle one is already in a typical internodal condition, each of the others consists of a curved band of typical 'nodal xylem'. Traced upwards these reticulate tracheides, the free ends of the band of reticulate wood, do not die out, but pursue an obliquely transverse course, passing in opposite directions round the circumference of the stele (Fig. 5, Pl. LXIV). Thus a mass of tracheides appears at different levels in all the bundles. When the two strands of reticulate tracheides and the phloem outside them have

girdled nearly the whole circumference of the stele they find themselves in adjacent bundles, and after becoming very closely approximated they die out without coming into absolute contact at a height of about 1.6 mm. above the first appearance of reticulate tracheides. When they die out the two strands are separated only by one or two parenchymatous cells. Each strand consists of the equivalent of a bundle, but while each may sometimes occupy the position of a single bundle it has of course to pass from one bundle to another, and frequently occupies a position between two bundles. While the masses of nodal wood have been journeying round the stele the number of bundles has increased from seven to ten, an increase very similar in amount to that found in many normal cones of *E. arvense*. It is interesting to note that this lower annulus, which only faintly recalled a leaf-sheath by its lobing on one side, possessed reticulate tracheides apparently identical in structure with those of an ordinary node; the distribution of these is of course different from their distribution in an ordinary node; but this is presumably due, in part at least, to the oblique insertion of the annulus. In one of the two bundles that first develop reticulate tracheides, a bundle situated on the side on which the annulus was most developed, there seemed to be indications of a reduced and abortive trace. A few phloem cells bend out into the cortex, and endodermal cells with exceptionally well-marked bands of cutinization may be seen cut longitudinally a little way out in the cortex. Moreover, one or two tracheides bulge out through the opening in the phloem and seem to be passing out into the cortex; unfortunately, two sections, each 10 μ thick, above the section showing these phenomena, were lost in mounting. If one or two tracheides did, as seems likely, pass out into the cortex they must have died out almost at once, for no further trace of them can be seen in other sections. The parenchymatous stelar cells that bend outwards, and those with endodermal markings, also die out ere long in the cortex; but for several sections they are distinctly discernible owing to the fact that they are cut longitudinally or very obliquely. No further indications of traces were observed in any of the other bundles.

Below the upper normal annulus there were ten strands, and the lowest whorl of the cone consisted of ten sporangiophores, so that there was no increase in appendicular members; yet six new meshes were formed above this annulus, two of which were closed at or just above the level of the lowest fertile whorl. No less than seven out of the ten meshes existing below the upper and normal annulus were closed in the region of its insertion. Thus the number of meshes closed and initiated in the region of the annulus was in the case of Cone F exceptionally high for *E. arvense*.

We may add that though annuli do not seem to have been described in most of the cones of the fossil Equisetales, Thomas records a possible example in *Calamostachys* (Thomas), and a structure which appears to

be of the same nature may be seen in one of Kidston's figures of *Pothocites* (Kidston, Pl. XII, Fig. 14).

GENERAL CONSIDERATIONS.

Equisetum is so isolated among existing plants that comparisons of the structure of its cone with the cones of recent plants seem at present to be futile from a morphological point of view. But the phylum of the Equisetales was well developed in the past, and a comparison with the varied cones of this great phylum offers the most promising field for conclusions as to the comparative morphology of the cone. The cones of the Equisetales may be divided into two great groups, those consisting only of fertile appendages, provisionally called sporangiophores, and those in which the cone also contains sterile appendages. Leaving abnormalities out of consideration the former group includes the cones of the recent *Equisetum*, those of the species of *Equisetites* in which the reproductive organs are known, namely, the carboniferous *E. Hemingwayi*, Kidston, the Liassic *E. Nathorsti*, Halle, and the Rhaetic *E. suecicum*, Nathorst (Halle, pp. 27-31); it also includes the cones of *Autophyllites furcatus*, Grand'Eury, *Bornia pachystachya*, Bureau, and perhaps of *B. transitionis*, Grand'Eury; these three species come from the Carboniferous (Jongmanns, pp. 265-7). In the cones forming the so-called genera *Calamostachys* (including Renault's *Calamodendrostachys Zeilleri*), *Palaeostachya*, *Huttonia*, *Cingularia*, and in *Volkmannia pseudosessilis*, Grand'Eury, sporangiophores and sterile bracts succeed one another on the axis of the cone (Jongmanns, p. 279). These types of cones are of Palaeozoic age; most of them certainly, probably all of them, represent cones of the Calamariae in the widest sense of the word. In *Calamostachys* bracts and sporangiophores form equidistant whorls; in *Palaeostachya* the sporangiophores are inserted in the axils above the bracts, while in *Huttonia*, in *Cingularia*, and in *Volkmannia pseudosessilis* they are situated below the bracts. *Archaeocalamites* (including *Pothocites* and *Bornia*, excepting perhaps *B. pachystachya* and *B. transitionis*) appears to be intermediate between the two groups, for its cone consists of whorls of sporangiophores, sometimes at least interrupted at considerable intervals by a whorl of sterile bracts. The best way of elucidating the anatomy of a cone is certainly by the study of its internal structure. But nearly all the cones mentioned above are known as impressions only; we are, however, acquainted with the anatomy of some species of *Calamostachys* and *Palaeostachya*. It has been customary of late years to regard the sporangiophores and bracts of these two genera as phylogenetically lobes of a compound leaf of sporophyll. Such a view is admittedly based partly on an analogy with the Sphenophyllales, in which group the sporangiophore, when present, is usually inserted on a sterile bract. This view has been somewhat widely held, and different modifications of it were

favourably considered by Scott (Scott, pp. 158-62)¹, Lignier (Lignier), Jeffrey (Jeffrey (1), p. 185), and others. Bower, however, was strongly opposed to it, regarding the sporangiophore as an organ *sui generis*, not only in the Equisetales, but also in the Sphenophyllales (Bower (2), pp. 381-4), while Seward supported him as far as regarding the sporangiophore, at least provisionally, as an organ *sui generis* (Seward, p. 15). There are certainly much stronger reasons for doubting that the sporangiophore represents a lobe of a leaf in the Equisetales than in the Sphenophyllales. In the former group we are at once met with the difficulty of explaining those cones in which the bracts are either absent or present only at considerable intervals. Those that regard the sporangiophore as a lobe believe that it has been displaced in *Calamostachys*; some years ago Dr. Scott pointed out that if such displacement occurred in a form in which, as in *Sphenophyllum fertile*, both lobes of the sporophyll bore sporangia, we should get a near approach to the *Equisetum* arrangement (Scott, p. 162). Jeffrey also remarks that there are many reasons for regarding the sporophyll in the Equisetaceous series as dorsiventrally lobed. He suggests that in this case the sporangiophores of *Equisetum* represent the result of fusion of ventral and dorsal segments, or that they are ventral segments, the dorsal having become obsolete. No known cone seems to show such an obsolescence of bracts, and the sporangiophores of *Equisetum* do not seem to be dorsiventrally double.

I was at first inclined to accept Dr. Scott's tentative suggestion that in *Equisetum* each sporangiophore might represent a separated lobe of a dorsiventrally lobed sporophyll; in this I was influenced by the analogy with the Sphenophyllales, but principally by the fact that I felt unable to escape the conviction that the sporangiophores of *Archaeocalamites* are the homologues of those of *Calamites*, and these sporangiophores seem very closely to resemble those of *Equisetum* (Browne, p. 16). But a comparative study of the cone of *Equisetum* seems to show that the sporangiophores are whole appendages and that their insertion marks the position of a node. It is true that though the cone has more internodal xylem than the stem, the ring of wood at a fertile node is only exceptionally complete; such a ring is, however, by no means rare in *E. arvense*. Moreover, at the insertion of the whorled appendages there is (except in cases of great reduction of the xylem) a marked increase in the amount of xylem, leading to the formation of bands or of a ring of xylem. Above the departure of the traces of the sporangiophores, and often very much at the same height as the breaking up of the xylem above the leaf-traces, these bands or this ring of xylem breaks up owing to the appearance of parenchymatous meshes.² In this

¹ Dr. Scott subsequently pointed out that the spore-bearing organ might be a whole leaf or a lobe of a leaf (Studies in Fossil Botany, 1909, p. 623). I have been led to adopt this view.

² The nodal xylem of the stem of course differs markedly from the xylem at a fertile node, for, except for the protoxylem, it consists of large reticulate elements and has a considerable depth radially, while the xylem at a fertile node consists entirely of relatively small annular and spiral tracheides and is very narrow radially.

respect, however, the cone varies much more than the stem, for a portion of the band of xylem may be continued upwards through the greater part or the whole of the internode, or it may break up relatively near the departure of the traces.

Thus the anatomy of the cone supports the view that the sporangiophores of *Equisetum* are whole appendages. On the other hand, the anatomy of the cone of *Palaeostachya* and *Calamostachys* seems to show that in these genera the sporangiophores and bracts are lobes of a leaf (Hickling, 1 and 2). This is a very fundamental difference, and it would seem that these genera do not lie at all near the Equisetal line of descent. The anatomical evidence is at present insufficient to decide whether the sporangiophores of *Archaeocalamites* were lobes, as were those of *Calamostachys*, or whole appendages, as those of *Equisetum* seem to be. The latter view seems to me the more natural. The bracts found at irregular intervals in the cone of *Archaeocalamites*, which I was formerly inclined to regard as indications of sterilization of fertile appendages (Browne, p. 17), would seem more probably to be reduced vegetative leaves, and their occurrence in the relatively ancient *Archaeocalamites* might be a primitive character, indicating want of definition of the strobilus.

The parenchymatous meshes found in the cone, like those in the vegetative internodes of *Equisetum*, do not, except at the reduced or immature apex of the cone, originate immediately above the traces. Thus they are not foliar gaps as defined by Jeffrey. Speaking of the tracts of parenchyma of the internode of the stem of *Equisetum* this author says, 'They lack, however, one important feature of foliar gaps, for they do not occur *immediately above the traces*, as should be the case with true foliar gaps. All other foliar gaps with which we are acquainted show this feature'¹ (Jeffrey (2), p. 252). If this definition of a foliar gap is to be applied in all cases, the tracts of parenchyma above the traces of certain recent Osmundaceae are not foliar gaps. Sinnott, seeking to defend Jeffrey's view that the traces of siphonostelic and dictyostelic Pteropsida always leave gaps, claims that when in recent Osmundaceae a trace appears to leave no gap in the wood at its departure the trace-bearing xylem-strands always break a little further up while the trace is in the cortex. This is exactly what occurs in the axis of the cone when a strand branches a little way above the departure of a trace; very much the same thing occurs in the stem when the nodal wood breaks up a little way above the insertion of the leaf-sheath. In cones which, like that of *E. limosum*, have very little xylem, the 'gap' or break usually occurs very close to, though not immediately above the trace, and thus the mesh of parenchyma approximates more closely to Jeffrey's conception of a gap. In the cones of *E. arvense* and *E. palustre*, when the xylem is broken above a trace, pith and cortex remain separated

¹ The italics are Jeffrey's.

by the endodermis, which in these species surrounds the stele. In the stem of *E. limosum* (and presumably in all cases in which the vascular strands are surrounded by separate endodermes) even this barrier is broken down; for at the breaking up of the nodal ring of wood the external and internal endodermes found in this region become involuted round each bundle, so that pith and cortex are in direct communication (Pfitzer, pp. 336-7). Definite endodermal markings are, however, very difficult to distinguish in the cone of this species. It would seem that, phylogenetically speaking, parenchymatous tissue first arose in the internodal part of the siphonostelic xylem of the cone of *Equisetum*. It is not surprising that this parenchyma should have arisen vertically above the traces, since the current of water, being deflected into the sporangiophores, would be diminished above them. From the dimensions of the fossil *Equisetites* we have good reason to believe that existing species of *Equisetum* are reduced, and reduction of the xylem would tend to make the mesh arise closer to the trace. This is exemplified in the cone of *E. limosum*, in which there is very little xylem; here the traces are often only surmounted by a very few lignified elements, though even in this species the parenchymatous mesh sometimes originates at a considerable distance above the trace.

In the preceding pages we have traced the phylogeny of the irregular network of strands of the cone of *E. limosum* from the more regular stele of *E. arvense*, which is imperfectly siphonostelic at the nodes and dictyostelic in the internodes. Considered separately, the irregular network appears to baffle interpretation; considered in the light of a comparative study of the cones of *E. palustre* and *E. arvense*, we see that it has arisen in the phylogeny by the reduction of xylem, this reduction being manifested by extension of the parenchymatous meshes upwards, downwards, and laterally.

In 1899 Jeffrey published a photograph of a cone of *E. arvense* cut longitudinally in two; this photograph was intended to show that the majority of the bundles of the cone do not alternate at the nodes (Jeffrey (1), Pl. XXX, Fig. 3). This feature was, he said, more or less marked in the cones of all the species of *Equisetum* that he had examined. Some years later he returned to this point, and after commenting on the greater conservatism of reproductive axes as compared with vegetative ones he proceeded: 'It appears to have been shown above and beyond any doubt that the equisetaceous strobilus perpetuates both the alternating strands and the complete absence of foliar gaps of the oldest Calamitean forms' (Jeffrey (2), p. 254). While, as Jeffrey remarks, it seems obvious from the data of Stur, which have never been called in question, that the oldest Calamariae were without alternation of the strands at the nodes, and while, according to Hickling, the bundles of the cone of *Calamostachys* did not alternate at the nodes (Hickling, 2, p. 10), and those of *Palaeostachya vera* seem to show no regular pectination, but probably occasional and irregular communication

(Hickling (1), p. 375), the non-alternation of the bundles in the cone of *Equisetum* seems clearly, from the comparative anatomy of the cone, not to be a primitive feature. Moreover, Renault says of his *Volkmannia gracilis*, which is clearly a *Palaeostachya* (cf. Jongmanns (1), p. 332), that the vascular bundles alternate from one internode to the next. It seems shown by the full discussion above that this non-alternation of the bundles at the nodes of the cone of *Equisetum* is due to the persistence of parenchymatous meshes on either side of a strand of xylem, and that this persistence is the direct result of poor development of xylem. More generally, when there is no marked reduction of xylem, and when the position of traces is not disturbed by changes in the number or size of members of successive whorls, the traces of successive whorls alternate with one another. When owing to reduction of xylem in the axis of the cone the traces are superposed, the sporangiophores which they supply still alternate regularly. This is, no doubt, due partly to exigencies of space in the young unelongated cone, but it may possibly be in part due to the retention of an ancestral feature. In Jeffrey's photograph of a cone of *E. arvense* cut in two, some of the strands may not have alternated at the nodes owing to persistence of parenchymatous meshes, while other strands may appear to be continued upwards above the node because the meshes of parenchyma originating above traces are generally narrow in this species, so that a longitudinal cut would not pass through many of them.

SUMMARY OF RESULTS.

1. The xylem at the node of a cone of *Equisetum* consists of a woody ring or of woody bands of varying width; in the internode the xylem usually breaks up into definite strands separated by parenchymatous meshes; these generally arise vertically above the points of departure of the traces, often close above them, but never, except perhaps in the reduced apical region, immediately above them.

2. When the xylem is relatively well developed these meshes are closed again in the neighbourhood of the next node; when less xylem is present some of the meshes tend to persist upwards through two or more internodes. When still less xylem is developed meshes of parenchyma tend to arise a little below and to one side of a trace; they also frequently become widened laterally by fusion with a mesh that has originated independently or by congenital fusion with a mesh above a trace departing from the edge of a strand of xylem.

3. The cones of *E. arvense*, *E. palustre*, and *E. limosum* form a series showing increased reduction of the xylem; *pari passu* with this decrease of the xylem the stele comes to form a more and more irregular network of strands.

4. The non-alternation of some of the strands of the cone at the node is due to poor development of xylem in this region causing the persistence of the meshes on either side of a strand.

5. The anatomy of the axis supports the view that the sporangiophores are whole appendages and not lobes of a sporophyll or leaf.

6. The branching of some of the vascular bundles in the neighbourhood of the insertion of the annulus affords an indication of nodal character at this level. This is confirmed by the anatomy of an abnormal specimen of *E. arvense*.

7. In the upper part of the fertile stem of *E. limosum* a diaphragm of the usual type was not found; instead there was an inverted hollow cone of dark brown cells, hanging freely down for a little distance in the central cavity and continuous upwards, above the breaking up of the nodal xylem with the locally somewhat thickened and dark brown endodermis.

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LITERATURE QUOTED.

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EXPLANATION OF PLATES LXIV AND LXV.

Illustrating Lady Isabel Browne's paper on the Anatomy of the Cone of *Equisetum*.

FIG. 1. Transverse section of the stele of a node of *E. arvense*, showing the bundles united into a ring of xylem and phloem. At the upper side of the photograph the ring is not quite complete; the complete ring of xylem persists a little way below and above the departure of the traces; on one side the section passes through a region where the ring of xylem is complete and no traces are departing. $\times 80$.

FIG. 2. Transverse section of part of the stele at the node of a cone of *E. arvense*. This photograph illustrates a case in which the traces depart from strands unusually far apart, and there is no formation of a ring or bands of xylem. A trace has just departed from a bundle on the reader's left hand. $\times 80$.

FIG. 3. Transverse section of part of the stele of the internode of the cone of *E. arvense*. The separate bundles are wider, compared to the parenchyma between them, than in *E. palustre* or in *E. limosum*. $\times 80$.

FIG. 4. Tangential longitudinal section through part of the cone of *E. arvense*. This photograph illustrates the fact that sometimes the strands alternate at the nodes and sometimes they pass uninterruptedly through the nodes. $\times 22$.

FIG. 5. Transverse section of part of the stele of the axis at the insertion of an abnormal annulus in *E. arvense*. Some of the bundles are in the condition typical of the vegetative internode, while two masses of reticulate tracheides and the phloem outside them are passing in opposite directions and obliquely round the stele. $\times 65$.

FIG. 6. Transverse section of the stele at the node of the cone of *E. palustre*. Two of the trace-bearing bundles are united, the others are separate though more approximated and larger than in the internode. In this species the strands often become united just above the node by their forking, and by the fusion of adjacent forks of neighbouring bundles; all the bundles do not give off traces at exactly the same level, so that the photograph of any single section does not show as much xylem as is present in the nodal region. $\times 65$.

FIG. 7. Transverse section of part of the stele of the internode of *E. palustre*, showing small bundles. $\times 80$.

FIG. 8. Transverse section of part of the stele of the internode of a large cone of *E. limosum*. $\times 80$.

FIG. 9. Transverse section of the stele in a small young cone of *E. palustre*, var. *polystachion*, showing ring of separate bundles. $\times 80$.

FIG. 10. Transverse section of stele just above the annulus of small young cone of *E. palustre*, var. *polystachion*, showing the formation of bands of xylem owing to fusion of bundles, unconnected with the departure of any traces. $\times 80$.

FIG. 11. Transverse section of the stele at the node of a small young cone of *E. palustre*, var. *polystachion*; as in the more typical specimens, some bundles are isolated and others fused. $\times 80$.

FIG. 12. Transverse section of the stele of large, mature cone of *E. limosum*. Some of the bundles are giving off traces, but owing to the irregularity of insertion of the sporangiophores, others have done so lower down or will do so higher up. Some of the bundles have already forked above the departure of traces and the branches have begun diverging, but have not yet fused with their neighbours (e.g. the two small bundles in the middle of the photograph on the reader's left); this accounts for the slight increase in number of the bundles; in the internode below there were eighteen, and this is also the number of the traces. $\times 55$.

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Piddock phot.

BROWNE — EUISETUM.

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BROWNE — Equisetum.

Paddock phot.

9.

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11.

12.

Ruth coll.

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