The Anatomy and Relationships of the Gnetales.

I. The Genus *Ephedra*.¹

BY

W. P. THOMPSON.

1851 *Exhibition Science Research Scholar, University of Toronto at Harvard University.*

With Plates XCIV-XCVII and two Figures in the Text.

THE question of the true affinities of the Gnetales, alluring in itself and yet hitherto so baffling, is being drawn into fresh prominence as morphologists turn to the great question of the origin of the Angiosperms. It is recognized that, aside from its own interest, a settlement of the Gnetalean affinities would mark a strategic advance in the attack on the ancestry of the dominant group of our modern seed-plants. Hitherto the chief attention of those who have added to our knowledge of the Gnetales has been focused on the reproductive structures, although even in this field much still remains to be done. The anatomical features have usually been dismissed with a bare reference to the occurrence of true vessels in the wood. There is accordingly great need of systematic study of the anatomy of the whole group, especially in accordance with the methods which have recently proven so fruitful of phylogenetic results when applied to the Conifers and lower Dicotyledones.

The results of such an anatomical study of the most primitive member of the family, the genus *Ephedra*, are given in the present contribution. It is hoped soon to complete the study of the other genera. In studying *Ephedra* the writer has had material of several species, including *E. altissima*, *californica*, *distachya*, *fragilis*, *Gerardiana*, *monostachya*, *trifurca*, *viridis*, and *vulgaris*. There is little specific variation, so that all the species may be treated together and important differences mentioned under the features concerned.

With regard to the history of the subject, it is contained chiefly in scattered references to individual features, particularly in general texts on anatomy. These will be mentioned as occasion arises.

¹ Contributions from the Phanerogamic Laboratory of Harvard University, No. 51.

PITH.

The pith of *Ephedra* is relatively very large, as may be seen in Pl. XCIV, Fig. 1, which is a photograph of a transverse section of an entire young branch. It is composed of dead, fairly thick-walled cells, many of which are filled with a hard brown substance. This substance is either homogeneous or of a foam-like structure (see Fig. 1). Often the cell-walls in certain places disappear, so that the dark masses become continuous, and, when the stem is broken, project as definite strands. This material is lacking at the node of the adult, and in both node and internode of the seedling. In a few species the pith also contains thick-walled fibres resembling those of the bast, which are confined to its periphery.

In certain places, notably in proximity to the nodes, the cells of the pith adjacent to the primary vascular bundles become differentiated. They are smaller and strongly lignified, and appear as definite strands extending inward from the protoxylem cluster. Fig. 2 gives their appearance in *E. trifurca*. It is plain that they might readily be mistaken for centripetal wood. Longitudinal sections, however, reveal their true character as lignified pith cells. It is possible, however, as Worsdell¹ holds for similar cells in *Welwitschia*, that they may represent modified centripetal wood. In *Ephedra* there is little evidence for such a view. The conditions just described emphasize the necessity for exercising the greatest care in identifying centripetal wood.

Another peculiar feature of the pith is the presence of a diaphragm of periderm-like cells a short distance above the node. In Fig. 3 the node is to be recognized by the constriction in the pith and the layer of thick-walled cells. Some distance above the node, the diaphragm may be seen extending completely across the pith and into the wood. The diaphragm is composed of vertical rows of three or more cells apparently formed by secondary divisions. It is sharply differentiated from the rest of the pith by the arrangement, size, and contents of its cells. Very frequently the branch breaks just above the node, and this layer always forms the line of separation. It serves no doubt to protect the surface exposed after the break. But on account of its extension into the wood it would also appear to be a device for cutting off young branches after the manner of an absciss periderm in leaf-fall. It recalls strikingly the similar structure found above the node in *Equisetum* and the Calamites.² In these forms, however, it is confined to the centre of the pith, not ordinarily reaching the periphery nor the surrounding wood. In the Calamites there was a diaphragm both above and below the node. Of course these peridermal diaphragms in

¹ Vascular Structure of the Flowers of the Gnetaceae. *Annals of Botany*, 1901.

² Williamson and Scott: *Phil. Trans. Roy. Soc.*, 1894.

Ephedra and the Equisetales can have no evolutionary connexion, but they furnish an interesting case of parallel development in plants of similar habit.

PRIMARY VASCULAR BUNDLES AND LEAF-TRACES.

The bundles of the primary wood, though not large, are rather conspicuous in transverse sections. Fig. 1 gives their appearance in *E. monostachya*. They may be seen to consist of two pairs of large bundles and two groups of three smaller ones. The groups of large and small bundles alternate regularly. The number and arrangement are constant for each species, but vary in the different species. The reasons for the appearance which they present in transverse sections are readily understood when one follows their course by means of a series of sections.

1. Course.

The simplest condition is found in *E. distachya*, and is represented diagrammatically in Text-fig. 1, which is a reconstruction drawn after a study of complete series of celloidin sections through the node.¹ As we shall see, it differs considerably from the conceptions arrived at by former investigators, but owing to the exactness of the method and the number of repetitions the writer feels certain of its accuracy. The ring of bundles is represented as split and turned into one plane. In the internode there are two pairs of large bundles as in *E. monostachya*, but the smaller bundles are also in pairs instead of groups of three. There are therefore two pairs of large bundles alternating with two pairs of small ones. As the node is approached, the smaller bundles flatten tangentially, and short tracheides appear between them. By this means they are soon united, so that a continuous band of primary wood results. The appearance of this band in another species is shown in Phot. 4. The original bundles are near the end of the band. Very soon the adjacent large bundle on each side becomes included in the same way. Meantime a similar band has been formed on the opposite side of the stem. Finally, these two bands become united by the extension of their ends. There results a complete girdle of nodal wood broken only by the exit of the leaf-traces. Often the position of the internodal bundle is indicated by a slight thickening of the girdle.

The leaf-traces, of which there are two at every node to supply the pair of opposite leaves, are in all cases double. The double character is shown in *transverse* section in Figs. 5 and 6, and in *tangential* section in Fig. 7. In the latter figure the two strands of the trace are below the centre of the field which is occupied by the large branch gap. The transverse sections

¹ The sections as they came from the microtome were arranged in order on a large slide and mounted in glycerine in which they were kept indefinitely for further study. By this means the accuracy of the work is rendered just as great as with the similar paraffin series used for soft material.

also show that the two strands are inserted separately. Each arises directly above one of the smaller internodal bundles, a piece of the girdle at this point simply turning out to form a strand (see Text-fig. 1). Sometimes a thickening of the girdle runs up from the small bundle and out with the trace, indicating that the small bundle as a whole originally formed the trace.

That part of the girdle between the two strands of each trace continues up as a definite bundle, so that in transverse sections the two strands are separated by a block of wood. This feature is shown in Fig. 5. The same bundle is seen in tangential section in Fig. 7. Above the traces it divides, and each part unites laterally with the girdle to form the outgoing branch.

TEXT-FIG. 1. *E. distachya*. Reconstruction of the course of the primary fibro-vascular bundles.

The bundles of the succeeding internode are organized from the nodal wood in a definite manner and position with respect to those of the lower internode. On each side of both branch gaps a large bundle is organized. The two pairs of large bundles of each internode are thus accounted for. Between the pairs of large bundles two small ones are then formed, and the two pairs of small ones are then accounted for. The result is the same organization as in the lower internode, except that the large bundles are now in the position of the lower small ones and vice versa. At the succeeding node the story is repeated, except of course that the leaves alternate with those below.

It is obvious that the bundles of the upper internode, although their position with respect to the lower ones is definite, cannot be regarded as continuations of them. Nor can it be said that any bundle of the internode passes out definitely as a leaf-trace. It is true that in some specimens

the continuous thickening of the girdle would indicate that this was originally the case. But as a rule it may be said that the leaf-traces are organized from the ring of nodal wood.

Another species possessing this organization of the primary vascular bundles is *E. vulgaris*. In *E. trifurca* the leaves are in whorls of three, so that in each internode there are three pairs of large bundles alternating with three pairs of small ones. The girdle and traces, however, are usually organized in the same way as in *E. distachya* and *E. vulgaris*. Occasionally, however, the intercalary bundle between the two strands of the leaf-trace is absent. Such a trace with its two strands leaving the stele side by side is photographed in Fig. 6. The condition here is similar to that of other plants which have the double leaf-trace. It is no doubt the primi-

TEXT-FIG. 2. *E. altissima*. Reconstruction of course of primary fibro-vascular bundles.

tive condition, for it obtains exclusively in the traces to the reproductive bracts.

A more complicated condition of the whole primary system is found in such species as *E. altissima*. Text-fig. 2 is a reconstruction of the bundle course in this species. As the leaves occur in whorls of three, the internode has three pairs of large bundles alternating with three groups of smaller ones. But in this case each of the smaller groups contains three bundles instead of two. Accordingly the total number of bundles is fifteen. The nodal ring is organized in the same way as before. The most striking difference is that the strands of the leaf-trace arise, not above the small bundles of the internode, but above the spaces between them. The intercalary bundle is then directly above the central small bundle of the group, and the traces arise over the spaces which separate the central bundle from its fellows. In this case, at least, the traces cannot be considered as continuations of the internodal bundles. In addition to the origin of the leaf-traces, the most striking difference is the presence of three small bundles

instead of two in each group. This is no doubt a specialized feature, for in the seedling (see Pl. XCVI, Fig. 27) one finds the simpler type of organization.

The observations of former investigators differ considerably from those just outlined, and also differ materially from each other. Geyler,¹ the pioneer in this sort of work, observed the girdle at the node in *E. equisetiformis*, but did not consider it of importance. He believed that the bundles were continuous through two internodes, the leaf-traces attaching themselves laterally at that distance below their exit. In reality they run through only one internode where they are formed from the girdle. He also made the mistake of considering the large internodal bundles as the leaf-trace bundles of the succeeding node. Van Tieghem² observed the intercalary bundle between the leaf-trace strands which Geyler failed to see. He thought that it was derived from the traces and divided into two to give the proper number of bundles for the next internode. Strasburger,³ while considering that the bundles ran through two internodes, correctly observed the origin of the intercalary bundle from the girdle. All these investigators examined species, *E. distachya*, *vulgaris*, and *equisetiformis*, which belong to the simplest type described. As we have seen, the conditions existing in many other species are quite different, although intermediate stages exist.

In spite of the disagreement in regard to details the course of specialization may readily be traced. There are indications that in the ancestral form the internodal bundles were as in the simpler type, and the small bundles ran out intact to form the leaf-traces. The intercalary bundle was absent. From this condition the girdle increased, the intercalary bundle developed, and the traces lost their connexion with the internodal bundles. Finally, the third small bundle of the internode developed, and the traces came to alternate with the internodal bundles.

Some of the features just described are of importance from the standpoint of relationships. The small number and simple regular course of the bundles through the internode are quite different from the conditions in the Cycads and Bennettitales, with which there has recently been a tendency to connect the Gnetales. It is well known that all the Cycadophyta had their primary vascular system arranged in the form of an irregular trellis from which the leaf-traces departed in a haphazard manner. The conditions in *Ephedra* resemble much more closely those of the Coniferales and Dicotyledones.

The double leaf-trace is a feature on which much stress has been laid. There appears to be general agreement as to its primitive character, for it is present in the ancient Cycadofilicinean forms. In *Ephedra* it differs from the double trace of many Gymnosperms in that the two strands of which it

¹ Gefässbündelverlauf und Laubblattregion d. Coniferen. Pringsheim's Jahrbücher, 1867.

² Anatomie des Fleurs des Gymnospermes. Ann. de Sci. Nat., Bot., 1889.

³ Die Coniferen und die Gnetaceen, 1872.

is composed do not unite before entering the stele, but are inserted separately. In this respect it resembles the Cycads and *Ginkgo*. It is doubtful, however, whether any importance can be attributed to this point, for even in many of those ancient forms of which it is characteristic the two parts unite before entering the stele (*Lyginodendron*), while in others they remain separate (*Poroxylon*). On this basis the primitive Conifers can claim just as close an affinity to *Ephedra* as can the Cycads, for they also have a double trace. Furthermore, the Bennettitales, which on account of their floral organization have a much stronger claim than their modern representatives on the Gnetalean ancestry, had only a single trace, as Wieland¹ has shown. This fact has been overlooked in much recent work. For example, Miss Sykes,² in her work on *Welwitschia*, considered its double leaf-trace indicative of Cycadean affinities. It is obvious that the argument which involves the floral organization is quite contradictory to that which involves the double leaf-trace, and one or the other must be abandoned.

The bundle intercalated between the strands of the leaf-trace is a feature not found in other Gymnosperms. This fact and its absence in certain cases in *Ephedra* indicate that it is a specialization. It is possibly another condition in which *Ephedra* approaches the Dicotyledones in which the several traces to a single leaf arise at various points in the circumference of the young stele and are separated by masses of wood.

The girdle of tracheides at the node is a special feature with no significance in respect to relationship. It recalls strikingly the nodal wood of *Equisetum*, but of course this can be only a case of parallel development. This feature and the medullary diaphragm of both forms are probably correlated in some way with their similarity of habit.

2. Structure.

Each primary vascular bundle is roughly triangular, the innermost angle being occupied by the smallest protoxylem elements (Pl. XCIV, Figs. 1 and 2). The succession of elements from this point outward to the secondary wood is of the usual type. There is no centripetally developed wood, so that the bundles are of the endarch type. As has been noted above, a band of lignified elements which might easily be mistaken for centripetal wood often extends from the protoxylem for some distance into the pith (Fig. 2), but in no case was true centripetal wood found in the internode.

At the node, however, centripetally developed tracheides are occasionally to be found. They occur in the pith about the level of the exit of the leaf-traces. In this position they are not of the usual type, but bear a close resemblance to transfusion tracheides of the leaf. Fig. 8 shows one

¹ American Fossil Cycads. Carnegie Institute, 1906.

² Anatomy and Morphology of the Leaves and Inflorescences of *Welwitschia mirabilis*. Phil. Trans. Roy. Soc., B., 1910.

such element separated by at least two pith cells from the xylem. By following a series of sections one finds that they occur in strands attached to the protoxylem below, but diverging centripetally above. The lowermost elements are most like tracheides, but the upper ones rapidly assume the characters of transfusion cells. It is probable that they represent the original centripetal wood which was present universally in the ancestral types, and has been lost from the internode as in so many other plants, but in this case retained in a modified condition at the node.

At the edges of the primary bundles of the internode one often finds in *E. monostachya* and *E. vulgaris* typical transfusion tracheides like those of the leaf. They are adjacent to the pith, and often reach across from one bundle to the next. In Fig. 9 two primary bundles may be seen at the extreme right and left, and between them three or four of the scattered transfusion tracheides with their characteristic bordered pits and thickening bars. Their presence is probably due to the fact that the cortex of the young plant functions as a leaf.

Having described the origin of the leaf-traces in connexion with the course of the primary bundles, it may be well at this point to take up its structure. In all cases the trace is very small, consisting of but a few elements. Its tracheides are nearly all spiral or scalariform, although occasionally one may find a pitted element. In all cases the arrangement is endarch, i. e. the protoxylem elements are on the adaxial side of the bundle, and the metaxylem is all centrifugal. The endarch character may be distinguished in Fig. 7, in which the protoxylem elements of the trace are uppermost. In no case was centripetal xylem found. The structure is then identical with that of the trace of the Angiosperms and Conifers. It is vitally different from that of the Cycads and older Gymnosperms. In the Cycads, as is well known from the work of Scott and the earlier studies of Mettenius, there is always a large amount of centripetal wood which is considered to be retained from a primitive condition in which it occurred in the stem as well as in the leaf. At the same time the centrifugal primary wood is very small in amount and diminishes in the petiole. In *Ephedra* the conditions are exactly reversed; the centripetal wood has been completely lost and the centrifugal wood developed. In regard to the structure of the leaf-trace, therefore, *Ephedra* is as remote as possible from the Cycads, and is in agreement with the Conifers and Dicotyledones. In view of the general agreement as to the importance of the leaf-trace as a seat of ancestral characters, this is a point which should be emphasized in all phylogenetic studies.

SECONDARY WOOD.

It has long been known that the secondary wood of *Ephedra* consists of tracheides, vessels, wood parenchyma, and rays. But an intimate study of each of these constituents is necessary, especially in the light of recent

similar studies on the wood of Conifers and Dicotyledones. A transverse view in which the general characteristics and arrangement of all the elements may be distinguished is shown in Fig. 10.

1. Tracheides.

The pitting of the tracheides is usually uniseriate with the individual pits well separated (see Fig. 11). In this respect it agrees with that of all the Conifers except the Araucarians, and is sharply distinguished from that of the Cycads and Bennettitales. In the latter group the pits were almost always of the very primitive scalariform type,¹ while in the Cycads the multiseriate pitted condition is the dominant one, although the scalariform condition is not uncommon.

The structure of the individual pits presents additional points of difference. The pit mouths in *Ephedra* are circular, as in the majority of the Conifers, whereas in the Cycads they are more or less slit-shaped. The torus is also very well developed (Fig. 11), while in the Cycads it is absent.

Although the pits are usually well separated, conforming thus to the 'Abietinean' type, one often finds the mutually compressed type or 'Araucarian' condition. This is represented in Fig. 12. It is most frequent at the ends of the tracheides. Often also the more typical Araucarian condition with two alternating rows of compressed pits is to be found. Rarely are more than two rows present.

In association with the Abietinean pitting the tracheides possess a feature which has been shown recently to be of primary importance, namely, the so-called bars of Sanio. These structures, named in honour of their discoverer, are horizontal bars or folds of cellulose crossing the tracheide wall between the pits. Stained in haematoxylin they appear as dark bands. They may be distinguished in the central tracheide of Fig. 11. Miss Gerry² has shown that they are present in all Conifers except the Araucarians, i. e. wherever the Abietinean type of pitting occurs. Outside the Conifers they are to be found only in *Ginkgo*, which also has uniseriate separated pits. Naturally they cannot exist where the pits are closely compressed. Their presence in *Ephedra* serves to distinguish this genus sharply from the Cycadales, and associate it rather with the Coniferales and Ginkgoales.

The bordered pits and bars of Sanio are not confined to the radial walls of the tracheides as in most woods, but are found also on the tangential walls, as may be seen in Pl. XCV, Fig. 13. In the Conifers tangential pits, when present at all, occur only in the summer wood, but in *Ephedra* they are to be found throughout the year's growth. They are usually somewhat smaller than those of the radial wall.

¹ Wieland : loc. cit.

² Distribution of the 'Bars of Sanio' in the Coniferae. *Annals of Botany*, Jan., 1910.

The tracheide walls sometimes show tertiary spiral striations such as are characteristic of *Taxus* and *Pseudotsuga*, and according to Bailey¹ are of sporadic occurrence in all the Pineae. Fig. 14 gives their characteristic appearance in *E. californica*. They appear to be of very sporadic occurrence. Their presence is not a specific character, nor are they more frequent in young wood, as Bailey found to be the case in the Pineae. They supply one more point of resemblance to the tracheides of the Conifers.

Another type of spiral thickening to which Boodle and Worsdell² has called attention is photographed in Fig. 15. These thickenings are broader and less numerous than those of the other type. Boodle and Worsdell observed that they appear to be continuations of the mouths of the pits. The relation to the pits is plainly shown in Fig. 15, especially in the upper part of the field. In many places the relation is not so obvious on account of the fact that the section may not include the underlying pit. It is plain that these thickenings have no connexion whatever with those of the usual type. They have also been observed in the genus *Widdringtonia*, one of the Cupressineae.

Still another feature which occurs sporadically in the tracheides of the Coniferales and only in that family is present in *Ephedra*, namely, the so-called trabeculae. By this term is meant a series of lignified septa occurring all in the same horizontal line in a single radial row of elements. When seen in radial section (Fig. 16), they present the appearance of a continuous row of lignified bars crossing the field. Their occurrence is so uncommon and sporadic in any wood that little account is taken of them in the literature of wood structure. They serve, nevertheless, as another addition to the list of Coniferous characters possessed by *Ephedra*.

There is just one other point in connexion with the tracheides of *Ephedra* to which attention should be called, namely, the frequent presence of resin plates. Resin is often deposited in the tracheides in the form of spool-shaped plates. In Fig. 16 the small tracheide at the left of the large central vessel contains several of them. Although this is the prevailing form, the resin is sometimes deposited in globules or larger masses. The spool-shaped plates bear a strong resemblance to those of the wood of certain Conifers, notably the Araucarians, in which they become a characteristic feature.

All the characteristic features of the tracheides of *Ephedra* are, then, also characteristic of the tracheides of the Conifers; the arrangement of the pits, the structure of the individual pits, the bars of Sanio, tertiary spirals, trabeculae, and resin plates. No single family of the Conifers possesses all these features, so that it would be difficult to connect *Ephedra* from the

¹ The Structure of the Wood in the Pineae. Bot. Gaz., July, 1909.

² L. A. Boodle and W. C. Worsdell. Annals of Botany, 1894.

standpoint of evolution with any special members of that family. It would seem rather to be related to some generalized ancient form.

2. Vessels.

The fact that *Ephedra* possesses true vessels is perhaps its best known anatomical feature. It is also well known that the perforations of those vessels correspond to the bordered pits of tracheides. The further fact that there are interesting transitions between bordered pits and perforations has been emphasized by Strasburger¹ and by Boodle and Worsdell.² The writer's study has shown that the transitions between tracheides and vessels are much more complete than was suspected, and has revealed additional structural features. For the sake of completeness some facts already known will be briefly recapitulated.

The lumina of the vessels vary from that of a tracheide to many times that size (Pl. XCVI, Figs. 27 and 29). The pits on the lateral walls are identical with those of the tracheides, though arranged more often in two rows. In addition the vessels show the bars of *Sanio*, tertiary spirals, and trabeculae characteristic of the tracheides. The perforations of the end walls are seen in transverse section (Pl. XCIV, Fig. 10) to be simply enlarged bordered pits in which the border has become narrow and the torus has disappeared. In the radial section (Fig. 12 and Pl. XCVI, Fig. 25) these points are also visible, although the border is not so clear. The perforations may be in two or three rows which are opposite or alternate. Perhaps the clearest ideas may be obtained from the tangential section which has been photographed in Pl. XCV, Fig. 17. In this figure the slanting end wall, the open communication between the conterminous elements, and the border of the perforations are clearly shown.

From the appearances presented in these figures the conclusion is natural that the perforations represent modified bordered pits. This assumption is rendered a certainty by the fact that one frequently finds true bordered pits in series with the perforations (see Fig. 20). The latter in such cases occupy the position of the bordered pits of a normal tracheide. This condition is shown in tangential view in Fig. 18, in which the two bordered pits at the bottom of the end wall have well developed borders and tori.

The transitions between tracheides and vessels are in fact remarkably complete, especially in the first few annual rings. In Fig. 19 is represented an element which differs from a tracheide only in the absence of the torus and narrowness of the border of *one* of its enlarged central pits. The other pits, while showing a slight decrease in the border, are still true bordered pits. A further stage is represented in Fig. 20, and many other figures could have been presented showing all stages up to the completed vessel of Pl. XCVI,

¹ Über den Bau und die Verrichtungen, &c.

² loc. cit.

Fig. 25. But a single vessel is often sufficient to show clearly the gradual disappearance of the torus and border. In Pl. XCV, Fig. 20, at the end of the vessel the pits have a typical border and a deeply stained, well-marked torus. Towards the bottom of the field, i. e. towards the centre of the end wall of the vessel, the torus becomes gradually fainter until it disappears, and there results an open communication through the pits. The decrease in breadth of the border is equally gradual. Usually the conditions are not so diagrammatic as this. Sometimes the torus and border do not disappear at the same rate, but the latter may be quite well developed when the former has completely vanished. Diagrammatic cases are sufficiently numerous, however, and the various stages presented by different elements are so often repeated that there can be no doubt as to the origin of the perforations, in *Ephedra* at least.

In those cases in which the torus is only partly developed, it may have become so in one of two ways: either in the course of ontogeny it has ceased to grow at that stage in its development, or it may have continued to the complete condition, and later have been partially resorbed. The writer was unable to determine which of these alternatives is correct.

If the vessels have developed in the manner indicated it might be expected that the seedling would present primitive conditions approaching tracheides. As a matter of fact the seedling possesses very few vessels of any kind, the mass of wood consisting almost exclusively of tracheides. This fact is shown strikingly in Pl. XCVI, Fig. 27, which is a photograph of a transverse section through the base of the seedling stem of *E. altissima*. Very few vessels can be recognized, and even those which can are extremely small. The absence of vessels is also shown in longitudinal view in Fig. 28. Of course, as one examines the upper parts of the seedling it is found that they gradually increase in number. Moreover, the vessels which are present have only a single row of perforations, and these are usually of the transitional type. Such facts furnish another striking example of the recapitulation in the seedling of ancestral characteristics.

It should also be noted that in the first annual ring of adult branches the few vessels which are present usually have a single row of perforations which are often transitional to bordered pits. Evidence is thus added to that which has recently been accumulated showing that this region is also the seat of retention of ancestral features.

Boodle and Worsdell¹ state that the node also lacks vessels. For the species which the writer has examined this statement does not appear to hold good, although the number in that region may be slightly less than in the internode. The presence of vessels in the node of *E. altissima* is shown by photography in Pl. XCIV, Fig. 7, especially at the right.

We have here seen the structure of the primitive vessels of *Ephedra*

¹ loc. cit.

and of the typical ones; there remains a more highly developed condition which is occasionally to be found, but which has not yet been described. It is illustrated in Pl. XCV, Fig. 21, which is a photograph from *E. distachya*. The upper two perforations appear from their shape to have resulted each from the horizontal fusion of a pair of perforations. This inference is confirmed by the condition of the pair of opposite perforations below, for the latter are separated by an extremely thin part of the wall (compare with Fig. 20). It is clear, therefore, that a fusion of perforations sometimes occurs, resulting in the formation of still larger perforations. The resulting vessels bear a much closer resemblance to those of the Angiosperms, especially to the ones with scalariform end walls which are characteristic of the lower Dicotyledones.

In spite of this resemblance, however, it must be admitted that the vessels of *Ephedra* differ essentially from those of the Angiosperms. The perforations of the Angiospermic vessels by no means correspond to modified bordered pits. It may be stated here, however, that the vessels of *Gnetum* to a large extent clear up the difficulty.

3. Wood Parenchyma.

Wood parenchyma is very abundant in *Ephedra*, the number of its elements often nearly equalling the number of tracheides. It is sometimes scattered irregularly throughout the wood (Pl. XCIV, Fig. 10), but is more often arranged in definite tangential bands. The banded arrangement is visible in Pl. XCVI, Fig. 29, in which the parenchyma cells appear dark owing to their deeply staining protoplasmic contents. There are usually two rows of tracheides separating the successive bands of parenchyma cells, although often, especially in root wood, only a single row of tracheides intervenes. Sometimes, indeed, the bands of parenchyma cells themselves become two or three rows in thickness.

The individual cells are identical with tracheides in length and shape (Pl. XCV, Fig. 23). They are also lignified in the same way and to the same extent as tracheides. Moreover, in the vast majority of instances they have no cross-walls as do those of Conifers. Therefore, the only features which serve to distinguish them from tracheides are the character of the pitting and the possession of protoplasmic contents. When in dry material the protoplasm disappears, the distinction is often difficult to make.

As for the other distinguishing feature, namely, the character of the pits, it is usually simple. This is always true in the case of pits between adjacent parenchyma cells. In some cases, however, where the parenchyma cell adjoins a tracheide or vessel the pits show a small border on the parenchyma side as well as the usual large one on the tracheide side. The small border is shown in Fig. 22. The parenchyma cell adjoining the vessel

on the right is charged with a black resinous mass which has penetrated through the pits into the lumen of the vessel, where it remains as little globules. The deep colour of this material emphasizes sharply the doubly bordered character of the pits as well as the fact that the border on the vessel side is wider than that on the side of the parenchyma cell.

A peculiar fact in connexion with these wood parenchyma cells is that they are often multinucleate. Fig. 23 shows a parenchyma cell in the wood of *E. monostachya* which in the short extent shown in the photograph obviously contains two nuclei. This condition obtains quite frequently, although it is often hard to demonstrate. Three and four nuclei have been observed in a single parenchyma cell. It would seem that the distance from the centre to the ends of such an extremely long living cell is too great to enable the single nucleus to perform its proper functions. Accordingly the original nucleus divides and the daughter nuclei become scattered along the cell. In fact, in the proper material it is possible to observe that the nucleus is actually undergoing division. Such a case is photographed in Fig. 24. The details of nuclear divisions were impossible to distinguish.

In a few cases, as Strasburger¹ has pointed out, the parenchyma cells are further distinguished from tracheides by the presence of cross-walls such as exist in the parenchyma of most other woods. Such a wall is shown in Pl. XCVI, Fig. 25, at the centre of the field. The inclination is typical. As a rule, however, septa are rare, and in some species were never seen. They are most abundant in *E. monostachya*. In no case was more than one septum seen in a single parenchyma cell, a condition which is in sharp contrast to that of the parenchyma of most woods.

The typical wood-parenchyma cell of *Ephedra* is then, except for its pitting, merely a tracheide which has retained its protoplasmic contents. And in some cases we have seen that even its pitting resembles that of a tracheide. From these facts, and also from the entire absence of wood parenchyma in the ancient Gymnosperms, it may be concluded that the wood parenchyma of *Ephedra* has been derived from tracheides. Each parenchyma cell would therefore represent a modified tracheide.

It is to be noted that this type of parenchyma differs essentially from that of the Conifers. The latter consists of short cells, a number of which together give the shape and size of a tracheide. In fact, Bailey¹ has recently brought forward evidence to show that this type was also derived from tracheides. The real difference then consists in the presence of numerous septations in the Coniferous cells. We have seen that in *Ephedra* a single septum is sometimes present, so that the distinction is not really so profound. The Conifers appear to have carried the process of septation much further.

The cells which resemble them most closely, however, are to be found in the Angiosperms, where they have been called fibrous cells or substitute

¹ loc. cit.

fibres. In fact, de Bary¹ concluded that they fell naturally into this category. It should be noted, however, that the Angiospermic fibrous cells, as their name indicates, resemble the woody fibres rather than tracheides. They are much longer and have thicker walls. Although the lack of septa is common to the two, it is doubtful whether they are homologous structures.

4. Wood Rays.

The ray structure of *Ephedra* has hitherto been passed over with the simple statement of Strasburger² that they are multiseriate. In reality the conditions which they present are no less significant from an evolutionary point of view than those of the vessels to which the whole attention has been devoted in the past. The fact that they are multiseriate is in itself of supreme importance, for in connexion with other facts it emphasizes their close relationship to those of the Dicotyledones.

The multiseriate condition is shown in transverse section in Pl. XCIV, Fig. 10 at the left and in tangential section in Pl. XCV, Fig. 13. The number of rows of cells varies from one to ten, but the average number is four or five. There is considerable specific and regional variation in this respect. In tangential section they are found in most cases to be solid homogeneous masses which extend vertically to considerable heights. They are not so high, however, as those of the Oak, but have a more fusiform outline (Pl. XCVI, Fig. 32).

The individual cells are extremely variable in size and shape. They may be isodiametric or elongated radially or vertically. As these variations may be found within a small area, they give the ray a peculiarly irregular appearance, as is shown in Fig. 26, and especially in Pl. XCV, Fig. 13. Furthermore, in old wood, all the cells of the marginal rows often become elongated obliquely to the course of the ray, a condition which no doubt results from the slow growth of the ray in comparison to that of the surrounding wood.

Each cell is strongly lignified, resembling in this respect the ray cells of Conifers and Dicotyledones and differing from those of the Cycads and Bennettitales. The simple pits, like those of the Dicotyledones, occur on all walls and are very small, being merely fine pores. Their character may be distinguished in Pl. XCVI, Fig. 26, especially at the top of the field. All these features give an appearance in radial section strikingly like that of a large ray of the Dicotyledones.

The conditions of the rays in the young stem are quite different from those just described for the adult. At the pith one finds only uniseriate rays similar to those which are characteristic of the Conifers (Figs. 27 and 29). From this condition the broad ray of the adult is produced in two

¹ Comparative Anatomy of Phanerogams and Ferns.

² Über den Bau, &c.

ways, first by the enlargement of the uniseriate rays, and secondly, by their fusion. The first process, that of enlargement, is itself effected in two ways. The cells of a uniseriate ray may simply divide radially to produce a biseriate one, which in turn continues the process, or the adjacent tracheides may be transformed into ray parenchyma. The latter method is much more common, and indeed many rays originate by this transformation in the wood and do not extend to the pith. During the process the tracheides retain their contents and become septated irregularly. As one examines the sections from the pith outwards one finds that the compartments into which the tracheides are divided become gradually shorter and arranged irregularly. Fig. 28, which is a photograph of a tangential section near the pith of *E. altissima*, shows the formation of a number of rays in this manner. The ray cells are all very much elongated vertically, and some of them are obviously segments of tracheides. Indeed, in some places, it is difficult to distinguish the limits of the rays.

The second method in which the broad rays are formed is the significant process of fusion of small rays. Two or more small rays become joined into one large one, while the intervening fibres are either pinched out or transformed into ray parenchyma. Later, other rays may be added laterally in the same way, so that rays of various sizes are found in the compounding area. Fig. 29 shows the compounding process taking place in *E. monostachya*. Two of the large rays are obviously in the process of formation by a fusion of similar ones. Fig. 30 shows the same thing taking place in *E. californica*. The completion of the process usually requires a number of annual rings. Often it is very slow, and the included fibres remain intact for a long distance. Indeed, in some cases the fusion appears never to become complete, for tangential sections may reveal the presence of fibres and even vessels in the rays of very old wood. Such a tangential section of *E. californica* is represented in Fig. 31. The numerous included fibres show that this broad ray has resulted from the fusion of smaller ones. A similar condition from *E. trifurca* is shown in Fig. 32. Broad rays such as these containing fibres are homologous with the so-called false rays of many lower Dicotyledones, e. g. *Alnus*, *Carpinus*, *Betula*.

The formation of broad rays by the compounding process is exactly what Eames¹ has recently described as occurring in the oak. He has shown that in the seedling and in the young branch of some species the characteristic broad oak ray is not present, but develops later in a manner exactly similar to that just outlined for *Ephedra*. From these facts and from fossil evidence he concluded that the broad type of ray found in Angiosperms is not a primary structure representing the gap between the original primary vascular bundles, as has been supposed, but is really derived secondarily from an aggregation of uniseriate rays of the Coniferous

¹ Eames, A. J.: Origin of Broad Ray in *Quercus*. Bot. Gaz., March, 1910.

type. Bailey¹ emphasized the transitions in the compounding process furnished by the false rays of the Cupuliferae which, as we have seen, likewise have their counterpart in *Ephedra*. He further showed that the compounding took place primarily around the leaf-trace. The development of broad rays is obviously an adaptation for the storage of assimilates manufactured in the leaf, and the most convenient place for their storage is in the stem adjacent to the leaf-trace. From their original position around the trace he considers that the broad rays have spread throughout the wood.

Not only in the possession of broad rays, therefore, but also in their origin does *Ephedra* resemble the lower Dicotyledones. It should be noted, however, that the compounding process bears no obvious relation to the leaf-traces, but may give rise to rays which do not touch a trace at any point. In fact, it seems to be quite independent of the leaf-trace, and is likely to result in the formation of a broad ray on any radius of the stem. It is true that the trace is accompanied by a broad ray, as may be seen in Pl. XCIV, Fig. 7, but this ray is neither so broad nor so high as the usual type of compound ray. Moreover, it rarely shows the fusion process. In fact, it represents rather the leaf-gap of other woods. The reason for its poor development is probably to be found in the non-functional character of the leaves. In practically all cases the leaves are merely small scales which have little or no chlorophyll, and have given over their function of assimilation to the cortex of the young plant which is abundantly supplied with chlorophyll and stomata. Not the restricted area around the leaf-trace, therefore, but the whole circumference of the branch would feel the need for storage. Of course it is quite possible that the original position of ray development was in the vicinity of the leaf-traces, and that with the reduction of the leaves and the functioning of the cortex in assimilation the rays may have lost their original connexions. Indeed, the occasional occurrence of compounding around the trace and the constant presence of a ray in that position would justify such an inference. In any case the resemblance both in regard to the history of development and adult form between the rays of *Ephedra* and those of the lower Dicotyledones is remarkably close.

Just as in many oaks the compounding process is visible only as a passing phase in the seedling, the broad rays of other regions extending right to the pith, so in certain regions of *Ephedra* the broad ray has worked back almost or quite to the pith. This is particularly true of those regions in which storage is greatest, namely, in roots and underground stems. In these places the broad ray develops at a very short distance from the pith, and may indeed be quite continuous with the pith. Pl. XCVI, Fig. 33, which represents a transverse section of a subterranean stem of

¹ Bailey, I. W.: Relation of the Leaf-trace to the Origin of Compound Rays in the Lower Dicotyledons. Ann. Bot., Jan., 1911.

E. monostachya, shows a very early development of several broad rays. Some of them which lack cell contents are to be distinguished as areas in which there are no vessels. As a rule, however, the broad rays do not appear until a considerable zone of wood has been formed.

With the increase in circumference of the young stem the rays become proportionately broader. If the increase went on indefinitely the rays would soon become too broad for the proper organization of the stem tissues. In *Ephedra* the stems rarely become large enough to cause this difficulty, but when they do it is met by the secondary obliquely vertical division of the rays. In tangential view the rays are found to be divided by oblique strands of fibres into a number of segments which then become scattered horizontally through the wood, as the strands of fibres increase in size. This division of broad rays with the increase in diameter of the stem is similar to that described by the writer¹ as occurring in certain of the Fagaceae and Casuarinaceae. Zilztra² has observed the same phenomenon in several Dicotyledonous plants. It was used in the former contribution in support of the theory that the smaller multiseriate rays of the Dicotyledones have been derived from the broad aggregate ray by the diffusion of the latter throughout the wood. In *Ephedra* the stems rarely become large enough to make the dissection process a necessity, but its occasional presence shows that the same rule holds as in the Dicotyledones.

Bailey³ has shown that oak wood formed immediately after an injury is likely to present primitive conditions of ray structure. In such areas one may find only uniseriate rays, and these later undergo the compounding process to form broad rays again. These phenomena are in agreement with the well-established principle that traumatic areas tend to revert to primitive conditions. In *Ephedra* such a reversion is extremely rare, although it is occasionally to be seen. For the most part, however, wounding has very little effect on ray structure, the rays continuing about the same size as before the wound. Occasionally, indeed, the wound causes the enlargement of rays already present, and even the introduction of new ones. As Bailey has suggested for a similar phenomenon in the oak the wound appears in these cases to stimulate the development of broad rays. On the whole, however, the effect of wounding is very indefinite.

One other respect in which the rays of *Ephedra* resemble those of the Dicotyledones is their retarding effect on the growth of the stem. In the oak the growth is slower in the vicinity of the broad ray, and the result is manifested in a distinct 'dip' in the contour of the annual rings which

¹ Thompson, W. P. : Origin of the Multiseriate Ray of the Dicotyledons. Ann. Bot., October, 1911.

² Die Gestalt der Markstrahlen im sekundären Holze. Recueil des Travaux Botaniques Néerlandais, vol. v, 1908.

³ Bailey, I. W. : Reversionary Characters in Traumatic Oak Woods. Bot. Gaz., Nov., 1910.

increase with the diameter of the stem. As Bailey¹ has shown this has had an important effect on the structure of the stem, for it has resulted in the production of the so-called depressed segments alternating with projecting ones. The depressed segments had formerly been considered to represent the 'interfascicular' wood. Fig. 30 shows the presence of the dip in *E. californica*, and its increase in the successive annual rings. Owing to the lack of association between broad rays and leaves in *Ephedra* the depression has not the regularity which it exhibits in the oak.

To summarize the important features of ray structure: The most primitive condition is obviously that presented by the first-formed secondary wood which has uniseriate rays, the individual cells of which are lignified. In both these respects, the uniseriate condition and the lignification, the rays differ from those of the Cycads and Bennettitales, and resemble those of the Conifers. For the rest the relationship is with the lower Dicotyledones, as is manifested by the process of compounding, the ultimate multiseriate condition, the presence of false rays, their retardation of the growth, the form and arrangement, and especially the pitting of the individual cells. A condition typically Dicotyledonous has therefore been derived from a condition typically Coniferous in a method which is to be expected from a study of Dicotyledonous anatomy.

The different constituents of the secondary wood which we have been considering show very little specific variation, so that a diagnosis on the basis of wood structure would be very difficult to make. What variation exists is mainly one of degree. Thus *E. monostachya* has more septated wood parenchyma cells than the others; *E. Gerardiana* and *E. monostachya* exhibit a greater tendency towards the ring-porous arrangement of the vessels; *E. californica* usually presents a larger number of 'false' rays, &c. But these features vary greatly in different pieces of wood and in different regions of the same plant. Accordingly, it is very difficult to make a specific diagnosis with any degree of certainty. But this difficulty is only in keeping with the recognized conservatism of vascular structures.

BAST.

The bast of *Ephedra*, unlike the wood, shows little indication of Angiospermous affinities. Indeed, except for the presence of broad rays, it is typically Gymnospermous.

Fig. 34 represents a transverse section of the bast as well as the cambium and a little secondary wood. The biseriate ray in the centre of the field is seen to broaden out in a characteristic manner. In addition to the ray parenchyma there are other bast parenchyma cells which are arranged in radial rows and elongated vertically. They do not bear the

¹ loc. cit.

relationship of companion cells to the sieve-tubes, but are arranged rather in groups.

The sieve-tubes themselves are visible in this photograph as smaller cells which lack contents and are somewhat collapsed. They are never present in abundance, but, as shown here, are usually confined to small patches. In very large stems of the American species which have been examined they become proportionately much more numerous. In longitudinal section they are found to lack well-defined end walls, but to be long and tapering, as is typical of Gymnospermous sieve-tubes. This feature is shown in the tangential section photographed in Fig. 35. The sieve areas are not confined to the end walls of the tubes, but are scattered rather uniformly along the lateral radial walls, as may also be distinguished in Fig. 35. The same condition is shown in radial section in Fig. 36, in which the sieve areas appear in face view.

Outside the zone of actively functioning bast many of the cells collapse, but others become strongly sclerified. The latter are scattered singly or in small groups. They represent part of the parenchyma of the living bast.

The bast of *Ephedra*, then, in all the characters of its sieve-tubes and in most of those of its parenchyma, possesses no Angiospermous affinities, but is typically Gymnospermous. Strasburger¹ states that in its general appearance and arrangement it resembles most closely the bast of *Araucaria*.

CORTEX, EPIDERMIS, ETC.

As may be seen in the transverse section of the entire young branch (Pl. XCIV, Fig. 1) the external surface is strongly ribbed. Each rib marks the position of a bundle of sclerenchymatous fibres immediately below the epidermis (Fig. 1 and Pl. XCVII, Fig. 37). The fibres are extremely hard, and do not take the usual lignin stains. Others of the same type are scattered either singly or in groups through the rest of the cortex, and large groups occur in contact with the primary phloem. The outermost living cells are arranged more or less in the form of a palisade and are abundantly supplied with chloroplastids. Beneath this layer the tissue is more irregular and contains air-spaces. Thus the structure of the cortex is remarkably like that of a leaf, whose function it performs.

The epidermis is thick-walled and heavily cutinized. It is abundantly supplied with stomata like a leaf, but these are confined to the furrows between the projecting ridges (Fig. 37). The guard cells are strongly lignified, and deeply sunken under overarching accessory cells (Fig. 37).

The periderm formation which eventually throws off the cortex begins just outside the soft bast and inside the primary bast fibres. Its radial rows of cells are in line with those of the bast.

¹ loc. cit.

ROOT.

The root of *Ephedra* presents few features of special interest. The primary wood is diarch and small in amount. In the large primary root near the base of the stem it is arranged in two triangular masses whose outermost apices are occupied by the two protoxylem groups, and whose broad bases are separated by a lignified pith. In the secondary roots the primary wood is very small in amount and extremely difficult to recognize. Indeed, in most cases it appears to have completely disappeared, as has the fundamental parenchyma, so that the centre of the root is occupied by a solid mass of secondary wood.

This secondary wood is in all essentials like that of the stem, differing chiefly in the relative amounts of the various constituents. Thus the wood parenchyma is more abundant and the rays larger, features which are to be anticipated from the function of the root in storage. The vessels are also more frequently of the primitive type, and the bars of Sanio more conspicuous.

LEAF.

The leaves of *Ephedra* occur in opposite decussating pairs or in whorls of three according to the species. They are extremely reduced, in most cases being small brown functionless scales a few millimetres in length. In seedlings and young plants they may be much better developed, probably reverting to an ancestral condition. They then consist of a sheathing base and long needle-shaped extremity.

A section through the sheathing base of one of the best developed leaves is represented in Fig. 38. Only the thickest part of the leaf in the region of the vascular bundles is included. Laterally, where it joins its fellow of the opposite side the leaf is only two or three cells in thickness. Stomata are exceedingly rare, but when present are deeply sunken like those of the stem. The mesophyll is not differentiated into layers and contains at best very little chlorophyll.

Such a leaf as this is enormously developed in comparison with the ordinary adult leaves, which are only three or four cells thick. Moreover, the cells soon become thick-walled and perish. In most cases sclerenchymatous fibres are scattered throughout the substance and may occasionally be arranged in bundles as in the stem.

The tissue of the leaf is early separated from that of the stem by the development of a layer of absciss periderm. The whole of the sheathing base is involved. In Fig. 42 the dark band across the centre represents the periderm layer, below which is the tissue of the cortex and leaf-trace, and above is the empty thick-walled mesophyll of the leaf. The presence of the absciss periderm is a distinctly Angiospermous character.

The vascular system of the leaf consists of two bundles, the continuations of the double trace whose course we have already examined. The two strands continue distinct and unbranched to the apex of the leaf. They are visible at low magnification in Fig. 38, and one of them is shown more highly magnified in Fig. 39. Each bundle is without a sheath of any kind and is flattened in a dorsiventral direction. The tracheides, which are very few in number, are arranged in radial rows. There is no trace of centripetal wood, all the larger elements being developed centrifugally to the protoxylem. The phloem is very poorly developed. At the edges of the bundle, as Strasburger¹ has noted, there is an occasional transfusion tracheide, one of which can be distinguished in Fig. 39 by its bordered pits and thickening bars. The bundle figured is better developed than is usually the case, for as a rule the tracheides are very few in number, the bast practically absent, and the transfusion tracheides rare. Such a bundle with its lack of centripetal wood and possession of transfusion tracheides is exactly like a reduced Coniferous bundle, and quite unlike that of the Cycads with its large development of centripetal wood.

In their basal portion the long needle leaves of the seedling have the same vascular organization as the typical adult leaves. But in their tips this organization becomes modified. The secondary wood of the two bundles diminishes (Fig. 40) until it quite disappears (Fig. 41). Meanwhile, the transfusion tissue increases laterally, and also develops centripetally. In the latter position it increases in amount towards the tip until it forms a solid mass between the two fast vanishing groups of centrifugal wood (Fig. 40). As it increases in amount, the form of its cells also changes; they become longer and more like true tracheides. Finally, in the extreme tip of the leaf the centrifugally developed tracheides have completely disappeared, and only a group of the centripetal ones remain (Fig. 41). Some of the latter are like typical transfusion tracheides, and some of them are more like ordinary tracheides, and might for this reason be considered centripetal wood.

The conditions just described might be used to support Worsdell's contention² that the transfusion tissue has been derived phylogenetically from the centripetal wood of the ancient Gymnosperms. The transitions between centripetal wood and transfusion tissue which he observed in several forms, notably in *Cycas* and *Araucaria*, are duplicated here. The evidence is thus the same as he presents. It should be emphasized that the leaves in which these conditions are found are the abnormal seedling ones, and that the elongated tip to which the centripetal wood is confined is not ordinarily present.

The structure of the vascular bundles of the leaf strongly indicate Coniferous affinity. The development of centrifugal and typical absence of

¹ Über den Bau, &c.

² Origin of Transfusion Tissue. Trans. Linn. Soc., 1895.

centripetal wood are quite like the conditions in Conifers, and quite unlike those in Cycads. The small amount of centripetal wood in the abnormal seedling leaves has its counterpart in several of the Conifers.

CONCLUSIONS AND RELATIONSHIPS.

A complete discussion of the affinities of the Gnetales as indicated in an anatomical study is deferred until the other members of the group have been subjected to a similar study. Certain facts brought out in this investigation, however, may be emphasized here.

As we have already noted, there is an increasing tendency at the present time to regard the Gnetales as derived from Cycadalean stock. The opinion has no doubt sprung from the conviction of many botanists that the Angiosperms have had the same origin, namely, from the Bennettiales, and that there is a real affinity between the Angiosperms and Gnetales. The fullest expression of this idea has been given by Arber and Parkin,¹ whose conclusions have been reached almost entirely from a consideration of floral organization. They maintain that these two great groups have developed along parallel lines from a common ancestor which was in turn derived from forms like Bennettiales. Deferring the consideration of the Angiospermic relationship, let us see what bearing the results of the present study have on the idea of a Bennettitalean origin for the Gnetales.

It may be stated at once that on the anatomical side there is very little evidence for connecting the Bennettiales with *Ephedra*, although this genus, being the most primitive of the Gnetales, is the one where the evidence ought to be found. The only notable feature of resemblance is the possession by both of multiseriate rays, but, as we have seen, those of *Ephedra* have undoubtedly been developed from a condition quite different from the Bennettitalean one, namely, from a uniseriate lignified condition. Therefore the only real anatomical point of resemblance proves valueless in establishing a connexion.

On the other hand, there are a great many differences so vital as to make any real affinity extremely doubtful. Among those differences should be mentioned the course and arrangement of the primary bundles, the pitting of the tracheides, bars of Sanio, tertiary spirals, wood parenchyma, primitively lignified uniseriate rays, adult rays derived by fusion, double leaf-trace, absence of centripetal wood, and development of centrifugal wood in the leaf-trace. Thus almost every tissue presents grave obstacles to this view. All these differences constitute too great a mass of evidence to be overlooked, especially since there appear to be no anatomical resemblances on which to base a relationship.

¹ Studies in the Evolution of the Angiosperms: The Relationship of the Angiosperms to the Gnetales. Ann. Bot., 1908.

With regard to the more recent Cycads they possess one feature of resemblance lacking in the Bennettitales, namely, the double leaf-trace whose two strands were inserted separately in the stele. But as the double leaf-trace is common to so many groups of Gymnosperms it might be used with equal force to connect any of them with the Gnetales. As for the fact that the two strands are inserted separately in the stele, we have seen that this is a variable feature, even the ancient Gymnosperms showing both a condition of separation at the stele (*Poroxylon*), and one in which the strands unite before entering (*Lyginodendron*). Miss Sykes, in her study of *Welwitschia*, brought forward other points of resemblance to Cycads, namely, the occurrence of centripetal wood in the peduncle and of inversely oriented and concentric bundles in the reproductive axis. A preliminary study of the reproductive organs of *Ephedra* has failed to reveal any of these features. On the whole it may be said that the differences between *Ephedra* and the modern Cycads are almost as strongly marked as between *Ephedra* and the ancient Bennettitales. Moreover, if the Gnetales have been derived from Cycadalean stock, most botanists would agree from the evidence of floral organization that it must have been from the Bennettitales, so that any advantages of the modern over the ancient members of that alliance should not have weight.

With the growth in favour of the idea of Cycadalean affinity the older view of the Coniferous relationship of the Gnetales is being supplanted. The present study has led the writer to conclude that the older view had much more in its favour than the more modern one. Every one of the points enumerated as opposed to the Cycadalean relationship may be used in an argument for the Coniferous relationship. To emphasize only the strongest points one should mention the arrangement and structure of pits of the tracheides, bars of Sanio, tertiary spirals, trabeculae, primitive uniseriate and lignified rays, lack of centripetal and development of centrifugal wood in the leaf-trace, and the structure of the vascular bundles of the leaves. These points of remarkable resemblance do not prove a descent from any modern group of Conifers. Indeed, such a descent seems difficult to establish. Opposed to it is the very generalized character of the secondary wood combining many characters found in the various groups of Conifers, such as Araucarian and Abietinean pitting, bars of Sanio, tertiary spirals, trabeculae, resin plates, and wood parenchyma. These points would rather indicate an affinity with that Abietinean-Araucarinean stock which it is now generally conceded gave rise to the modern Conifers. Of course it is possible that the Gnetales represent a line of development paralleling to a considerable extent that of the Conifers. But, however opinions may differ as to the exact point of origin of the Gnetalean line, there is a large mass of evidence to indicate an affinity with the base of the Coniferous line of descent.

Evidence from other sources supports this view. Hill and de Fraine,¹ from their study of the vascular system of the seedlings, conclude that in this respect *Ephedra* strongly resembles *Araucaria* and the Podocarps. Miss Sykes states that the transition phenomena between root and stem in *Welwitschia* strongly resembles that in *Araucaria*.

If the anatomical evidence leads to these conclusions the gametophytic evidence is just as conclusive. According to Land's² description the male gametophyte is typically Coniferous in all details. The female gametophyte differs from that of Coniferales only in the long neck of the archegonium and presence of a pollen-chamber, features which he explains on a physiological basis.

Thus all the essential features, both gametophytic and anatomical, indicate some relationship to the Conifers. Opposed to these and in favour of the Cycadalean affinity we have so far only the evidence of floral organization.

With regard to the Angiospermous relationship *Ephedra* presents several points of interest. Prominent among these is, of course, the possession of vessels. But, as has been pointed out, the vessels of *Ephedra* exhibit vital differences from those of the Angiosperms, although the rare occurrence of fusion of perforations lessens this difficulty. An equally striking feature and one which has been overlooked is the possession of broad rays like those of the lower Dicotyledonous woods, and especially their origin by compounding. This is really a feature of first importance. Among those of lesser value one should recall the separation of the leaf-traces on the stem and the presence of an absciss periderm in the leaf.

SUMMARY.

The pith presents two striking features in the presence of a peridermal diaphragm at the base of each internode and occasional patches of lignified cells simulating centripetal wood.

The primary vascular bundles run regularly through one internode and lose themselves in a nodal girdle of tracheides. Throughout the internode their structure is endarch, but at the node occasional elements like transfusion tracheides are present in a centripetal direction. Transfusion tracheides also occur laterally to the bundles in the internodes of some species.

The leaf-traces are double and the two strands are inserted separately, usually with a vascular bundle between. In structure they are endarch throughout.

The tracheides of the secondary wood are characterized by the arrangement of the pits in both the Abietinean and Araucarinean fashion, structure

¹ On the Seedling Structure of Gymnosperms, IV. Gnetales. Ann. Bot., 1910.

² Spermatogenesis and Oogenesis in *Ephedra trifurca*. Bot. Gaz., 1904.

of pits typically Coniferous, tangential pits, bars of Sanio, and occasionally by tertiary spirals, trabeculae, and resin plates.

The vessels possess all the features just enumerated for the tracheides, and have also perforations which represent bordered pits. The transitions between tracheides and vessels are remarkably complete, all stages in the disappearance of torus and border being visible even in single elements. The vessels are very few in number and of a primitive character in the seedling, and more numerous though of the same character in the first-formed secondary wood of the branches. Fusion of perforations may be observed rarely.

The wood-parenchyma cells, which occur abundantly either scattered or in tangential rows, resemble tracheides in size, shape, lignification, and sometimes in pitting, and have probably been derived from tracheides. They are often multinucleate. They appear to resemble most the so-called fibrous cells of Angiosperms.

The medullary rays of the first-formed secondary wood are uniseriate, and from these the broad rays of the adult are derived either by simple enlargement, addition through the transformation of tracheides to ray parenchyma, or by compounding. The latter process is the same as in Dicotyledones. False rays are common. The individual cells are lignified and pitted like those of Dicotyledones. The broad rays have a retarding influence on the growth of the surrounding wood.

The bast is typically Gymnospermous.

The cortex is abundantly supplied with chlorophyll and functions as a leaf. The stomata in the epidermis of the stem are numerous, and are confined to furrows between projecting ridges due to hypodermal bundles.

The leaves are small and non-functional, except a few on the seedling. The vascular bundles are two in number, small and endarch. Transfusion tracheides are common. At the tip of the seedling leaves the transfusion tracheides develop centripetally and become more like centripetal wood.

The idea of Cycadalean and Bennettitalean affinity receives little support from the anatomy of *Ephedra*. On the other hand, there are many points which are opposed to it, and in favour of Coniferous relationship: the arrangement of the primary vascular bundles, double leaf-trace, arrangement and structure of pits on the tracheides, bars of Sanio, tertiary spirals, trabeculae and resin plates, primitive uniseriate lignified rays, wood parenchyma, and endarch vascular bundles of the leaf. The Gnetales do not appear to have arisen from any modern group of Conifers, but rather from or close to the base of the Coniferous line.

An Angiospermous affinity is indicated by the possession of true vessels, broad rays, formation of broad rays by fusion, and separation of the leaf-traces on the stem.

This investigation has been carried on by the writer in the Phanero-

gamic Laboratories of Harvard University, as an 1851 Exhibition Science Research Scholar of the University of Toronto. He is indebted to Professor E. C. Jeffrey for material and advice.

EXPLANATION OF PLATES XCIV-XCVII.

Illustrating Mr. Thompson's paper on the Gnetales.

PLATE XCIV.

- Fig. 1. *E. monostachya*: transverse section of entire young branch. $\times 60$.
 Fig. 2. *E. trifurca*: transverse section, showing group of pith cells simulating centripetal wood. $\times 125$.
 Fig. 3. *E. altissima*: radial section through region of node, showing peridermal diaphragm. $\times 30$.
 Fig. 4. *E. altissima*: transverse section through lower part of node, showing girdle of primary tracheides. $\times 125$.
 Fig. 5. The same: section through node at exit of trace, showing the double character and separation of strands by a block of wood. $\times 125$.
 Fig. 6. *E. trifurca*: nodal section, showing double trace whose strands are not separated by wood. $\times 100$.
 Fig. 7. *E. altissima*: Tangential section through node, showing two strands of leaf-trace separated by wood. $\times 125$.
 Fig. 8. *E. vulgaris*: centripetal transfusion tracheide at node. $\times 667$.
 Fig. 9. *E. monostachya*: transfusion tracheides in internode. $\times 667$.
 Fig. 10. *E. monostachya*: transverse section of secondary wood. $\times 500$.
 Fig. 11. *E. trifurca*, root: radial section, showing Abietinean pitting and bars of Sanio. $\times 667$.
 Fig. 12. *E. distachya*: compressed Araucarian pitting and normal vessel. $\times 500$.

PLATE XCV.

- Fig. 13. *E. trifurca*, root: tangential pits, bars of Sanio, and broad ray. $\times 500$.
 Fig. 14. *E. californica*: tertiary spirals. $\times 667$.
 Fig. 15. *E. Gerardiana*: thickenings around pits. $\times 500$.
 Fig. 16. *E. trifurca*: showing trabeculae. $\times 500$.
 Fig. 17. *E. altissima*: tangential section, showing perforations in end wall of vessel. $\times 500$.
 Fig. 18. *E. Gerardiana*: tangential section near pith, showing perforations in association with bordered pits. $\times 500$.
 Fig. 19. *E. gerardiana*: tracheide showing first stage in transition to a vessel. $\times 667$.
 Fig. 20. *E. monostachya*: vessel showing gradual loss of torus and border. $\times 500$.
 Fig. 21. *E. distachya*: vessel showing fusion of perforations. $\times 667$.
 Fig. 22. *E. californica*: parenchyma cell whose pits are slightly bordered. $\times 667$.
 Fig. 23. *E. distachya*: wood-parenchyma cell with two nuclei. $\times 500$.
 Fig. 24. *E. trifurca*: wood-parenchyma cell, showing nucleus dividing. $\times 500$.

PLATE XCVI.

- Fig. 25. *E. monostachya*: septated wood-parenchyma cell and normal vessel. $\times 500$.
 Fig. 26. *E. distachya*: radial section of medullary ray. $\times 500$.
 Fig. 27. *E. altissima*, seedling: transverse section. $\times 60$.
 Fig. 28. *E. altissima*, seedling: tangential section near pith, showing formation and enlargement of medullary rays by transformation of tracheides. $\times 125$.
 Fig. 29. *E. monostachya*: transverse section, showing compounding of rays and dip in annual rings. $\times 30$.
 Fig. 30. Transverse section of wood of *E. californica*. $\times 10$.

- Fig. 31. *E. californica*: tangential section of false ray. $\times 125$.
 Fig. 32. *E. trifurca*: 'false' ray. $\times 250$.
 Fig. 33. *E. monostachya*: subterranean stem, showing broad rays extending to pith. $\times 250$.
 Fig. 34. *E. Gerardiana*: bast and cambium. $\times 125$.
 Fig. 35. *E. altissima*: tangential section of bast, showing tapering sieve-tubes and lateral sieve-plates. $\times 250$.
 Fig. 36. *E. altissima*: radial section of bast, showing sieve-tube with sieve-plates in face view. $\times 667$.

PLATE XCVII.

- Fig. 37. *E. monostachya*: young stem showing epidermis and cortex. $\times 330$.
 Fig. 38. *E. altissima*: leaf-base. $\times 60$.
 Fig. 39. The same: vascular bundle with transfusion tracheide. $\times 667$.
 Fig. 40. The same: seedling leaf, showing centripetal transfusion tissue and bundles disappearing. $\times 500$.
 Fig. 41. The same: seedling leaf-tip with group of centripetal tracheides. $\times 667$.
 Fig. 42. *E. Gerardiana*: longitudinal section of leaf-base, showing absciss periderm. $\times 500$.

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<https://doi.org/10.1093/oxfordjournals.aob.a089432>.

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