## 5. The Development, Structure, and Affinities of the Genus Equisetum.

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### Introductory.

De Bary in his masterly Comparative Anatomy of the Vegetative Organs of Vascular Plants expressly renounces the consideration, of what he terms the *voir venir*, the course of development, and practically confines his attention to the structure of mature organs. It may be assumed, that this was done more to limit a task which he describes as a labor of the Danaids, than from any real distrust of the developmental methods, which yielded in his hands such splendid and lasting results in the study of Fungi. Since the appearance of De Bary's text-book there have been many researches on the development of the sporangia, spores, prothallia, archegonia, antheridia, embryos, and meristemata of vascular plants, and on the mature structure of their less accessible tropical representatives, and the still rarer fossilized remains of past ages; but in the midst of all this activity one developmental study has been almost entirely overlooked.

In his presidential address before the botanical section of the British association for the advancement of science, at the meeting of 1896, Dr. D. H. Scott (p. 2) makes the following remarks: — "The embryological method has so far received scant justice from botanists. * * * In the cases which have been investigated perhaps excessive attention has been given to the first division of the ovum, the importance of which, as Sachs showed long ago, has been overrated, while the later stages when the differentiation of organs and tissues is actually in progress have been comparatively neglected."

Convinced of the truth of this statement, the writer has devoted considerable attention to the study of the development of the young sporophyte, in all the various groups of vascular plants and his investigations have led to conclusions, which seem to have a not unimportant bearing on certain problems of the morphology and phylogeny of the phanerogams and vascular cryptogams.

The present memoir is devoted to the development and structure of the genus Equisetum alone; but in order that the questions presented by the ontogeny and anatomy of the Equisetaceae may be fully appreciated, it is necessary to indicate in a general way the relevant morphological conceptions which now prevail, and to state as briefly as possible,

the writer's position towards these conceptions, as the result of the studies mentioned above.

Further since the genus Equisetum may be considered in the light of the many and brilliant palaeobotanical researches of recent years, as the last degenerate survivor of a phylum, which begins in the petrifactions of the Silurian period, and extends with important modifications down to the present time, it will be necessary likewise to outline the structure of the various calamitean forms, with special reference to those features, which afford an adequate explanation of the peculiar anatomy of Equiseta, or which on the other hand can themselves only be understood by an accurate comprehension of the organization of the living representatives of the calimarian stock.


## Morphology of the Central Cylinder.

Sachs (Lehrbuch der botanik, 1882, p. 74 *et seq.*) in the second edition of his Lehrbuch divided the tissues of the higher plants into three groups, the integumentary, fibrovascular, and fundamental. De Bary in his Comparative anatomy already referred to adopted the same morphological standpoint. In his conception the fibrovascular strands consist of Nägeli's xylem and phloem, and according as the xylem is completely surrounded by phloem, or by radially arranged clusters of phloem, or has the phloem applied only to one side, or to two opposite sides, he speaks of concentric, radial, collateral, and bicollateral bundles respectively.

In recent years Van Tieghem (Sur la polystélie, Ann. sci. nat. bot., sér. 7, tom. 3, p. 275; Traité de botanique, 1891, p. 673; Eléments de botanique, 1898, p. 83) has set up a very different hypothesis of the morphology of the fibrovascular system of the higher cryptogams and the phanerogams. The primitive type of vascular axis, according to his view, consists of a centrally placed stele (concentric fibrovascular bundle of De Bary), limited by a specialized inner layer of the cortex, the endodermis. This simple type of stele, which he calls monostelic, may be modified in various ways. It may for example divide by repeated dichotomy into two, four, eight, etc., exactly similar strands and thus become polystelic (Van Tieghem, Eléments de botanique, p. 179; Traité de botanique, p. 1370); or secondly, it may become enlarged and develop a central pith and radiating medullary rays, the parenchyma of which, is morphologically different from the fundamental tissues outside the stele. The fibrovascular strands which appear externally as the result of the formation of the medulla and its rays, are not morphologically comparable to the concentric steles of the polystelic type. This sort of central cylinder or stele, is found characteristically among the higher vascular plants, but occurs occasionally among the Pteridophyta, *e. g.* Osmunda and Todea; thirdly, in this type the endodermis

may become infolded between the bundles and breaking in the bottom of the sinuosities, may unite round the individual collateral strands. The pith by this process is supposed to become continuous with the fundamental tissues of the outside cortex. This type of axis is denominated astelic and is said to be characteristic of the Equisetaceae, the Ophioglossaceae, and many limicolous phaenogamous orders e. g., Ranunculaceae, Nymphaeaceae, Alismaceae, etc. This account by no means exhausts Van Tieghem's types, but is sufficient for the present purpose.

Strasburger (Histologische beiträge 3) in a recent comprehensive investigation of the anatomy of vascular plants, adopts Van Tieghem's views except in the case of the so-called astelic type, which he prefers to consider as monostelic, regarding the individual endodermal sheaths, which surround the bundles in this type, as not morphologically equivalent to the general endodermis, surrounding the complex of bundles in monostelic axes. This view is the result of two considerations; first, he is of the opinion that it is difficult to conceive that the pith of different species of the same genus should lie sometimes within and sometimes without the stele, as for example in the case of the Equisetaceae and Ranunculaceae; and, secondly, since he attributes a great physiological importance to the pith, in connection with the conductive functions of the central cylinder, he thinks it impossible to consider it as in any case separated from the bundles.

His first objection had really been anticipated by Van Tieghem (Journ. de bot., 1890, p. 365), however, in the case of the Equisetaceae. Van Tieghem there shows that the stem of the Equisetaceae is always astelic in the adult plant and that the pith is consequently always continuous with the cortex. Van Tieghem's theory however would scarcely allow of this explanation in the case of the Ranunculaceae, but it is not necessary to consider that group in the present connection. In the Equisetaceae, he has shown from Pfitzer's researches and his own, that the individual endodermal sheaths of the bundles and the internal general endodermis, where they occur, are at intervals continuous with the outer endodermis, and as Strasburger admits the morphological value of the outer endodermal layer, he must necessarily grant the same value to its inward extensions. In regard to his objection to separating the pith from the bundles very little need be said. The former is frequently absent or composed of dead cells, especially in perennial plants, so that in general it can scarcely have any very important conductive functions. Zenetti (Leitungssystem von *Osmunda regalis* Bot. zeit., 1895) has moreover recently shown that in *Osmunda regalis* where the presence of a distinct endodermis surrounding the leaf-bundles, makes it easy to decide, there are no strands of medullary tissue, accompanying the leaf-traces on their upward course, as Strasburger has suggested in connection with the important conductive functions, which he has assigned to the pith. We may accordingly conclude that Van Tieghem's conception of astely, in the case of the Equisetaceae at least, is not open to the objections suggested by Strasburger.

Van Tieghem's ideas, more or less modified by Strasburger's criticisms described above, have met with general acceptance and they are now found in almost all botanical text-books. As a consequence the morphological conceptions of Sachs and De Bary have been almost universally abandoned.

It is necessary to examine, whether these new ideas are really more in accordance with the facts, than those of Sachs and De Bary, and that this may be done more definitely the following citation from Van Tieghem's (Traité de botanique, 1891, p. 765) writings is put before the reader. " Le cylindre central étroit et sans moelle de la région inférieure de la tige, au lieu de se dilater, comme dans le cas ordinaire, au lieu de se rompre en faisceaux libéroligneux distincts, comme dans la structure astélique, s'élargit quelquefois en un ruban, qui bientôt se divise en deux par un étranglement médian. Chaque moitié s'aplâtit plus haut à son tour et se divise en deux et ainsi de suite." This is his description of the mode of development of his polystelic type.

In his essay on polystely (Van Tieghem, Ann. sci. nat., Bot., sér. 7, tom. 3) we do not find any specific instances, of the development of cryptogams, illustrative of the polystelic type. In a later publication, however (Traité de botanique, 1891, p. 1372), he gives the following brief account of the development of the stem of *Pteris aquilina.* " La Ptéride aquiline, par example n'a d'abord, jusque vers sa septième feuille, q'une stèle axile, plus haut, cette stèle se divise en une stèle dorsale et une stèle ventrale, formant un cercle unique ; c'est plus tard seulement que ces stèles produisent des branches qui séjournent dans l'écorce et y constituent un second cercle en dehors du premier." As this is the only example so far as I am aware, of a description on his part of the development of a cryptogamous stem of his polystelic type and as *Pteris aquilina* presents the greatest complexity of bundle-arrangement found among our common ferns, the writer proposes to describe briefly his own investigation of this form. The account here given does not depend on the study of isolated sections, but on that of numerous complete series of sections of the young stem, from the region of the foot to that where the characteristic arrangement of the bundles of the adult is reached.

Above the exit of the first leaf-trace the young vascular axis is a bundle-tube, which at first is so narrow, that no fundamental tissue is enclosed by it. Consequently in passing inwards we meet, first the external phloem, then the ring of vessels and innermost a core of phloem. At the height of origin of the fourth or fifth leaf, a core of fundamental tissue makes its appearance inside the internal phloem. Immediately above the point of origin of each leaf-trace there occurs a break in the continuity of the fibrovascular tube, which may be called the foliar lacuna. In the younger region of the stem, the internal and external bast-elements communicate through these lacunae, but, when the stem has reached the stage described above, where there is present internally a core of fundamental

tissue, the latter communicates periodically also with the fundamental tissue outside the tubular axis. The writer has not been able to discover here any indication of the repeated dichotomous division which Van Tieghem describes as characteristic of the stele of the young polystelic axis. On the contrary, if his observations are correct, there is present from the very first, a hollow tubular fibrovascular axis.

After from nine to twelve leaves have been formed in this way, the young stem, which up to the present has grown perpendicularly upwards, bifurcates and the two equal divisions plunge into the soil, and henceforth pursue the horizontal course, which is characteristic of the adult rhizome. In consequence of this horizontal course, the leaves no longer originate in a spiral manner, as in the younger upright axis, but come off alternately from the sides of the young rhizome. As a result, the foliar lacunae occur on opposite sides of the fibrovascular tube and frequently overlap, so that in certain planes of cross-section, there is presented the appearance of independent dorsal and ventral steles.

In the meantime a rod of brown sclerenchyma, oval in transverse section, has made its appearance in the midst of the fundamental tissue occupying the center of the stelar tube. At a point about two or three centimeters from the region of bifurcation of the young rhizome, the dorsal wall of the stelar tube becomes involuted, and gives off a bundle into its cavity, which is quickly surrounded by a tubular sclerenchymatous sheath, formed by the bending round it from below, of the rod of brown sclerenchymatous tissue already mentioned. The ensheathed single central vascular strand gives off branches to the leaves and is from time to time reinforced by additions from above. Subsequently it divides dorsiventrally into two, in a manner which need not be described here, and the original vascular tube having in the meantime become transformed into a complex tubular network of strands, the state of affairs which is characteristic of the adult is reached.

As the result of the observations described in the foregoing paragraphs, the writer has reached the conclusion that the outer bundles are not cortical, as is stated by Van Tieghem, and that the two large inner ones, which he appears to have confused with the dorsal and ventral primary strands of the younger horizontal rhizome, are in reality medullary strands. That the outer series is primitive is indicated, moreover, by the fact that both the root-traces and the leaf-traces are attached to it.

The above account gives little support to Van Tieghem's theory of polystely, since the young vascular axis is first and always a tube and does not become successively divided into two, four, eight, etc., strands, as he describes. It might be supposed that the state of affairs in *Pteris aquilina* is possibly abnormal, but the writer is in the position to assert, from the examination of the development of a large number of vascular cryptogams, belonging to the most different groups, that the course of development in *Pteris aquilina* is quite typical, and that there is no evidence in any case which has come under his notice

of the repeated dichotomy of the primitive strand which has been indicated by Van Tieghem. The writer's results in the example described moreover agree with those of Leclerc du Sablon (Ann. sci. nat. bot., sér. 7, tom. 11) for his figures and descriptions of the *younger* stages of the stem of *Pteris aquilina* are quite in harmony with the statements above. He has made the curious mistake, however, of regarding the mature rhizome of this species, as derived from an adventitious bud on the young plant, although Hofmeister's (Higher cryptogams, Ray soc., p. 213) account is correct in this respect.

The writer's study of the development of the stem in a wide range of North American and exotic Pteridophyta has led to the result that, in the vascular axes of stems, there are just two primitive types of stelar structure, *viz.*, the single concentric strand, and the tubular concentric strand, and moreover that all the varied complexities of the mature stem may readily be derived from these by the study of development in the individual cases.

There can be little doubt that the simple concentric strand is the more primitive type, and that the tubular concentric strand was subsequently derived from it. The writer is inclined to attribute the origin of the tubular type to the action of mechanical causes, but it would be out of place to discuss this subject at the present time. The two primitive types of stele described above may, however, be appropriately designated, protostelic and siphonostelic respectively.

In the protostelic axes of the Hymenophyllaceae we generally find the concentric type of stele, but in the genus Hemiphlebium (Prantl, Die Hymenophyllaceen, Plate 4, figs. 61, 62) the bast disappears on the lower side of the stele, which thus becomes collateral. The Ophioglossaceae afford examples of this unilateral degeneration of the bast in siphonostelic stems. From a study of the development of the young stem of species of Ophioglossum and Botrychium the writer is able to state that there occurs here the same stelar tube as in the young stem of *Pteris aquilina*. The two types differ only in the absence of internal bast in the former. The researches of Poirault (Recherches anat. sur les crypt. vasculaires, Ann. sci. nat., bot., sér., 7, tom. 8), and Van Tieghem (Journ. de bot., 1890) have demonstrated the presence of an internal endodermis in the young stem of various Ophioglossaceae. It is interesting also to note that the leaf-traces of *Botrychium virginianium* are concentric, and like those of the cycads retain in all probability a primitive type of organization, which has disappeared in the bundles of the stem.

Our examples have up to the present been drawn from the Filicales. The primary vascular axes of living Lycopodiales rarely present the phenomena of siphonostely. A good example, however, is to be found in *Selaginella laevigata* Blk., var. *lyallii* Spr. The stelar tube in this case resembles that of *Pteris aquilina* and has likewise a pair of medul-

lary strands. In a photograph 1 (Pl. 27, fig. 1), the stelar tube appears with a lacuna in its side, where the vascular strand of a branch has been given off, this gap is the ramular lacuna. The leaves originate from the stelar tube, however, without causing any break in its continuity. Photograph 2 (Pl. 27, fig. 2) shows the restoration of the integrity of the tube below the point of origin of a subsequent branch.

In photograph 3 (Pl. 27, fig. 3), we have a copy of Williamson's figure (Phil. trans. roy. soc., 1881, Pl. 52, fig. 9) of the tubular stele of *Lepidodendron harcourtii*. The vascular tissues in this form are likewise arranged in a tubular fashion. The leaf-traces are small and cause, according to his description, no interruptions in the walls of the tube. Where a branch is given off on the contrary, as in the figure, there occurs a ramular lacuna. Both Renault (Cours de bot. foss., tom. 2, p. 71) and Gibson (Annals of bot., vol. 8, p. 192) have been struck by this resemblance between *Selaginella laevigata* var. *lyallii* and *Lepidodendron harcourtii* (other species of Lepidodendraceae had similar peculiarities, *e. g.*, Halonia, Ulodendron, and species of Sigillaria, etc.), and Bertrand (*Phylloglossum drummondii*, Arch. bot. Nord France, 1885, p. 71) considers his Centradesmideae (in part) as belonging to the same type.

In comparing these instances with the examples taken from the Filicales, it is to be observed, that while both cases represent siphonostely, there is this marked difference between them: in the filicineous stems the siphonostely is characterized by the occurrence of foliar lacunae, while in the lycopodineous axes it is related to ramular lacunae. Without going further into the matter at the present time, the hypothesis is presented that siphonostely has a mechanical significance, and that in the case of the Filicales, the siphonostelic modification of the vaso-skeletal tissues arose in connection with the support of large leaves. Among the Lycopodiales it made its appearance on the contrary, in relation to the support of secondary axes. We may consequently call the siphonostely of the Filicales phyllosiphonic, and that of the Lycopodiales cladosiphonic.

At this stage we come naturally to the discussion of the bearing of these morphological conceptions, assuming that they are well founded, on the phylogenetic position of the Equisetaceae. In this connection it is necessary to examine with some care both the structure and development of the genus Equisetum, and since certain of its features can only be understood in the light of a knowledge of its ancestors, it will likewise be necessary to refer as briefly as may be to the organization of the Calamites and Sphenophyllales. It will conduce to clearness and brevity of exposition to begin with the extinct groups and subsequently to describe their living representatives.

## CALAMITES.

The Calamites first make their appearance in the Silurian deposits (Stur, Sitzungs-berichte akad. d. wissensch. Wien, bd. 83, p. 409) but their petrified relics and casts are so rare in these earlier strata, that the upper Devonian and lower Carboniferous beds give us the first definite idea concerning the organization of the more primitive representatives of the group. One of the oldest Calamites of which we possess any detailed information is the genus Archaeocalamites Stur. (Stur, Abh. d. k. k. geol. reichsanstalt, Wien, bd. 8. Heft 1. Culm-flora d. mährischen-schlesischen dachschiefers. Heft 2 Culm-flora d. ostrauer u. waldenburger schichten.) In this form there is present the jointed stem which is characteristic of the modern Equiseta. The ridges and channels of the stem, however, differed from those of Equisetum in not alternating at the nodes. The leaves which originated in the nodal region and were not united into sheaths, but were quite free from one another and dichotomously divided. The roots also appeared in relation to the nodes and were often forked like the leaves. Branches were frequently present in the nodal region, but they do not seem to have been very numerous. Of the nature of the strobili of this genus, very little is known, as they have been very imperfectly preserved. The vascular frame-work, with which we are fairly well acquainted, as the result of the investigations of Göppert, Renault, and Solms-Laubach, had the same general features as that of Equisetum, differing only in its continuous strands, and its secondary growth in thickness by means of a typical cambium.

The Calamites proper, differed from Archaeocalamites in their generally undivided leaves, and the continually more pronounced (in more recent strata) alternation of their vascular strands at the nodes. They possessed, like the older type, a cylinder of secondary wood. Their strobili are comparatively well known and vary greatly in structural details, presenting throughout a marked contrast to Equiseta, in the probable division of their sporophylls into dorsal sterile, and ventral generally peltate sporangia-bearing segments (Scott, Cheirostrobus, Phil. trans. roy. soc., 1897, B). According to Williamson and Scott (Phil. trans. roy. soc., 1894, B. p. 864, 868, 890) their branches originated, in contrast to those of Equisetum, above the nodes. From Weiss (Steinkohlen-Calamarien, Heft 2, p. 34), we learn that the roots of the Calamites were attached either at the nodes or slightly to one side (he does not say, however, which side).

Most frequently calamitean remains occur as casts of the medullary cavities. These casts represent accurately the inner configuration of the fibrovascular cylinder and are consequently constricted at points corresponding to the nodal woody rings and channelled along the course of the primitive bundles. As the primary rays between the primitive bundles were bridged over more or less rapidly by the secondary wood, they appear

merely as broad, rounded, longitudinal elevations on the cast between the depressions above mentioned. At one side of the nodal circular depressions and on the ends of the rounded ridges corresponding to the primary medullary rays, there occur frequently knob-like projections. Sometimes less marked tubercles appear in a similar position on the other side of the node.

Brongniart (Hist. des végétaux fossiles) who did not realize that he was dealing with casts, explained the larger nodules as representing rudimentary branches and roots (p. 109), and curiously enough considered them to occur on the upper side of the node, although he was clearly aware that in *Equisetum fluviatile*, which he used as the basis of his comparison, the roots and branches come off below the articulations, and alternately with the leaves (p. 103). The other and often absent zone of tubercles he explained as undeveloped leaves (Brongniart, *op. cit.*). His ideas concerning the rudimentary character of the organs represented by the tubercles probably originated from the observation that in specimens, which are otherwise apparently well preserved, the nodules in question are frequently entirely absent. Subsequent investigations, which need not be detailed here, established the fact that in branching rhizomes, the orientation of which can be inferred, the more conspicuous nodules of the cast occur below the node and at the upper end of the longitudinal ridges.

It has not been so easy to settle the nature of the anatomical features of the calamitean woody cylinder, which gave rise to the ring of more prominent tubercles. In photograph 4 (Pl. 27, fig. 4), which is copied from Williamson (Phil. trans. roy. soc., 1871, pl. 26, fig. 22), we see a tangential section of the primary bundles of a Calamite, which is so close to the medulla that the carinal canals of the protoxylem of the bundles are laid open. It is to be noticed, that the course of the bundles is the same as in Equisetum, except, that on the left of the figure no alternation takes place at the node. Above the node are represented the vascular strands belonging to branches, or as has been stated more recently (Williamson and Scott, Phil. trans. roy. soc., 1894, B., p. 876) to leaves.

It is to be observed that these writers assume for the Calamites a different relation of the branches to the nodes, from that obtaining in Equisetum, *i. e.*, that they originated above the node and not from the node, as in the latter (Williamson and Scott, *op. cit.*, p. 890). In the medullary rays, below the nodal wood, the parenchyma is seen in spots *l* to be somewhat disintegrated. In photograph 5 (Pl. 27, fig. 5) which is a copy of a figure (Williamson, Phil. trans. roy. soc., 1878, plate 20, fig. 23) representing a more external longitudinal section passing through the secondary wood, may be seen the branch-traces *m* (or leaf-traces as they were later called) no longer running free in the upper medullary rays, but arched over more or less by strands of secondary wood. In the lower rays disintegration has gone so far that actual cavities, *l*, have made their

appearance. Such cavities were considered to be definite canals by Williamson (*op. cit.*, 1871, 1878), and he accordingly called them infranodal canals. He expressed the opinion that the larger series of tubercles described above, as occurring on the pith-casts of Calamites are moulds of these canals in stone. Subsequently in collaboration with Scott (Phil. trans. roy. soc., 1894, B., plate 78, fig. 11) he published a figure, which is reproduced in our photograph 6 (Pl. 27, fig. 6), which may be considered as representing a tangential plane of section, somewhere between those of the two former figures, reproduced in our photographs 4 and 5 (Pl. 27, fig. 4, 5). In this figure the traces making their exit in the superior medullary rays, are no longer considered as belonging to branches, but on the contrary to leaves (Phil. trans. roy. soc., 1894, B., p. 876).

Stur (*op. cit.*) from the study of the casts of various Calamites and of the stem of their modern representatives, the Equiseta has reached certain conclusions which it will not be profitable to consider fully. He states, however, that Williamson's figure, reproduced in our photograph 4 (Pl. 27, fig. 4), is inverted, and that the areas of disintegrated parenchyma, which by the inversion of the figure in question, he places in the upper medullary rays are due to the disappearance of leaf-traces. He enforces this contention by objecting that Williamson's figures make the branches arise above the node and not below it, as he thinks should be the case, from the analogy of Equisetum. He comes to the conclusion that the infranodal canals of Williamson are consequently supranodal indications of leaf-traces, and that the large nodules of calamitean casts, already referred to, are as a result above the node, which hardly follows from his course of argument. It is, moreover, in many cases certain that the larger nodules are below the nodal constrictions of the casts, for reasons which have been already indicated.

Weiss (Steinkohlen-Calamarien, Heft 2) has more recently discussed the vexed question of the tubercles, and after calling attention to Stur's inversion of the casts, expresses his opinion that the disputed nodules, probably represent the points of attachment of either roots or leaves. He realizes that their occurrence below the nodes, and in alternation with the vascular strands, makes it difficult to regard them as related to the leaves. This would seem to lead to the alternative, that they are the indications of the attachments of roots. He does not draw this inference, however, although he records the fact that the nodules are absent entirely, or very imperfectly represented, on parts of Calamites which are undoubtedly aerial (*op. cit.*, p. 24). He leaves the question of their interpretation open, having previously stated that he does not regard the nodules as casts of Williamson's infranodal canals.

Solms-Laubach (Fossil botany, Eng. ed., p. 301–315) discusses at length the organization of the calamitean stem, and the nature of calamitean casts. As a result of the consideration of all the evidence, he comes to the conclusion, that the more conspicuous

series of nodules on the medullary casts of the Calamites are really infranodal, and agrees with Williamson in regarding them, as the result of the regular disappearance of tissues in the lower medullary rays, but considers that the disintegration is due rather to unequal maceration, than to the presence of any special organs or canals. The opinion of Graf zu Solms in such matters rightly carried great weight, and after its expression practically in favor of Williamson's view, the latter thought it no longer necessary to defend his hypothesis (Williamson and Scott, Phil. trans. roy. soc., 1894, B., p. 888).

Seward in his recent admirable treatise on fossil plants (1898, p. 324) adopts Williamson's explanation as quite proved, and does not even discuss the other views.

Renault (Etudes des gîtes minéraux de la France, fasc. 4, atlas) has recently published figures of tangential sections through the inner part of the secondary wood of Calamites, in which are represented the usual more or less constantly alternating vascular strands. Above the nodal anastomoses, and at the bottom of the upper medullary rays, are indicated radiating traces, $o$, which are stated in the description of the plates to be "aquiferous organs." Below them are represented smaller traces, $f$, embedded in the vascular strands, which are regarded by this author as leaf-traces. His "aquiferous organs" are undoubtedly the homologues of the "leaf-traces" of our photograph 6 (Pl. 27, fig. 6) copied from the monograph of Williamson and Scott. In the full descriptive text, which appeared three years after his plates Renault (Etudes des gîtes minéraux de la France, fasc. 4, p. 93) informs us that his figures, one of which is copied in our photograph 1 (Pl. 28, fig. 1) should be inverted, and that his "aquiferous organs" are really "organes rhizifères" which he regards as the equivalents of Williamson's infranodal canals. He states also that he has found roots in connection with the organs in question. These observations open up again the whole subject of the infranodal canals, and it is to be regretted that Renault has not given us reasons for the subsequent inversion of his figures.

As will be shown in the sequel, a consideration of the structure of Equisetum gives us criteria for explaining all the foregoing conflicting accounts and apparently for settling this much-disputed question.


## Sphenophyllales.

There remains to be said something concerning the organization and structure of the Sphenophyllales. Like the Calamites and Equisetaceae, they had a regularly jointed and furrowed stem. The ridges of the stem did not alternate. The leaves somewhat resembled those of Archaeocalamites in being dichotomously divided, and were arranged in superposed whorls. The branches, according to the account of Renault (op. cit.,

p. 170), originated at the nodes, and he tells us that they came off from the stem between the leaves, and consequently like those of Calamites and Equisetaceae were not axillary.

The fructifications of the Sphenophyllales were cones of superposed verticils of sporophylls. These consisted of a dorsal sterile segment, and one or more ventral sporangiferous segments, bearing as a rule on their upper surface a single sporangium which hung inwards towards the axis of the cone. Solms-Laubach (Jahrbuch geol. reichsanstalt, 1895, vol. 45, p. 239) has recently described an interesting strobilus, *Bowmanites römeri*, belonging to this group, in which the sporangiophores are transversally peltate like those of the cycad Encephalartos.

The most interesting cone of this class, however, is that of which Scott (Cheirostrobus, Phil. trans. roy. soc., 1897, B.) has still more recently given an account. The sporophylls of Cheirostrobus are arranged in superposed verticils of twelve members. Each sporophyll consists of a dorsal and a ventral tripartite segment. The former is sterile, and the latter has each of its three divisions developed into a typical peltate sporangiophore bearing four sporangia. This author calls attention to the marked resemblance of his cone to the calamitean Palaeostachya and Calamostachys.

The internal features of structure in the stem of the Sphenophyllales were remarkable. There was a protostelic triarch, hexarch, or dodecarch (Cheirostrobus) central cylinder. The groups of protoxylem were generally distinguished by the presence of carinal lacunae as in Equisetum. The central cylinder was further characterized by the presence of a peculiar secondary wood. Other points of anatomy need not be considered here.

## Observations on the Genus Equisetum.

The development of the prothallus of Equisetum has been very elaborately studied by Buchtien (Entwick. prothall. von Equisetum), and the writer's investigations accord in their results with his, so far as they have gone. The gametophyte consists of a median vertically growing fleshy axis terminated by meristematic tissue, in which it is not possible to make out a definite apical cell. From this terminal, actively dividing tissue lateral lobes are produced, to which the sexual organs have a definite relation. The main axis seldom forks in *E. limosum* and *E. arvense*, but frequently does so in the large prothalli of *E. hiemale* chiefly studied by the writer, and there may be as many as four or five secondary axes in the latter species.

The antheridia are formed at the tips of the lobes in a manner which has been often described and need not be referred to here. The antherozoids likewise do not

require special description, as they have been fully investigated in recent years by Buchtien and Belajeff.

The archegonia, however, require more attention. They originate, as has been observed by other writers, frequently, but not invariably, near the base of a prothallial lobe. A superficial cell becomes more rich in protoplasm than its neighbors, and undergoes transverse division into nearly equal parts, in this respect presenting a contrast to the mother-cell of the archegonium of the isosporous Filicales, where the first division results in the formation of a shallow outer cell and a much deeper inner one, Pl. 26, fig. 1. The young archegonium in the two-celled stage resembles closely that of *Lycopodium clavatum* (Bruchmann, Ü. d. prothal. u. d. keimpflanzen mehrer. europ. Lycopod., Pl. 3, fig. 12; I am indebted to Dr. G. L. Goodale for calling my attention to this recent work) of the same age. Treub (Annales du jardin bot. de Buitenzorg, tom. 4, 5) unfortunately does not figure such early phases in the case of *L. cernuum* and *L. phlegmaria*. In Pl. 26, fig. 2, is represented a later stage, in which the inner cell has become equally divided by a second transverse wall. The outer cell at nearly the same time becomes bisected by a perpendicular wall. Frequently the outer cell at this time is still undivided, and in such cases the perpendicular row resembles the three cells of the young archegonium of the isosporous Filicales, but the significance of the cells in the two cases is very different, in the former they are cervical cell, cervical canal-cell and central cell; in the latter, cervical cell, central cell, and basal cell. It was probably an archegonium at this stage of development somewhat obliquely cut and consequently showing only part of the central cell, which led Campbell (Delt. of mosses and ferns, p. 430, fig. 223b) to make the statement that a basal cell sometimes occurs in the Equisetaceae.

Janczewski (Bot. zeit., 1872, p. 420), Sadebeck (Schenck, Handbuch d. bot., bd. 1, p. 196), and Buchtien (*op. cit.*, p. 25), all agree in stating that there is no basal cell in the archegonium of the genus Equisetum, and with this assertion my own observations on a large number of examples of *E. hiemale*, *E. limosum*, and *E. arvense* are quite in accord. Pl. 26, fig. 3, represents a young archegonium of *E. hiemale*, in which the central cell has already given off the ventral canal-cell, and as a result has become the egg-cell. The neck has become further developed and the cervical canal-cell is beginning to push its way upwards. In Pl. 26, fig. 4 is represented a nearly ripe archegonium. The neck remains short in *E. hiemale*. The cervical canal-cell has become longitudinally divided into two, a peculiarity which has only been described elsewhere in *Lycopodium phlegmaria* (Treub, Ann. du jardin bot. Buitenzorg, tom. 5, pl. 21, figs. 9 and 10). The ventral canal-cell has already begun to degenerate. Around the egg-cell cells are cut off from the prothallial cells, by walls parallel to its surface, a feature first observed by Hofmeister and confirmed

frequently by subsequent writers. The development of the archegonium in *E. limosum* and *E. arvense* is practically identical with that of *E. hiemale*, which has been described above, and they have the same peculiar longitudinally divided cervical canal-cell. Pl. 26, fig. 5 represents a nearly ripe archegonium of *E. arvense*. In the two last mentioned species the neck is very much longer than in *E. hiemale* and consists of three or four tiers of cells. The uniform occurrence of longitudinal division in the cervical canal-cell of these three species is interesting and probably indicates that this feature will be found to be common to the group. Campbell (Mosses and ferns, p. 427), however, figures a transverse division for *E. telmateia*. Sadebeck (Engler u. Prantl, Nat. pflanzenfam., teil 1, abteil 4, p. 2) has recently published a figure of the archegonium of *E. arvense* which does not at all agree with Fig. 5, but as he does not represent in it the divisions of the prothallial cells parallel to the surface of the egg, and the cuneate insertion of the neck of the archegonium which have been noticed by practically all other observers, beginning with Hofmeister, his representation must be regarded as somewhat diagrammatic.

The first division of the egg is transverse, the basal wall being generally somewhat oblique. The inclination of the basal septum is sometimes towards the apex and sometimes towards the base of the prothallus, more frequently, however, towards the former. It has not been possible to absolutely settle the order of the next two divisions, but it is probable that the median wall is formed first. The transverse wall often does not extend at first entirely across the embryo, especially in the hypobasal half. The apical cell is early formed in the epibasal portion, and in the hypobasal half, an apparent apical cell is also differentiated. These features are shown in Pl. 26, fig. 6, which is almost identical with Hofmeister's (*op. cit.*, Pl. 39, fig. 2) illustration of a similar stage. The development of an apparent apical cell in the lower half of the embryo, and a tacit homologizing of that region with the corresponding region, as regards the substratum of the leptosporangiate embryos, with which he was familiar, led him into the error of regarding it as the embryonic primary axis. As its regular segmentations soon cease, and it is thrust aside by the growth of the upper portion of the embryo, he regarded the primary axis of Equisetum as abortive. The real primary stem-apex in the upper part of the embryo of Pl. 1, fig. 6, he regarded as that of a secondary shoot, an error which has been recognized by Sadebeck (Pringsheim's Jahrbücher, bd. 11, p. 581), and subsequent observers. Sadebeck (*op. cit.*) informs us that in the case of *E. arvense* and *E. palustre*, the development of which he has studied, the epibasal cell gives rise immediately to the primitive shoot-axis, from which the first whorl of leaves is derived exactly as are the subsequent ones. This statement I am not able to confirm exactly, for in *E. hiemale*, which I have particularly studied, the rudiment of the first root appears very early, next the apical cell, and on the side of it which faces the apex of the prothallus. Pl. 26, fig. 7, shows an embryo at this stage, the

cells of which have been outlined with the camera lucida, *a* is the apical cell and *r* is the rudiment of the root. It might be thought that another cell, further down on the right of the young embryo, is really the radical rudiment, but that such is not the case may be determined from the next figure, which is a lrawing of an older embryo made with the camera lucida. The upwardly directed arrows in the two last mentioned figures indicate the direction of the neck of the archegonium, and those pointing downwards, the position of the embryos in relation to the substratum, as inferred from the course of the prothallial root-hairs. It will be seen from these figures, that the root appears very early in *E. hiemale*, and in all probability is derived from the epibasal region of the embryo. It presents in the latter feature a close correspondence to the state of affairs observed by Treub (*op. cit.*) and Bruchmann (*op. cit.*) in the embryos of *Lycopodium cernuum*, *L. phlegmaria*, *L. clavatum*, and *L. complanatum*. The segmentations of the apical cell become numerous before the first whorl of leaves makes its appearance in embryos of nearly twice the size of that of Fig. 8. It is accordingly not easy to trace the members of the first foliar whorl to the epibasal octants by allowing, as is usually done, one for the apical cell, and one for each of the three primary leaves. It would seem to be a more reasonable procedure to compare the embryo of Equisetum rather with those of the Lycopodiales, concerning which we have in recent years so much information, which was entirely lacking when the fashion of comparing all embryos with those of the probably highly specialized leptosporangiate ferns originated. Such a comparison would lead to our deriving both root and shoot from the epibasal half of the embryo, and leaving the whole hypobasal portion for the foot. Without, however, attaching too much importance to this comparison, it may be safely stated that the primitive root of *E. hiemale* originates high up on the side of the embryo and in close relation to the primitive shoot. As the embryo develops, the root gradually descends, and finally as it begins to push its way out, becomes the most inferior organ of the embryo. The young root is directed towards the apex of the gametophyte and alternates with the two anterior leaves of the first foliar whorl. The first so-called adventitious bud originates above the point of origin of the first root, and likewise between the two primary leaf-traces. The secondary axis differs from the primary in not producing the rudiment of the root, till the first foliar whorl is clearly indicated, as a fold round the secondary stem-apex. About the time of the appearance of the first adventitious bud, and when three or more whorls of leaves have been formed on the young axis, the shoot breaks through the calyptra, the root having previously in the case of *E. hiemale* and *E. arvense* made its way into the soil. In *E. limosum* the root develops very slowly and does not enter the soil till long after the shoot has made its way out. This is probably the result of its amphibious mode of life, as many plants of this habit have a poorly developed primary root e. g., *Nelumbium luteum*. The writer has not a sufficiently

complete series of embryos of *E. arvense* and *E. limosum* to describe completely the embryogeny of these species. Moreover, the examination of the earlier phases of development is rather to be passed over in this essay since a good deal of attention will be given to the later stages which have been almost entirely neglected by previous writers.

The first shoot of *E. hiemale*, after bursting through the calyptra, forms from six to twelve segments, and then ceases to grow. Some time previously, however, the first so-called adventitious shoot has emerged below the point of attachment of the first foliar whorl of the primary axis. This secondary axis is terminated inferiorly by a root which originates below its primary whorl of leaves or ochreola. The secondary axis is followed by a tertiary axis which springs from below its first sheath and between two leaf-traces. These features are represented in Pl. 26, figs. 9, 10. The next figure shows us a somewhat older plant, in which a number of shoots have been successively formed in the order indicated by their numeration. It is to be observed that each shoot has a corresponding root. In the stouter later shoots the nodal buds, which develop normally as shoots, are no longer confined to the basal nodes, but appear also in relation to the higher articulations, as may be learned from Pl. 26, figs. 10, 11. As each new axis originates well down towards the attachment of the root of its predecessor, the later formed shoots are continually more deeply buried in the soil, Fig. 11. In *E. hiemale* twelve or more erect shoots are formed before a horizontal rhizome makes its appearance, from the base of one of the larger and more deeply buried secondary upright axes. It would be interesting to discover if the depth of the parent axis in the soil has anything to do with the formation of these plagiotropic shoots; the writer, however, has not made any experiments in this direction. The first shoot of *E. hiemale* has foliar sheaths of three members, the second shoot has frequently similar sheaths, but more often has whorls of four united leaves, then follow axes with verticils of four, five, and six members.

The writer's cultures of *E. limosum* did not produce plants of more than two developed shoots. It is apparently difficult to secure the proper conditions for the continued growth of this species, for, unlike *E. hiemale*, it does not live long under greenhouse conditions. Here the first shoot may have leaf-whorls of only two members; in fact, the plants grown from spores obtained from a swamp about fifty miles northeast of Toronto, were practically all characterized by this peculiarity. Buchtien (*op. cit.*, p. 40) has noticed a similar peculiarity in the case of *E. variegatum*. Sporophytes from spores gathered by the writer from plants on the border of Howard Lake in High Park, Toronto, had, on the other hand, almost invariably sheaths of three members. A study of the sporogeny showed that in the former case a considerable number of spore-mothers became disintegrated after the tetrad division had taken place. This did not occur in the material from High Park. It is possible that, in the first instance, too large an amount of spo-

rogenous tissue had given rise to spore-mothers and too little to the formation of tapetal cells, and, as a consequence, the resultant spores produced only depauperate plants. A series of observations in this direction might prove interesting in connection with Bower's theory of the origin of the sporophyte. Pl. 26, figs. 12 and 13, sufficiently illustrate the external features of the young sporophytes of *E. limosum,* and show that they do not differ essentially from those of *E. hiemale,* except in their greater delicacy, and in the smaller number of segments formed in the first shoot.

Turning our attention now to the internal development of *E. hiemale,* we find that in the first axis of the young sporophyte there is a gradual transition from the typical arrangement of the tissues in the root, to that obtaining in the base of the young stem. The central cylinder of the first shoot makes its appearance as an unbroken tube of reticulated tracheides. There are no typical protoxylem elements, although the internal tracheides are formed first. The primitive vascular axis, in fact, starts out with a similar organization to that which is found subsequently to recur at the nodes. The center of the vascular tube is occupied by parenchyma, which may be considered in the light of what is to follow, as belonging to the pericycle. Outside the ring of reticulated vessels occurs a zone of phloem, terminated by a typical endodermis, with the usual radial lignified bands. The rudiment of the second shoot causes an interruption in the continuity of the vascular cylinder of the primary axis above its point of origin which disappears again, at about the level of exit of the leaf-traces from the central cylinder. The latter do not cause any gaps in the vascular ring as they pass off, and it is only at a measurable distance above their points of origin, that the so-called foliar lacunae make their appearance. The first shoot-bud originates between two leaf-traces as do all the subsequent ones. The foliar lacunae described above, if they may so be called, divide the fibrovascular tube into three distinct strands which alternate with the leaves. These three strands differ from the woody ring below in having typical protoxylem elements, which lie in more or less characteristic carinal lacunae. They are surrounded by a common external endodermis. At a point two or three millimeters above the exit of the leaf-traces of the primary whorl, a cell makes its appearance in the midst of the internodal bundles, which is characterized by having endodermal markings on its walls; still higher up this gives place to a radiating group of cells, which have endodermal dots about the middle of their radial walls. Just above the exit of the leaf-traces of the next whorl, that is at the base of the next internode, the internal endodermal elements disappear. They again become evident at a short distance above this point, only to disappear again above the exit of the leaf-traces of the next internode. These variations recur in all the segments of the first shoot and need not be further described. In the higher internodes, however, the internal endodermis shows a tendency to unite with the outer one, just below the continuous rings of reticulate vascu-

lar tissue which mark the nodes. It is impossible, however, even in the unbroken series of thin sections, which the writer has studied, with the aid of phloroglucin and hydrochloric acid, to be sure that such a union actually takes place, as the indications consist only of somewhat irregular endodermal streaks radiating out from the internal endodermis, at the points described above. From the state of affairs in the adult stem (Pfitzer, Pringsheim's Jahrbücher, bd. 6; Van Tieghem, Journal de botanique, 1890, p. 365 *et seq*), it might be expected that we should find similar indications just above the nodes, but they do not occur.

The first node of the second shoot has likewise a pith of pericyclic origin. Here again the internal endodermis makes its appearance only above the primary node. The internal endodermis of the second shoot, however, is continuous throughout the secondary axis and does not disappear at the nodes. It clearly unites moreover with the outer endodermis below the nodal vascular rings. In subsequent shoots the internal endodermis is likewise continuous and finally in shoots of five or more bundles it is found also in the primary node and is continuous with the internal endodermis of the parent axis. It is in shoots of five bundles that the internal endodermis first unites with the external, above as well as below the nodes, as in the adult plant. The primary axis does not develop nodal buds other than the basal one, except in some of its higher nodes, and these seldom under ordinary conditions give rise to branches. The second, third, and subsequent shoots have one or more dormant nodal buds at all their nodes. Quite frequently there is an increase in the number of vascular strands in passing from a lower internode to a higher one. In one example, where four strands were present in the first internode, five were found in the second and six in the third, after which the number remained constant. This feature is interesting, as repeating on a small scale a phenomenon which was of common occurrence among the Calamites.

*Equisetum limosum* is very similar to *E. hiemale* in the particulars of its internal development. The only differences which need to be noticed are those which have reference to the distribution of the endodermis. In the first shoot of this species, whether bifascicular or trifascicular, there are no indications whatever of an internal endodermis, although as may be seen from photograph 2 (Pl. 28, fig. 2) the outer endodermal sheath is well developed. The second shoot of *E. limosum* in my specimens was too immature to show the endodermal marking.

The arrangement of the endodermis in the young stems of these two species of Equisetum does not appear to offer very much support to Van Tieghem's (Journ. de botanique, 1890, p. 370) hypothesis of astely, for in accordance with his conception of the origin of astely, the primitive type had above the first whorl of leaves, bundles individually surrounded by endodermal zones, and these individual zones

becoming subsequently fused gave rise to a continuous outer and a continuous inner endodermis. It is not unreasonable to expect to find some evidence of this in the young stem. If anything may be argued from these embryological results, the primitive condition would seem to have been one in which there was both an outer and an inner endodermis. This subject, however, will be more satisfactorily discussed at a subsequent stage.

Having examined the external and internal development of the young sporophyte of Equiseta we may now turn our attention to certain features of the adult, which are either in themselves interesting, or which are of importance in coming to any conclusions concerning the affinities of the Equisetaceae.

Photograph 3 (Pl. 28, fig. 3) represents a transverse section through the nodal region of the subterranean stem of *E. hiemale*. On the outside of the stem and on the carinal ridges are to be seen certain projecting organs, *a*, of a parenchymatous nature. These are situated opposite the points where the leaf-traces leave the central cylinder to pursue their upward course in the foliar sheaths. They were noticed by Brongniart (*op. cit.*) in *E. litorale*, but apparently have not been elucidated since. At *b* in the same photograph may be seen the origin of a root-trace. At *c* there is present a shoot-bud. This has several roots attached to its lower end which do not appear in the plane of section. Photograph 4 (Pl. 28, fig. 4) represents more highly magnified one of the organs referred to above. The sclerenchymatous cortex of the rhizome is here interrupted by a strand of parenchymatous tissue which extends from the leaf-trace outwards. These organs may be conveniently called nodal organs. Their constituent parenchymatous tissue is of a loose and spongy nature, and their organization is quite similar to that of the lenticels which occur on the roots of the higher plants, and we probably shall not go very far astray in considering that these peculiar nodal organs of certain Equiseta have the function of permitting an interchange of gases through the otherwise impervious integument of the rhizome. They make their appearance on the subterranean parts of quite young plants of *E. hiemale* as well as in the adult.

Photograph 5 (Pl. 28, fig. 5) shows an entire thin transverse section through the nodal region of *E. silvaticum*. At *a* are the nodal organs similar to those of *E. hiemale*. The origin of root-hairs from the epidermis of the rhizome may also be clearly made out. The outer zone of the cortex is parenchymatous, and internal to it occurs a ring of brown sclerenchyma, the continuity of which is broken by the spongy parenchyma of the nodal organs or by root-traces, *b*. Inside the sclerenchymatous zone occurs a third, which is of a parenchymatous nature and adjoins the bast of the fibrovascular bundles. The central cylinder is seen to give off six processes, five of which are root-bases and one a dormant branch, *c*. Alternating with these and much smaller are the leaf-traces, *d*, subtending

internally the nodal organs, *a*, where these are present. The central cylinder in the nodal region, as has been often described, forms a continuous ring in which the vascular tissue, instead of being scanty and separated into individual bundles, each characterized by an internal lacunar protoxylem, as is the case in the internodes, is massive and entirely devoid of typical protoxylem elements. At the lower side of the photograph the leaf-traces have quite cleared the central cylinder, and it is to be noticed as a feature of importance, which will be subsequently referred to more at length, that the nodal vascular ring is quite unbroken by their exit. In the upper part of the figure, the medulla is seen to extend outwards into the root-bases.

Photograph 6 (Pl. 28. fig 6) is of a section through the nodal region of *E. arvense*. The nodal organs are absent in this species, but the rhizophoric buds, *c*, are better developed than in *E. hiemale* and *E. silvaticum*. The fact that the so-called foliar lacunae do not appear immediately above the leaf-traces, as they should from the analogy of the Filicales, but are separated from them by the nodal wood, may also be inferred from this section, which on the whole closely resembles that of *E. silvaticum*. Nodal organs have been found by the writer only in *E. hiemale* and *E. silvaticum*, and are absent in *E. variegatum*, *E. arvense*, and *E. limosum*.

In the next photograph (Pl. 29, fig. 1) is shown part of the section through the node of *E. limosum*. In this species all the nodal buds develop as rhizophoric organs except one or two. At *c* is the single large ramular bud and at *b* are the rhizophoric organs. The other features of the section need not be described.

Turning our attention now to the longitudinal topography of the stem of Equisetum we have in photograph 2 (Pl. 29, fig. 2) a tangential section of the nodal region of *E. hiemale* the plane of which is sufficiently deep to lay open the vallecular canals, *l*, of the lower internode; a branch, *c*, is making its way out through one of these. The magnification is sufficient to show that the medulla of the branch is composed of brown sclerenchymatous cells, and that its wood, which is no doubt to be regarded as the nodal wood of the first segment of the branch, is devoid of lacunae, such as occur in the internodes, and forms a ring, the vessels of which are still immature on the upper side. Above the branch are present four leaf-traces, *t*, which are about to assume an upward course in the foliar sheath of the main stem. The more profound tangential section of photograph 3 (Pl. 29, fig. 3) shows clearly the arrangement of the fibrovascular bundles at the node. Each bundle from the lower internode widens out at the node and the contiguous strands become thus united. From this ring of nodal wood the bundles of the upper internode take their origin in alternation with those of the inferior internode. A branch, *c*, is starting from the lower border of the nodal wood between two lower vascular strands, and, although the plane of section is so deep

as to pass through the very base of the branch, there is still a wide brim of nodal wood above the latter. The leaf-traces, as may be learned from the examination of a series of tangential sections, originate on a level with the lower surface of the branch-traces, but as they pass outwards, rapidly pass above the latter, as may be inferred from photograph 2 (Pl. 29, fig. 2).

A deep tangential section is likewise represented in photograph 4 (Pl. 29, fig. 4). The arrangement of the bundles at the sides is the same as in the preceding photograph, but the two central bundles, between which a cluster of thick-walled cells indicates the starting-point of the medulla of a branch, do not alternate but are continued with those of the internode above. This phenomenon is not rare in *E. hiemale* and is of interest both because it has apparently not been noticed before in Equiseta, and because it exemplifies a mode of fascicular arrangement which was common at the nodes of the Calamites.

Radial sections show more clearly than tangential ones the relations of the branches to the nodal wood, and it is the more necessary to devote some attention to these features, because the opinion prevails that the branches of the Calamites in contrast to those of Equiseta originated above the node. Photograph 5 (Pl. 29, fig. 5) shows the topography of a radial section of an aerial stem of *E. hiemale*, at the point of origin of a branch. At *d* is the partially sclerified nodal diaphragm of the main stem, and below it at *n* is the nodal wood. From the lower half of the nodal vascular ring comes off a branch, *c*. The diaphragm of the first node of the branch is very deep, and is somewhat sclerified at the ends. Two roots, *r*, and a nodal bud, *k*, are attached to the basal node of the branch. The first leaf-sheath, or ochreola, is present inferiorly, but is abortive on the upper axial side. It is manifest that the aerial branch of *E. hiemale* arises neither above nor below the node but from the lower region of the nodal wood. Photograph 6 (Pl. 29, fig. 6) illustrates the topography of the origin of a rhizophoric bud from a node of the rhizome. The same general features obtain as in the last photograph, and it may readily be seen that here, too, the potential secondary axis originates from the lower region of the nodal wood. The lettering is the same as in the preceding photograph. A feature which is worthy of note is that, the first sheath of the bud, the future ochreola, is normally developed, as is generally the case in branches derived from the subterranean stem. The next photograph 1 (Pl. 30, fig. 1) illustrates the mode of origin of a stout upright branch from a deep horizontal rhizome; as before, *d* is the diaphragm, *n* is the nodal wood, and *r* is a root. Here, too, the branch arises neither above nor below the node but from the nodal wood, and since in this case the base of the secondary axis is very broad, it covers the whole of the node.

The next photograph 2 (Pl. 30, fig. 2) is of a radial section through the nodal

region of the rhizome of *E. silvaticum*. The branch, as in the other cases, originates from the lower region of the nodal wood.

From all these examples it will be sufficiently obvious that in Equisetum the branches arise neither above nor below the nodal wood but from it, and in the case of the smaller branches, from its lower border, and in that of the larger ones, more or less exactly from its central region. In *E. limosum* at the subterranean nodes, whether of upright or horizontal stems, there are present one or two branch-buds and a number of rhizophorous buds. From the latter as many as six or seven roots grow out into the soil, and the stem-region of the buds more or less completely degenerates. That these root-bearing pedicels are the morphological equivalents of branches is obvious for two reasons : in the first place they possess a typical medulla like the shoot-organs, and are thus distinguished from the pithless roots which are characteristic of the modern Equiseta; secondly, by examining the successive nodes of an upright branch, beginning below the soil and passing upwards, it is possible to distinguish all phases of transition between rhizophoric organs and typical leafy shoots These results are only confirmatory of those of Janczewski (Recherches sur le dév. des bourgeons dans les prêles. Mém. soc. nat. sci. Cherbourg, 1876, tom. 20), but it is important to have independent evidence in these matters as will appear in the sequel.

It has already been stated that the leaf-traces originate from the protoxylem of the bundles of the lower internode. Photograph 4 (Pl. 30, fig. 4) demonstrates the accuracy of this statement. The leaf-trace is separated rather widely from the surface of the nodal wood, and the endodermis forms a deep bay on the outer side of the node, between it and the leaf-trace, as is represented in Pl. 26, fig. 14.

Before leaving this part of the subject one interesting feature may be referred to. Photograph 5 (Pl. 30, fig. 5) represents a section of the nodal diaphragm of *E. hiemale*. It is easy to make out that the cells of the upper portion of the diaphragm are arranged in perpendicular rows, and that the lower members of the rows have become thick-walled, forming the characteristic sclerification of the diaphragm. These features are of considerable interest, because peridermal tissue has been recently described as occurring in the diaphragms of Calamites by Williamson and Scott (Phil. trans. roy. soc., 1894, B., p. 889). In the Calamites, however, there was no subsequent sclerification of its cells, the nodal diaphragms of this group being entirely parenchymatous (Williamson, Phil. trans. roy. soc., 1871, p. 505). A similar sclerified periderm has been found by the writer in *E. limosum*. In *E. silvaticum, E. arvense*, and *E. variegatum*, on the other hand no nodal periderm is present. The presence or absence of this feature may be of some use in the difficult task of tracing the relationships of the modern Equiseta. The palaeobotanical writers above referred to compare the periderm of calamitean diaphragms

with that abnormally formed in the pith of certain Campanulaceae, etc. It is probably equally justifiable to compare it with that occurring in certain cryptogams. Russow (Vergleich. untersuch., p. 117), for example, has described the existence of periderm in the Marattiaceae and the Ophioglossaceae and the writer (Trans. Can. inst., 1898, p. 284) has called attention to a similar formation at the bases of fallen leaves in *Botrychium virginianum*. The frequent separation of the stem of equisetoid plants at the nodes, as the result of normal or exceptional conditions, would make such a protection at these points of considerable importance. In this connection it is interesting to notice that the sclerified diaphragms of *E. limosum* extend to the outer margin of the vallecular canals. They thus surround the vascular bundles, just as is the case with the abciss-periderm of the leaf-stalks of Hippocastanum, etc.

Some of the results described in the foregoing paragraphs seem to the writer not to be without importance in connection with certain disputed points of calamitean anatomy referred to in the Introduction. The two features which are most worthy of consideration in this connection are the mode of insertion of the branches of the Calamites, and the nature and position of the organs which gave rise to the inferior series of nodules on calamitean medullary casts.

## The Branches and Infranodal Canals of Calamites.

Beginning with the first of these, the statement is commonly made by palaeobotanical writers that the branches of the Calamites in contrast to those of Equiseta originated above the node. Photograph 6 (Pl. 30, fig. 6) of the present memoir is a copy of a rare and beautiful specimen of a calamitean stem showing external features, figured in Weiss's admirable monograph (Steinkohlen-Calamarien, Heft 2, atlas, pl. 16, fig. 6). Several nodes are present, to which leaves are attached and the scars of a number of fallen branches are to be seen in a single horizontal row. On the lower margin of the branch-scars are smaller scars, which Weiss interprets as belonging to fallen leaves, but when he tells us that these fallen leaves are the appendages of a node which comes immediately below the branches, it is probable that the botanical reader, remembering the state of affairs in Equisetum, will hesitate to follow him. If a node is present in this position it is certainly not very obvious and is irregularly placed. Moreover, in similar specimens figured in an earlier monograph (Weiss, Steinkohlen-Calamarien, Heft 1, atlas, pl. 17, figs. 1 and 2), where the leaves were represented only by their scars, in accordance with the conviction that the branches arise above the node, he has considered the smaller scars, related to scars of fallen branches, as dipping down underneath the branches and coming up to the nodal line again in the intervals between the branches. In the example fig-

ured here, since the attached leaves are obviously situated in some cases immediately above the scars of the branches, he abandons that position, and assumes the presence of an intercalated node corresponding to the crescentic series of smaller scars on the lower margins of the branch-scars. The writer suggests that the crescentic rows of scars of the figure, copied in photograph 6 (Pl. 30, fig. 6), really belong to the basal whorls or ochreolae of the fallen branches and that as a consequence, so far as can be judged from external appearances, the branches of Calamites had the same relation to the node as those of Equiseta. The ochreolae of the Calamites were not continuous sheaths as in Equisetum but were composed of separate leaves. The ochreolae of the Equiseta not infrequently lack fibrovascular bundles and are often obsolete on the upper axial side of the branch. The occurrence of similar features in the Calamites is not improbable and these would account for the absence of leaf-scars on the upper margin of the branch-scars and for the non-retention of the ochreolar leaves, together with the normal leaves of the nodes of the parent axis in photograph 6 (Pl. 30, fig. 6).

But without attaching too much importance to the above explanation, it will be well to consider the internal relations of the branches to the nodes, as described in recent works on calamitean anatomy, and, at the same time, to examine the statements as to the nature and disposition of the organs which gave rise to the infranodal tubercles of certain calamitean casts.

In photograph 6 (Pl. 27, fig. 6), a copy, the original of which has been already indicated (Williamson and Scott, Phil. trans. roy. soc., 1894, B., pl. 78, fig. 11), is a representation of the nodal arrangement of the vascular strands of a Calamite, as seen in tangential section. It will be observed that these have, generally speaking, the same relation to each other at the node as is exemplified in our photograph 3 (Pl. 29, fig. 3) of *E. hiemale.* In the lower ends of the upper medullary rays are situated certain structures which Williamson and Scott (*op. cit.,* p. 876) consider to be leaf-traces. In photographs 4 and 5 (Pl. 27, figs. 4, 5), which are taken from Williamson's earlier memoirs (Phil. trans. roy. soc., 1871, pl. 26, fig. 22; ibid, 1878, pl. 20, fig. 23), these are represented as being the vascular strands of branches. The changed interpretation of the later memoir need not be considered for the present, although, as will be indicated subsequently, it is of some importance. In the later memoir already referred to, Williamson and Scott (Phil. trans. roy. soc., 1894, B., pl. 78, fig. 11) make the statement that the leaf-traces in the Calamites originated from the protoxylem of the bundles of the lower internode, and consequently, it may be assumed, below the nodal wood, since they inform us that the protoxylem came to an end below the node in Calamites, just as it does in the Equisetaceae. Returning now to the statement that the leaf-traces are found in the upper medullary rays and consequently above the nodal wood, it may be asked how they have got into this supranodal

position. It can be only in one of two ways: they must pass up on either the inside or the outside of the nodal wood. But before considering either of these possibilities, one of their figures (*op. cit.*, pl. 78, fig. 7) shows the leaf-trace running directly outwards from the protoxylem of the lower vascular strand and consequently below the node. This is a difficulty in connection with either of the above suggestions. Let us suppose that it does not exist, however, and imagine the leaf-trace to pass upwards inside the nodal wood. But this would involve the presence of ringed and spiral woody elements on the inside of the nodal wood, since the leaf-trace consists largely of these elements. They state, however (*op. cit.*, p. 872 and 877), that protoxylem· is absent from the inside of the nodal wood of the Calamites just as it is in Equisetum. These difficulties make us turn to the other alternative, that the leaf-traces pass to their supranodal position on the outside of the nodal wood. Photograph 4 (Pl. 27, fig. 4) is a reproduction of a figure from one of Williamson's memoirs (Phil. trans. roy. soc., 1871, pl. 26, fig. 22). The section which it represents is so profoundly tangential that the carinal canals of the protoxylem are laid open. The so-called leaf-traces are nevertheless already in their supranodal position, and consequently cannot have passed up external to the node. If, in spite of all these difficulties, the leaf-traces are still maintained to start outwards in the lower ends of the supranodal medullary rays, other difficulties make their appearance. All figures which indicate the internal relations of calamitean branches represent their vascular strands as running in the medullary rays and at the same time above the nodal wood. Since, according to William-son's and Scott's statement (*op. cit.*, 1894, B., pl. 78, fig. 11), the leaf-traces also run in the same rays and in the same relation to the nodes, the branches must originate in the axils of the leaves, which is not only contrary to the arrangement in Equisetum, where the branches originate between the leaf-traces, but also to the statements of Williamson and Scott themselves (*op. cit.*, p. 864, 868, 890) that a similar state of affairs obtained in the Calamites. There is, in fact (Williamson, *op. cit.*, 1871, pl. 28, fig. 38), a figure of a branch in this anomalous position in one of Williamson's older memoirs, but the joint authors of the later memoir already referred to (*op. cit.*, 1894, B., p. 890) tell us that this represents an arrangement which was exceptional. It is not easy to see, however, why it should not have been present whenever the strands alternated at the node, as they inform us they generally did (*op. cit.*, p. 868, 876, 877), since in such cases the leaf-traces and the branch-traces would both run, according to their descriptions, in the superior medullary rays. If we return to Williamson's original statements (*op. cit.*, 1871 and 1878) that the strands running in the upper medullary rays belonged to branches, the difficulties are just as great; for here, too, since the strands of the lower internode gener-ally alternated with those of the upper, the branch falling in the interval between the two upper strands would be exactly over a lower strand, but from the lower strand the leaf-

trace originated and consequently the branch would lie in the axil of the leaf, which is not the case.

If the cause be sought of all the manifold contradictions, which, assuming the correctness of the writer's course of argument, are present in the figures and statements cited above, it is to be found in the fact, that the figures in question are inverted, in other words, in the fact, that, contrary to what is the case in Equisetum, the branches of the Calamites are represented as originating above the nodes, and by inverting the figures above mentioned all the difficulties which have been described at once disappear. It may be further stated, that it is only possible for the branches to uniformly alternate with the leaf-traces, whether the arrangement of the strands at the nodes is continuous or alternating, when the former originate between the strands which run up to the nodes, since it is from these same strands that the leaf-traces are derived both in Calamites and Equiseta.

But if the conclusions of the last paragraph be accepted as correct, Williamson's areas of macerated parenchyma no longer lie below the node, and consequently cannot be used as an explanation of the tubercles occurring below the nodal constrictions of calamitean medullary casts.

At this point the following quotation from Renault (*op. cit.*, p. 89) may be introduced apropos of photograph 1 (Pl. 28, fig. 1), copied from his monograph (*op. cit.*, atlas, pl. 47, fig. 7).

"Les lames de tissu fondamental qui séparent les coins ligneux s'élargissent à leur partie supérieure *o* planche 47 fig. 7, 8 (ces deux figures doivent être vues retournées) et forment une sorte de gouttière ou de canal allant de la moelle à la périphérie; en coupe transversale ces organes ont une section elliptique; il n'est pas rare de trouver une cavité dans la région centrale, produite par la disparition, de cellules polyédriques qui forment une sorte de moelle (M. Williamson les a désignés sous le nom de *infrano-dal canals*): les cellules qui composent la couche périphérique sont allongées dans le sens radial, prismatiques, polygonales sur une coupe transversale et rectangulaires sur une section faite suivant leur largeur, leurs parois portent des ornements ponc-tués; il est assez fréquent de voir des trachéides se détacher des coins ligneux, pénétrer au milieu de ce tissu particulier et se confondre avec lui, leur nombre est égal à celui des lames de tissu fondamental secondaire qui séparent les coins ligneux. Les racines adventives, quand elles se développaient, étaient en rapport avec ces organes, que nous considérons comme des organes particuliers expectants, que nous distingue-rons sous le nom d'organes rhizifères."

The three important features of this citation are, that Renault states that his figure, which is reproduced in our photograph 1 (Pl. 28, fig. 1), should be inverted,

that the traces running in the medullary rays are related to roots, and that they are equivalent to Williamson's infranodal canals. Renault gives no reasons for the inversion, but obviously the figure, in its original position, is open to the same objections as have been urged in a former paragraph against the orientation of the similar figures of Williamson and Scott. The observation that the organs, o, have a parenchymatous medulla which is surrounded by a zone of pitted cells comparable to the peculiar tracheary elements of the basal node of the branches, or of the walls of the rhizophorous pedicels of Equiseta is all the more interesting, because, as Renault informs us, roots are actually attached to these organs. It is possible to accept his first two statements, without admitting the accuracy of the third, viz., that the organs, o, are the equivalents of Williamson's infranodal canals. If the reasoning of a former paragraph is sound, the tracts of macerated parenchyma which Williamson called infranodal canals are not really below the node at all but on the contrary above it, consequently the organs described by Renault cannot be considered as their equivalents. If Renault's figure, reproduced in photograph 1 (Pl. 28, fig. 1), be compared with photographs 5 and 6 (Pl. 27, figs. 5, 6), it is not very difficult to decide that the organs situated in the upper (really lower) medullary rays of the three figures are equivalent, and since, if the course of reasoning adopted here' is correct, these organs in photographs 5 and 6 (Pl. 27, figs. 5, 6) are branches they must similarly be branches, or their homologues, in photograph 1 (Pl. 28, fig. 1). But Renault tells us, in the passage quoted above, that in this case they are related to roots, and the inference may be drawn, that they are the morphological equivalents of the rhizophoric buds of Equiseta, which have an identical relation to the vascular strands and to the nodes.

Renault (op. cit., texte, p. 92, 95, 107, 123) has not realized this, since both in his figures and the subsequently published explanatory text he makes the traces of the ordinary branches pass outwards above the leaf-traces and above the node, and not below the leaf-traces and at the node, as must be the case if the mode of the argument previously adopted by the writer is not fallacious.

At the beginning of the discussion of the relation of calamitean branches to the node, a figure from Weiss, our photograph 6 (Pl. 30, fig. 6), was cited, indicating, if the writer has properly interpreted it, that externally at least the branches of the Calamites had the same relation to the node as obtains in living Equiseta. A consideration of the internal features has led, moreover, to a similar conclusion in regard to the position of the branches in the ancestors of the Equisetaceae. In the case of the calamitean rhizophoric organs on the other hand, first from the evidence of internal structural arrangements, the conclusion has been reached that they are the equivalents of branches and have the same relation to the nodes, Pl. 26, fig. 17, which is a copy from Weiss (Steinkohlen-Calamarien,

Heft 1, p. 121) shows clearly that the roots and branches were on the same side of the node in the Calamites, externally as well. In the center of the figure to the left are seen a few small leaf-scars. Along the rest of the nodal line these have disappeared. Below the indications of leaf-traces stretches a line of scars, the smaller of which are root-scars the single larger one is a branch-scar, below which are the less distinct scars of its basal roots.

Assuming the correctness of the various arguments employed in attempting to solve these difficult questions of calamitean anatomy, the result is reached, that in the Calamites the branches and their morphological equivalents, the rhizophoric organs, had the same relation to the nodes as in living Equiseta. Further, the branches were more or less exactly centered on the node according as they were of greater or smaller size. The rhizophoric organs were attached along the lower margin of the ring of nodal wood, and their cylindrical medullary cavities, which, unlike those of normal branches, did not expand are consequently represented on the casts by nodules situated below the nodal constrictions. The infranodal tubercles are thus only to be found on subterranean stems, and this is in accordance with Weiss's statement (*op. cit.*, Heft 2, p. 24) referred to in the Introduction, that they are absent or inconspicuous on axes, which are clearly recognizable as aerial.

An attempt has been made in the foregoing paragraphs to explain certain features of the Calamites by reference to the corresponding features of living Equiseta. The writer will now employ the reverse method of attempting the explanation of certain structural features of the extant genus Equisetum by a consideration of the homologous ones of the ancestral and extinct Calamites.

## The Cladosiphony of the Equisetaceae.

Attention has been called in the early part of this essay to the peculiar relations of the leaf-traces in Equisetum to the nodal wood *viz.*, that they originate below it and yet without causing any gap or lacuna in its vascular ring, as might be expected from the analogy of the foliar lacunae of the Filicales, which occur immediately above the exit of the leaf-traces from the vascular tube. Yet, notwithstanding the fact that the lacunae do not begin at the level of exit of the leaf-traces, they do, nevertheless, occur opposite the outgoing traces, but only make their appearance above the nodal wood. These facts have already been referred to in connection with photographs 5 and 6 (Pl. 28, figs. 5, 6). They appear not to have been noticed by previous writers and are susceptible, nevertheless, of a somewhat interesting interpretation which is of importance from the standpoint of the phylogeny of the Equisetaceae.

In the Introduction attention has been called to the characteristic arrangement of the traces at the nodes in Archaeocalamites, which is diagrammatically represented in Pl. 26, fig. 16. It is to be noticed here that the leaf-traces are not opposite lacunae at all, but, on the contrary, the branches or their equivalents, the rhizophoric organs, are. In this primitive type of Calamite the leaf-traces were not subtended by any gaps in the vascular tissues, but the internodal lacunae were ramular lacunae and appeared immediately above the branches. In the Introduction the term cladosiphonic has been used to describe a tubular fibrovascular axis characterized by having ramular lacunae but no foliar lacunae, and consequently Archaeocalamites, like *Selaginella laevigata* and *Lepidodendron harcourtii*, is cladosiphonic. But Stur (*op. cit.*, p. 158) has shown that in the Ostrau beds, passing from lower to higher strata, a series of forms, *Calamites ramifer* Stur, *C. cistiformis* Stur, *C. approximatiformis* Stur, and *C. ostraviensis* Stur, represent transitions from the bundle arrangement of Archaeocalamites represented in Pl. 1, fig. 15, to that of Equisetum represented in Pl. 1, fig. 16. It will consequently be not unreasonable to infer with Stur, that the equisetal arrangement of the bundles was derived in the course of geological time from archaeocalamital arrangement. The final result of the shifting of the internodes upon each other at the nodes has been, that the lacunae primarily belonging to the branches no longer subtend the latter but on the contrary the leaf-traces, which still, however, betray their true morphological relations by the fact that their exit causes no break in the nodal wood. It may then be assumed, if the reasoning based on these facts is correct, that the apparent foliar lacunae of Equiseta are really ramular lacunae which have shifted from their original position during the course of evolution of the Equisetales, and that this group is accordingly cladosiphonic. The original state of affairs occasionally reappears even in modern Equiseta, as is shown in photograph 4 (Pl. 29, fig. 4). A much more striking example of the same ancestral phenomenon is shown by photograph 3 (Pl. 30, fig. 3), which reproduces the course of the vascular strands in the cone of *Equisetum arvense*. It will be noticed that the bundles in this case for the most part do not alternate. This feature is more or less marked in the cones of all the species of Equisetum which have been examined by the writer. In this connection may be mentioned a striking cambium-like arrangement of the cells in the young bundles of the cones of *E. hiemale* and *E. limosum*. It disappears, however, almost entirely in the comparatively massive bundles of the adult cone, and perhaps may also be regarded as an ancestral feature, since secondary growth was frequently present in the vascular tissues of the strobili of various Calamites.

It has been pointed out in the Introduction that protostelic and siphonostelic axes may be possessed by different species of the same genus e. g., *Lepidodendron selaginoides*

was protostelic and *L. harcourtii* was siphonostelic, likewise *Sigillaria vascularis* and *S. pulcherrima* had protostelic axes, while on the other hand *S. diploxylon, S. elegans,* and *S. spinulosa* had siphonostelic axes; a similar relation exists between *Selaginella martensii* and *S. laevigata.* In other instances different genera of the same natural order may exemplify the two types of stelar structure *e. g.,* in the Gleicheniaceae, Gleichenia is protostelic and Platyzoma is siphonostelic. Similar examples are afforded by the Hymenophyllaceae and Schizeaceae.

## The Ancestors of the Equisetaceae.

In this connection the question may properly be asked where are the protostelic Equisetales to be found. The Sphenophyllales immediately suggest themselves in reply to this question. Stur (*op. cit.,* p. 17) and Rothpletz (Botanisches centralblatt, Gratis beilage 3, pl. 11), have both called attention to their remarkable external resemblance to Archaeocalamites in their strobloid fructifications, their rigid and articulated stems, and whorled superposed dichotomous leaves. The branches of the Sphenophyllales also resembled those of the Equisetales in rising at the nodes, *between* the leaves (Renault, *op. cit.,* texte, p. 170). Solms-Laubach (*op. cit.*) has described the sporangiophores of *Bowmanites römeri* as peltate and Scott (*op. cit.,* 1897, B.) has compared the much more complex sporophylls of Cheirostrobus with those of the calamitean Palaeostachya, and makes the important suggestion that the comparison of the cone of the Equisetales with that of Cheirostrobus is likely to change considerably our views of the morphology of the former. He probably has in mind the extension of the comparison to Calamostachys, Paracalamostachys, Cingularia, etc., where the sporangiophore does not immediately suggest itself as the ventral segment of the sporophyll, as it does in Palaeostachya. Even in the latter genus the sporangiophore more often as in the case of the sporangium of the living Selaginella (Goebel, Bot. zeit., 1881, p. 697; Bower, Phil. trans. roy. soc., 1894, B., p. 523), appears to originate from the axis than from the ventral surface of the dorsal sterile segments. Weiss (Steinkohlen–Calamarien, Heft 2, p. 7) has pointed out that it is possible to arrange a series of calamitean cones, starting with forms which have the sporangiophore attached to the base of the dorsal segment, and ending with those which have it high up on the axis. It is interesting to note in this connection, that the number of vascular bundles in the axis of all calamitean cones yet examined is not greater than the number of sporangiophores, while the so-called sterile leaves are frequently twice as numerous as the vascular strands and consequently as the sporangiophores (Calamostachys). This feature, together with the fact that the sporangiophores were placed above and between the members of the reduplicated sterile whorl, and the fact that the nodes correspond in

position to the latter (Williamson and Scott, Phil. trans. roy. soc., 1894, B., p. 902, 906), point to the conclusion that the pairs of sterile leaves were really dichotomously divided dorsal segments of sporophylls, of which the sporangiophores were the ventral segments, and in this feature (*i. e.*, dichotomy) resembled the foliage leaves of Archaeocalamites.

The morphological nature of the sporangiophore of Equisetum would appear in this connection to be problematical. Is it to be regarded as the result of the fusion of dorsal and ventral segments, such as has been shown to exist by Van Tieghem (Ann. sci. nat., bot., sér. 5, tom. 10) and Strasburger (Coniferen u. Gnetaceen) in the interesting peltate sporophylls of certain Cupressineae, or is it not rather to be considered as a ventral segment, the corresponding dorsal segment of which has become obsolete? If the former supposition is correct, there is no indication in the form of vestigial vascular bundles, in the axis of the sporangiophore, to indicate its morphological nature. We must await further knowledge of the cones of Archaeocalamites before attempting to decide this point, for these oldest known calamitean strobili had, according to the imperfect data at our disposal, the same external organization as those of living Equiseta. If it ever becomes possible to examine their internal structure, the sporophylls of this genus may prove to be analogous in organization to those of the Cupressineae referred to above, *i. e.*, composed of fused ventral and dorsal segments. In any case, there are many reasons for regarding the primitive type of sporophyll in the equisetaceous series as composed of a dorsal and a ventral segment, as Strasburger (*op. cit.*) considers to be the case in the analogous series furnished by the Coniferae.

Although the Sphenophyllales and Equisetales resemble one another so closely in their vegetative organization and in the structure of their strobili, a striking difference exists between the two groups, as Seward (Fossil plants, p. 388) has pointed out, in the structure of their vascular axes. In the former group, the central cylinder is protostelic, while in the latter it is cladosiphonic; but it has already been shown that these two stelar types may coexist within the same order and even within the same genus. In view, consequently, of numerous remarkable points of resemblance, the writer is of the opinion that the sphenophyllaceous and equisetaceous forms should be regarded as belonging to the same natural group, the former series being only more primitive than the latter. If this conclusion is correct, the phylum Equisetales must be made to include a new order, the Sphenophyllaceae, thus : —

<div align="center">
Sphenophyllaceae.

Equisetales   Calamitaceae.

Equisetaceae.
</div>

We may now turn to the question of the affinities of the Equisetales in the larger sense above indicated. It has already been pointed out that the siphonostely of the Fili-

cales is phyllosiphonic, and that of the Lycopodiales, on the other hand, is cladosiphonic. The writer has reached the conclusion, for reasons indicated above, that the Equisetales are likewise cladosiphonic. Assuming that the occurrence of cladosiphony in the two groups is *prima facie* evidence of their relationship, it is necessary to add to this a number of other features of similarity before it can be considered as proved that the Lycopodiales and Equisetales are really somewhat closely allied.

Goebel (Bot. zeit., 1887) and Buchtien (*op. cit.*, p. 42) have both noticed the striking resemblance between the green gametophyte of *Lycopodium inundatum* and *L. cernuum* and that of the genus Equisetum; there are, in both cases, the same upright fleshy axis and the same characteristically numerous lateral lobes. Goebel (*op. cit.*) has noticed, too, that the archegonia of *L. inundatum* have the same relation to the lobes of the prothallus as those of Equisetum. The archegonia of Equisetum and Lycopodium are, moreover, alike, in that in both genera they are uniformly without the basal cell, which is found without exception in the archegonia of all the isosporous Filicales.

The antherozoids of the two groups differ in structure, those of the Lycopods being biciliate and moss-like, those of the Equisetaceae, on the other hand, being spiral and multiciliate. The embryo of *Equisetum hiemale*, as has been indicated in the earlier part of this essay, resembles that of Lycopodium in that root and shoot both originate from the upper (epibasal) region. But the resemblances are strongest in the sporophytic phases. Both groups are palingenetically microphyllous and have invariably strobiloid fructifications. In both these features they present a very marked contrast to the Filicales. Finally, both cohorts present the phenomenon of cladosiphony, and in this feature also are contrasted to the phyllosiphonic Filicales.

It may accordingly be assumed, if numerous features of resemblance are trustworthy indications of relationship, that the Equisetales in the larger sense indicated above and the Lycopodiales are closely allied, as indeed has already been suggested by Scott (Pres. address Brit. assoc., 1896, p. 15) in connection with the genus Sphenophyllum.

## Conclusions.

The conclusions of this research may be stated as follows: —

1. The writer's investigation of the development of the vascular axis of the stem of the young plant, in a large number of representative vascular cryptogams and phanerogams, has led to the recognition of two primitive types of vascular axes *viz.*, the protostelic type consisting primarily of a single concentric bundle in the sense of De Bary, and the siphonostelic type, in which the vascular tissues from the very outset form a bundle-tube. Of siphonostelic axes there are again two types *viz.*, phyl-

losiphonic axes, in which the tubular vascular axis is interrupted by foliar lacunae occurring above the points of exit of the traces of the large leaves, and cladosiphonic axes, in which there are no foliar lacunae corresponding to the palingenetically micro-phyllous leaves, but which on the contrary are characterized by ramular lacunae appearing immediately above the departing traces of the branches. As regards the general morphology of vascular strands the writer, as a result of his study of development, returns to the standpoint of Sachs and De Bary.

2. The writer finds, with Goebel and Buchtien, that the gametophyte of the Equise-taceae, in its vertically-growing fleshy axis and its characteristically numerous thin lateral lobes, presents a detailed and striking resemblance to the green autotrophic species of prothallia of Lycopodium *viz.*, those of *L. inundatum* and *L. cernuum*. Further, the archegonium of the Equisetaceae resembles that of the isosporous Lycopods in being uniformly without the basal cell, which is invariably present in the archegonia of the isosporous Filicales. The embryo of *Equisetum hiemale*, the only species fully studied by the writer, agrees with those of Lycopodia described by Treub and more recently by Bruchmann, in the fact that both root and shoot originate from the upper (epibasal) region. Further, the sporophytic phases of the two groups also present a close agreement, since in both cases there are, invariably, microphyllous leaves and strobiloid fructifications.

3. In Archaeocalamites the internodal lacunae of the vascular cylinder occurred above the branches (as may be learned from Pl. 26 fig. 15), and the leaves were inserted at the nodes without lacunae in the course of the continuous vascular strands. This genus was consequently cladosiphonic and in this respect resembles the higher Lycopods. During the phylogenetic development of the Calamites the segments of the stem were gradually rotated on each other, as has been shown by Stur, and as a consequence of this process the ramular lacunae were ultimately shifted, so as to coincide with the leaf-traces, but the latter give evidence of their true affinities, even in the modern Equiseta (Pl. 26, fig. 16), by the fact that their apparent foliar lacunae are separated from them by the whole depth of the nodal wood. Moreover, the writer's examination of the development of the young stele in Equiseta shows, that it is primi-tively tubular and not, as Van Tieghem suggests, dialydesmic. The data of phylogeny, ontogeny, and anatomy consequently all favor the view that the Equisetaceae are, like *Selaginella laevigata* and *Lepidodendron harcourtii*, cladosiphonic, and there are thus additional reasons for regarding the Lycopodiales and Equisetales as closely allied.

4. The Sphenophyllales are the protostelic ancestors of the Equisetales and agree with them closely in all particulars, except the structure of their stele. But as has been pointed out, protostely and siphonostely may occur in different genera of the

same family, and even in different species of the same genus. The writer consequently is of the opinion, that the Sphenophyllales cannot any longer, on that ground, be regarded as a separate phylum, but must be included with the Equisetales as an additional order, thus: —

<div style="text-align:center">

Sphenophyllaceae.

Equisetales   Calamitaceae.

Equisetaceae.

</div>

.5. The branches of the Calamites did not, as has been stated in recent years, arise above the nodes, but, like those of the Equisetaceae, originated either more or less exactly from the center of the ring of nodal wood, or from its lower border.

6. The more conspicuous series of nodules on the medullary casts of the Calamites are not impressions of Williamson's infranodal canals, but on the contrary of the short cylindrical medullary cavities of modified rhizophorous branches, homologous with those of living Equiseta.

7. Nodal periderm is present in certain species of Equisetum and is comparable to that described by Williamson and Scott as occurring in the nodal diaphragms of Calamites.

This investigation was completed in the Cryptogamic laboratory of Harvard university, and the writer offers his best thanks to Dr. W. G. Farlow and Dr. Roland Thaxter for their courtesy and advice. He is also under obligations to Dr. G. L. Goodale for material and the use of photographic apparatus belonging to his department, and to Dr. B. L. Robinson for cones of a large number of species of Equisetum from the collections in the Gray herbarium.

## Explanation of Plates.

### PLATE 26.

Fig. 1. Young archegonium of *Equisetum hiemale*.

Fig. 2. Older archegonium of *E. hiemale*.

Fig. 3. Older archegonium of *E. hiemale*.

Fig. 4. Nearly ripe archegonium of *E. hiemale*.

Fig. 5. Nearly ripe archegonium of *E. arvense*.

Fig. 6. Young embryo of *E. hiemale*.

Fig. 7. Older embryo of *E. hiemale*.

Fig. 8. Still further advanced embryo of *E. hiemale*.

Fig. 9. Young sporophyte of *E. hiemale*.

Fig. 10. Older sporophyte of the same species.

Fig. 11. Advanced sporophyte of *E. hiemale*.

Fig. 12. Young sporophyte of *E. limosum*.

Fig. 13. Older sporophyte of the same species.

Fig. 14. Diagram showing the relation of the leaf-trace to the nodal wood in *E. hiemale*. *n. w.* nodal wood; *e.* endodermis; *p. t.* protoxylem; *l. t.* leaf-trace.

Fig. 15. Diagram of the node of *Archaeocalamites*. *l.* leaf-traces; *b.* branches.

Fig. 16. Diagram of the node of Equisetum. *l.* leaf-traces; *b.* branches.

Fig. 17. Surface of a Calamite showing the scars of leaves, branches, and root. For explanation see page 181.

### PLATE 27.

Fig. 1. Stele of *Selaginella laevigata* showing the origin of a branch. ×25.

Fig. 2. Stele of the same species below the point of origin of a branch. ×25.

Fig. 3. Stele of *Lepidodendron harcourtii* at the point of origin of a branch. ×25. See page 161.

Fig. 4. Tangential view of the bundles at the node of a Calamite, copied from Williamson. See page 163.

Fig. 5. Tangential view of the bundles at the node of a Calamite, copied from another of Williamson's figures. See page 163.

Fig. 6. Tangential view of the bundles at the node of a Calamite, copied from a figure of Williamson and Scott. See page 164.

### PLATE 28.

Fig. 1. Tangential view of the bundles at the node of a Calamite, copied from Renault. See page 165. (In this figure there are leaf traces, *f*, only at alternate strands, a state of affairs not uncommon in the Calamites).

Fig. 2. Transverse section of a young trifascicular stem of *Equisetum limosum*. ×200.

Fig. 3. Transverse section of the stem of *E. hiemale* in the nodal region. *a.* branch; *b.* a root. ×25.

Fig. 4. Nodal organ of *E. hiemale*. ×200.

Fig. 5. Transverse section through the node of *E. silvaticum*. *a.* nodal organs; *b.* roots; *c.* a branch; *d.* leaf-traces; ×25.

Fig. 6. Node of *E. arvense*. *c.* branches; *d.* leaf-traces. ×25.

PLATE 29.

Fig. 1.  Transverse section of a node of *Equisetum limosum*. *c*. branch; *d*. leaf-traces; *b*. rhizophoric organs.  ×25.

Fig. 2.  Tangential section of the node of *E. hiemale*.  *c*. branch; *t*. leaf-traces; *l*. vallecular lacunae.  ×25.

Fig. 3.  Deep tangential section of the node of *E. hiemale*.  *c*. branch; *l*. vallecular lacunae.  ×25.

Fig. 4.  Deep tangential section of the node of the rhizome of *E. hiemale*.  *c*. a branch; *l*. vallecular lacunae.  ×25.

Fig. 5.  Radial section through an aerial node of *E. hiemale* at the point of origin of a branch.  *d*. nodal diaphragm; *n*. nodal wood; *c*. the branch; *r*. roots; *k*. nodal shoot of the branch.  ×25.

Fig. 6.  Radial section of a terrestrial node of *E. hiemale* at the point of origin of a nodal bud.  *d*. nodal diaphragm; *n*. nodal wood; *c*. nodal bud; *r*. root.  ×25.

PLATE 30.

Fig. 1.  Radial section of a terrestrial node of *Equisetum hiemale* at the point of origin of a large vertical branch.  *d*. nodal diaphragm; *n*. nodal wood; *c*. branch; *r*. root.  ×25.

Fig. 2.  Radial section of a node of a terrestrial branch of *E. silvaticum*; lettering as in Fig. 2.  ×25.

Fig. 3.  Course of the bundles in the cone of *E. arvense*.  ×4.

Fig. 4.  Tangential section passing through the leaf-trace of *E. hiemale* and showing its mode of origin from the protoxylem of the internodal bundle.  *px*. protoxylem; *mx*. metaxylem; *lt*. leaf-trace; *n*. nodal wood.  ×200.

Fig. 5.  Section through the nodal diaphragm of *E. hiemale*.  ×200.

Fig. 6.  The surface of a Calamite, copied from Weiss, showing four whorls of attached leaves a nda single row of scars of fallen branches.  The latter have scars of fallen leaves along their lower margin.

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