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INVESTIGATIONS ON THE PHYLOGENY OF THE ANGIOSPERMS

I. The Anatomy of the Node as an Aid in the Classification of Angiosperms

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It is generally recognized that during the course of evolution among vascular plants certain rather definite organs or regions of the body have changed much more slowly than others and hence retain many ancient characters which have been lost elsewhere. One of the most important tasks before the student of comparative plant morphology is to determine where these regions are and in what features they are conservative, and thus to aid the phylogenist in picking out those primitive and constant characters on which he may construct a natural system of classification.

The reproductive organs, root, young plant, first annual ring, leaf and node in various families have all been shown to be regions which in a greater or less degree are apt to be conservative in their internal or external structure. Among these the anatomy of the leaf, particularly at the node where leaf and stem unite, often retains in a most striking way features which have been lost elsewhere in the plant. The ancient centripetal or "cryptogamic" wood has persisted in the foliar bundle of Equisetum (3), the cycads (5), and Prepinus (4) after it has disappeared in all other regions, save occasionally in the reproductive axis. The presumably primitive number and arrangement of leaf bundles persists at their point of insertion at the node in the sigillarians, ferns (6), cycads, Cordaitales, Ginkgo and the broad-leaved conifers although it has changed greatly in the petiole and blade.

Since the vascular system of the leaf in the lower orders appears so generally to be a region which is slow to change, it is reasonable to suppose that in the angiosperms as well it will display a similar

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conservatism. The structure of the angiospermous petiole, indeed, has been the subject of numerous and careful studies by different anatomists, and it has been found that in a few families and even in certain genera the petiolar structure is sufficiently peculiar and conservative to be used as a diagnostic character for the group. In general, however, the number and arrangement of the petiolar bundles is too much dependent on the size and texture of the leaf to be of very great taxonomic importance; and even where these characters are reasonably constant, it is very hard to draw phylogenetic conclusions from them and to determine which particular type is the most primitive. The fact that the node of several of the lower orders, rather than the petiole, seems to be a notably conservative region suggested that in the higher seed plants, as well, it might be worthy of study. The present investigation has therefore had as its object an examination of the nodal structures of the angiosperms with the hope of discovering simple and constant anatomical features which will be of value in determining broad lines of relationship.

In the Lycopodiales, ancient and modern, the vascular supply for the leaf is at its base almost invariably a single strand. In the ferns, cycads, Cycadofilices, Cordaitales, Ginkgoales and conifers the foliar bundle, although often single, seems primitively to have been a double one. This double trace, especially in the ferns, has often been broken up into a wide arc of strands. In these lower vascular plants the foliar supply, whether single, double or multiple, causes typically but a single gap (if any) in the continuity of the vascular ring (*fig.* 1). Thomson (7) has observed, however, that in very vigorous specimens of Agathis the two bundles of the leaf-trace are separated at their insertion by a tiny segment of the secondary wood and thus cause a double gap in the cylinder (*fig.* 2). Among the Gnetales the genus Ephedra, which most closely approaches the conifers in other respects, has like them a double leaf-trace, but the two portions as in Agathis are separate at their insertion (*fig.* 3). The node of Gnetum is much more complex for here there are from seven to eleven strands passing off into each leaf and every strand causes a gap of its own in the cylinder.

Such a condition where there is an odd number of bundles, each departing from a distinct gap in the vascular ring, is typical of the Angiosperm node, and has apparently arisen as an adaptation to the increased transpiration current passing to the broad leaves. The

particular number of bundles and gaps is extremely constant among related forms, and almost every family has a characteristic nodal formula which is subject to little variation.

As to what was the primitive structure of the node among angiosperms we cannot be sure, but in all probability the earliest condition was rather plastic and variable. It seems clear, however, that a foliar supply of three bundles, each causing a gap of its own in the stem cylinder, is certainly a very ancient type among the dicotyledons. We may designate this as the *trilacunar* condition (*figs.* 4, 5, 11, etc.). It characterizes most of the members of the Piperales, Salicales, Myricales, Juglandales, and Fagales—in short, of the former Amentiferae; and is present in the great majority of the Ranales and Rosales, as well. Since in all likelihood one of these great groups approaches the primitive angiosperms (or at any rate the primitive dicotyledons) in its character, we may feel reasonably sure that the trilacunar condition became fixed in the angiosperm line very far back. This is rendered still more probable by the fact that all other variations of nodal structure in the phylum seem to have been derived, as we shall see, from such a three-bundled type. This type is not confined to the lower Archichlamydeae but also characterizes in general the Rhoedales, Geraniales, Rhamnales, Malvales and many Sapindales and Parietales among the Archichlamydeae; and the Plantaginales, Cucurbitales, Caprifoliaceae and Compositae among the Metachlamydeae, thus occurring in the majority of dicotyledons.

This ancient trilacunar condition has been modified both by reduction and by amplification. In many orders we find that only a single gap is left by the foliar supply, whether the latter is single or multiple (*figs.* 14, 16, 20 etc.). Such a single-gapped or *unilacunar* type of nodal structure characterizes all the Centrospermae, most of the Myrtiflorae and numerous families of the Sapindales and Parietales among the Archichlamydeae; and the Ericales, Primulales, Ebenales, Contortae, Tubiflorae and families in the Rubiales and Campanulatae among the Metachlamydeae. That this simple condition is not a primitive one, however, but has been derived by reduction from the trilacunar type is indicated by a study of the node in those few families which are transitional from one type to the other.

The Cruciferae are perhaps the best example of such a family. Most of the genera in the Thelypodieae, Sisymbriineae, Cochleariineae and Brassicineae, as well as scattering genera in other tribes, possess

a foliar trace of three rather distant strands, each causing a gap of its own in the stele. In certain genera and species, however, such as Sisymbrium leiocarpum (*fig.* 13), these three bundles approach each other very closely and are separated only by two very small segments of the cylinder. In all the other Cruciferae the departure of the foliar supply causes but a single gap in the wall of the cylinder, but in such cases the leaf trace itself almost always consists of three bundles (*fig.* 14). In the Cruciferae the three originally distant strands thus seem to have gradually become approximated until by the disappearance of the separating segments of the stele, they come off close together and cause but a single gap. In the Dilleniaceae a very similar transition is also evident.

In many of the groups of plants which are characterized by a unilacunar nodal structure the leaf-trace at its origin frequently consists, as in the Cruciferae, of three distinct strands or of a deeply three-lobed one (*photo.* 3). Such a structure is particularly common in those great unilacunar orders the Centrospermae and the Tubiflorae and indicates that the nodal condition in these and similar groups has arisen by reduction from the primitive three-bundled type.

In certain instances even this triple division of the leaf-trace has been lost in the older parts of the plant, as is shown by *figure* 8, which is a section through the mature stem of *Chenopodium album.* In the young plant, however, where the whole stem structure is simpler, the leaf-trace consists of three quite distinct strands (*fig.* 7). Such "recapitulations" are of frequent occurrence.

Among such families as the Amaranthaceae which are characterized by anomalous growth of the vascular tissue, the leaf-trace is often exceedingly complicated at maturity (*fig.* 10). In the simpler members of the family, however (*fig.* 9), and in the seedlings of the complex forms, the primitive triple condition is retained. The ancestors of such plants probably possessed the nodal structure of primitive angiosperms, with three isolated bundles departing to the leaf. These first became approximated and the gaps fused; and later the foliar supply underwent various further modifications.

The unilacunar condition seems to have been derived from the trilacunar, in certain families, by the abortion of the two lateral strands instead of their fusion with the central trace. In *Ilex opaca* (*fig.* 19), for example, the three typical bundles are usually present, but one or both of the lateral ones tend to be very small. In all other members

of this and other genera of the family, however, only a single bundle was observed (*fig.* 20). This shows no signs of being divided into three parts, and without doubt represents the median one of the original three strands. In various species of Myrica the two lateral bundles are usually small and have often disappeared. Spiraea, Exochorda and their immediate allies alone among the Rosaceae, as far as the writer has observed, possess but a single unlobed and undivided leaf-trace (*fig.* 16). In such closely related forms as Physocarpus, however, there are the three widely separated strands (*fig.* 15) and we are forced to the conclusion that the trace of Spiraea represents only the median one of these. This method of reduction seems to have been a common one. From the fact that the single bundle given off to the leaf in the Ebenales, Ericales, Contortae and certain other groups is continuous and undivided we may infer that the unilacunar condition in these forms has arisen by the loss of the two lateral traces rather than by the fusion of all three, as in the Centrospermae and Tubiflorae.

In these two ways, then, the presumably primitive trilacunar condition of the node has been reduced. In several groups, however, the opposite has happened and amplification has taken place. This tendency is shown in many forms but reaches its highest development in the Polygonales and Umbelliflorae. In these orders the leaves are typically sheathing and are supplied by a large number of bundles, each of which causes a gap of its own in the cylinder (*fig.* 6). In certain of the Polygonales, however, such as the dioecious species of Rumex (*fig.* 5), and the climbing forms of Polygonum, the node is trilacunar. In the Araliaceae, also, which are presumably more primitive than the Umbelliferae, the number of bundles and gaps is smaller than in the latter family, being as low as five in certain species. In young plants of the Polygonales and Umbelliflorae the first formed leaves are almost always supplied with three strands which are inserted separately on the vascular ring. In the Ranunculaceae, too, the more primitive genera have three bundles and gaps, and the more highly specialized ones, many. It therefore seems very probable that this *multilacunar* condition has been derived by the amplification of our hypothetically primitive trilacunar type.

If this supposition is correct, it furnishes evidence of much value in determining the relative antiquity of monocotyledons and dicotyledons. The typically sheathing leaf of the former group is supplied by a large number of bundles which come off around the entire peri-

phery of the stem, much as in the multilacunar dicotyledons save that, of course, a continuous vascular ring with typical leaf gaps is absent. In families which are admitted to be very primitive, however, such as the Potamogetonaceae, a much simpler condition prevails. The anatomy of various members of this family has been investigated by Chrysler (2), who comes to the conclusion that the genus Potamogeton is the most primitive in the group; and that its more robust species, such as *P. pulcher*, represent the original type from which the others have been reduced. The vascular tissue in this form is arranged in a cylinder, as in the dicotyledons. The foliar traces are three in number. After running for a short distance in the pith, they leave the cylinder from three distinct points (*fig. 29*), thus presenting a striking resemblance to the trilacunar type which we have regarded as primitive for the dicotyledons, and suggesting the way in which the more complicated nodal structure of the higher monocotyledons has arisen.

The young plants of many of these higher types show decided anatomical resemblances to the primitive monocotyledons and to the dicotyledons. Chrysler (1) has investigated the anatomy of the seedling in several groups, particularly the Araceae and Liliaceae. From his description and figures it is evident that in a great many instances the first few leaves are supplied with three bundles, each of which arises separately and causes a gap of its own in the cylinder which in these earlier stages much resembles the woody ring of dicotyledons. *Figure* 30 shows the node of a seedling of *Acorus calamus* with the three traces departing to one of the earlier leaves.

If such forms as the Potamogetonaceae are actually primitive among monocotyledons, and if the structure of the young plant is rightly regarded as displaying primitive characters—conclusions for both of which there seems to be ample evidence—then it would certainly appear that the monocotyledons have had their origin from plants possessing a medullated ring of vascular tissue and the trilacunar nodal condition which we have regarded as primitive for dicotyledons.

We have already remarked that almost every family of the dicotyledons has a particular type of nodal structure which is extremely constant. That it is almost entirely independent of the size, shape or mode of attachment of the leaf is also apparent. The large pinnate leaves of Fraxinus, Juglans and Daucus, which are essentially similar in size and shape, are provided, respectively, with one, three and many traces, each of which arises independently from the vascular cylinder.

The vascular supply to the large leaves of Catalpa comes off from a single gap, whereas that to the much reduced ones of certain of the Polygonaceae is made up of a considerable number of separately inserted strands. The sheathing leaves of the Polygonaceae and Umbelliferae are supplied by a large number of bundles, but in many instances in the Caryophyllaceae and other groups the leaves also encircle the stem with their bases but into each passes only a single strand from the stem. To be sure, there are a considerable number of instances where the leaf has been so much reduced from adaptation to xerophytic or hydrophytic conditions that it is supplied by a single bundle instead of by the three or more which may distinguish the rest of its family. In such cases, which of course are comparatively rare, the anatomy of the node is of little value in classification. The type for a family should be obtained from vigorous, unreduced species.

Let us now briefly compare the anatomy of the node in the various main groups of dicotyledons and endeavor to find what information a study of this region presents which will be of value in determining relationships.

Verticillatae[1]

Each of the much reduced, scale-like leaves of Casuarina is supplied with a single small trace.

Piperales

Among the Piperaceae the genus Peperomia has a normal vascular structure and a trilacunar trace. In Piper, where the stem anatomy is usually anomalous, the foliar supply consists generally of five or seven separate strands. Peperomia thus presumably represents the primitive condition for the family.

Salicales

In all species of Salix and Populus examined, the nodal structure was invariably trilacunar.

Garryales

The node of Garrya is trilacunar.

Myricales

The node in this group is doubtless primitively trilacunar, but the two lateral bundles are small and often absent.

[1] The nomenclature and classification is that of the last (7th) edition of Engler's "Syllabus der Pflanzenfamilien."

Leitneriales

Leitneria is trilacunar.

Juglandales.

The order is prevailingly trilacunar, although five bundles and gaps frequently occur in Pterocarya.

Julianales

This order is trilacunar.

Fagales

All species of the genera of the Betulaceae and Fagaceae examined had invariably three bundles and three gaps (*fig.* 4 and *photo.* 1).

It is thus evident that in all those plants grouped originally under the inclusive order Amentiferae the fundamental type of nodal structure is trilacunar. This may occasionally be expanded but in no case is there an approximation and fusion of the three gaps into one.

Urticales.

All the Ulmaceae and Urticaceae examined agreed in the possession of a trilacunar node. This seems also to be characteristic of most of the Moraceae, although in Ficus there are usually five bundles and gaps.

Proteales

In the six genera of Proteaceae examined the nodal structure was invariably trilacunar.

Santalales

In the Santalaceae and Loranthaceae there is apparently but a single bundle and gap to each node, but a trilacunar condition is characteristic of the Olacaceae and is therefore probably ancestral for the order as a whole.

Aristolochiales

The node of Aristolochia is trilacunar, but the bulk of the vascular supply to the leaf is contained in the central bundle. The two lateral ones are very small and arise close together on the *opposite* side of the stem from that where the leaf is attached, pass around the stem and thus enter the base of the leaf.

Polygonales

We have already spoken of the Polygonaceae as a typically multilacunar family. In Mühlenbeckia, Coccoloba, Fagopyrum and most species of Rumex and Polygonum examined there are a considerable number of strands passing off into the sheathing base of the leaf from the entire periphery of the stem (*fig.* 6). In young plants of these forms, however, there are only three bundles to each leaf, and this trilacunar condition, which also prevails in the dioecious species of Rumex (*fig.* 5) and the climbing species of Polygonum, is probably primitive for the order.

Centrospermae

In this great order a large number of species were investigated in all families save the Cynocrambaceae and Bassellaceae, and in every instance the departure of the foliar strand was found to cause but a single gap in the cylinder. In the Chenopodiaceae, Amarantaceae, Nyctaginaceae and Phytolaccaceae the stem structure is often anomalous, but even here the complex leaf-trace comes off from one definite region and is not inserted in various places around the stem (*figs.* 8 and 10). The simpler species in these groups (*fig.* 9), however, and the very young plants (*fig.* 7) display a single vascular ring with no anomalous bundles. Although the leaf-trace in such forms and in all the rest of the order (the Aizoaceae, Portulacaceae and Caryophyllaceae) never leaves but a single gap, it is almost always three-parted or three-lobed, thus indicating its probable origin from an approximation of the three strands of a trilacunar type. The fact that such a very large series of plants are characterized without exception by a single type of nodal structure is strong evidence for placing them together, especially since the unilacunar condition which they display is possessed by very few of the other lower Archichlamydeae. The Polygonales, with which some or all of the Centrospermae have frequently been included, even in the recent system of Hallier, possess a nodal anatomy so unlike that of the Centrospermae as to preclude any very close relationship, if the structure of the node is to be regarded as of much taxonomic value. Evidence from this region certainly supports the view that the Centrospermae as defined by Engler constitute a very natural order which is somewhat removed from the other lower Archichlamydeae.

Ranales.

The nodal structure of the Ranales is extremely various but seems to have been primitively trilacunar. The three genera Trochodendron, Tetracentron and Euptelea, included by Engler under the family Trochodendraceae, are characterized, respectively, by five, three and one traces and gaps. The Cercidiphyllaceae (Cercidiphyllum) are trilacunar. Among the Ranunculaceae, the presumably more primitive sections of the family (the Paeonieae and Helleboreae) are for the most part trilacunar. Such a condition distinguishes Paeonia (*fig.* 11), Caltha, Coptis, Delphinium and sometimes Aquilegia. Forms in which the primitively follicular ovary has been much reduced, as Actaea, Xanthorrhiza (*fig.* 12 and *photo.* 5) and Cimicifuga, have the base of the leaf supplied with a very large number of strands inserted separately around most of the periphery of the stem. Such a condition is present also in the Anemoneae (Ranunculus, Anemone and Thalictrum), which from their single-seeded fruits are regarded by Engler as the most highly specialized members of the family. Clematis is the only member of this subfamily with a trilacunar node. The trilacunar condition therefore seems to have been primitive for the Ranunculaceae; and reduction of the ovary and amplification of the nodal system have apparently progressed together. The Lardizabalaceae (Akebia and Sinofranchetia) are trilacunar. Among the Berberidaceae, *Berberis communis* and many other species are trilacunar but others, particularly *B. aquifolium*, may have as many as eleven bundles passing off to the leaf base. In Epimedium there are seven strands and gaps. The Menispermaceae seem to be exlusively trilacunar. The Magnoliaceae are perhaps more variable in nodal structure than any other family of dicotyledons. Illicium, Schizandra and Kadsura are unilacunar; Drimys and Tetracentron are trilacunar, and Liriodendron, Magnolia and Michelia are multilacunar. The Calycanthaceae are all trilacunar. The rest of the sub-order Magnoliineae which were observed (the Anonaceae, Myristicaceae, Monimiaceae, Lauraceae and Hernandiaceae) are entirely unilacunar, but in every case the leaf-bundle is three-lobed or tripartite (*photo.* 3), indicating that the nodal type was originally trilacunar.

The nodal structure of the Ranales seems to have been primitively trilacunar and to have progressed both toward amplification and toward reduction. The group as a whole is more variable in this respect than are most orders, a circumstance which seems to favor the idea that

it is relatively primitive in constitution, for it is among primitive types that any structure is apt to be found in its most plastic and variable condition.

Rhoedales

In this order the Papaveraceae seem to be invariably trilacunar, but it is noteworthy that the three bundles, at least in the smaller portions of the stem, come off very close together. The Capparidaceae are entirely unilacunar. The Cruciferae, as we have noted above, are both trilacunar and unilacunar (*figs.* 13 and 14), and from the number of intermediate conditions observable, this family furnishes one of the best examples of the way in which one type has been derived from the other. The Resedaceae are unilacunar.

In this order, therefore, the primitive condition was apparently one with three gaps and traces (since it occurs in the most generalized and primitive family, the Papaveraceae) and the whole tendency in the evolution of the group seems to have been toward the approximation and fusion of the various bundles constituting the foliar supply.

Rosales

Plants belonging to this order possess a nodal structure which is almost invariably trilacunar (*figs.* 15 and 17). Some of the more important exceptions observed were the following:—Schizophragma, Astilbe and a few species of Hydrangea, among the Saxifragaceae, have five or seven bundles and gaps; Spiraea, (*fig.* 16), Exochorda and their immediate allies among the Rosaceae are unilacunar and *Potentilla palustris* is multilacunar; among the Crassulaceae, all species of Sedum and Crassula investigated were unilacunar, but in Cotyledon there were in addition to the central bundle two small lateral ones; Eucommia is unilacunar; Platanus has seven bundles and gaps, and Phaseolus, Dolichos, Gymnocladus and a few other genera of the Leguminosae possess a foliar supply of five bundles. Evidence from the node, therefore, indicates that the Rosales are a good natural order.

Geraniales

The Geraniales resemble the Rosales in possessing, for the most part, a trilacunar nodal structure. This characterizes without exception all the members of the Geraniaceae, Tropaeolaceae, Oxalidaceae, Linaceae and Rutaceae which were observed. The Simarubaceae

(Ailanthus) possess seven bundles and gaps, and the Burseraceae and Meliaceae five. Erythroxylon is unilacunar. The Malpighiaceae are prevailingly trilacunar but a few genera (Bannisteria) have but a single gap. The Vochysiaceae, Tremandraceae and Polygalaceae are unilacunar. The large family Euphorbiaceae is prevailingly trilacunar, but certain genera (Ricinus) have more than three bundles and a few (Antidesma) only one. The order agrees with the great majority of Archichlamydeae in being fundamentally trilacunar.

Sapindales

Under the Sapindales are included a large number of sub-orders some of which are not very closely related to one another, and the anatomy of the node is consequently rather diverse among the various members of the order.

The sub-orders Empetrineae, Buxineae, and Coriariineae are evidently entirely unilacunar. Among the families included under the Celastrineae both types are represented; the Cyrillaceae and Celastraceae (*fig.* 18) being unilacunar and the Staphyleaceae trilacunar. Most of the Aquifoliaceae (Nemopanthus, Byronia and most species of Ilex) (*fig.* 20) are unilacunar but, as we have previously noted, *Ilex opaca* (*fig.* 19) has three bundles and gaps. The Aceraceae, Hippocastanaceae and Sapindaceae, included under the Sapindineae, are all trilacunar so far as observed save for a few species of Aesculus where there may be five bundles and gaps. The Balsaminaceae are entirely unilacunar but the single trace is clearly tripartite.

It is within such rather heterogeneous groups of plants as are included among the Sapindales that the anatomy of the node, which is so constant within individual families, will probably be found to be of much value in determining the composition and relationship of the various sub-orders. As at present constituted, the Sapindales apparently cannot be regarded as a very "natural" order.

Rhamnales

In this order the Rhamnales are entirely trilacunar, but the Vitaceae examined have three, five or seven bundles and gaps.

Malvales

The various families included under the Malvales seem to be very similar in their nodal structure, the Elaeocarpaceae, Tiliaceae, Mal-

vaceae and Sterculiaceae being characterized almost exclusively by a trilacunar node. The only exceptions noted to this were among a few of the Malvaceae which possessed five or more strands.

Parietales

The Parietales are another rather large and heterogeneous order. The families included by Engler under the Theineae are various in their nodal anatomy; the Eucryphiaceae and Ochnaceae being trilacunar, the Dipterocarpaceae having three or five bundles and gaps and the Marcgraviaceae, Theaceae and Guttiferae (*fig.* 21) being entirely unilacunar. The Dilleniaceae present another good example of a family which is intermediate between a trilacunar and a unilacunar condition. The genera Dillenia, Tetracera, Davilla, Curatella, Doliocarpus and Hibbertia have either three or five bundles and gaps at the node. They all belong to the sub-family Dillenioideae which, from the simple structure of the stamens and the partial freedom of the carpels, is with little doubt to be regarded as more primitive than the rest of the family. The other two sub-families, the Actinidioideae and Saurauioideae, are more specialized florally and the two genera Actinidia and Saurauia which compose them are both unilacunar in nodal structure. The Dilleniaceae thus present further evidence that the unilacunar condition of the node has been derived from a trilacunar one. All the Cistaceae examined are unilacunar, but the Bixaceae, included with them under the sub-order Cistineae, are trilacunar. All members of the Flacourtiineae investigated (Violaceae, Flacourtiaceae, Stachyuraceae and Passifloraceae) were trilacunar. The Caricaceae have from three to many bundles and gaps at the node. The number in the Begoniaceae is usually five.

Opuntiales

The Cactaceae are so much reduced that nodal anatomy is of little value in determining relationships.

Myrtiflorae

Aside from the Centrospermae, the Myrtiflorae are the largest order of Archichlamydeae to be overwhelmingly unilacunar. Most of the families grouped under the order by Engler were investigated and in all but three the departure of the foliar supply caused but a

single gap in the cylinder (*fig.* 22 and *photo.* 4). These three are the Nyssaceae, Alangiaceae and Rhizophoraceae, which are trilacunar. The first two have often been included under the Cornaceae, an affinity which the structure of the node supports. Nodal anatomy also indicates that the Rhizophoraceae should not be placed in the Myrtiflorae which, aside from these three families, seems to be a natural order.

Umbelliflorae

The Umbelliflorae of Engler include the families Araliaceae, Umbelliferae and Cornaceae. As we have previously noted, the first two of these families are almost invariably characterized by an amplified nodal structure, in which a large number of bundles, each leaving a separate gap, enter the base of the leaf (*fig.* 23 and *Photo.* 6). The Cornaceae, on the other hand, as far as has been observed are always trilacunar (*Photo.* 2). The anatomy of the node thus supports evidence from other sources which goes to show that this family should not be included in the Umbelliflorae but should be placed elsewhere. The order thus reduced to the Araliaceae and the Umbelliferae seems to be a very natural one.

Ericales

The various families included under this order (Clethraceae, Pirolaceae, Ericaceae, Epacridaceae and Diapensiaceae) are all unilacunar (*fig.* 24) save the Epacridaceae, in which each of the sheathing leaves is supplied by a considerable number of separate strands. If the anatomy of the node is a sound criterion of relationship, the Epacridaceae cannot be placed very close to the Ericaceae. This may well be an instance, however, where the structure of the flower is more dependable than that of the node.

Primulales

Members of all three families of this order are unilacunar.

Plumbaginales

The single family Plumbaginaceae included under this order appears to be entirely trilacunar.

Ebenales

The four families included under the Ebenales seem to be exclusively unilacunar (*fig.* 27).

Contortae

All genera examined of the five families included by Engler in the Contortae are unilacunar save Menyanthes which (with another genus) composes the sub-family Menyanthoideae of the Gentianaceae. In this case three or five bundles enter the base of each leaf from as many gaps. Either Menyanthes should not be included under the Gentianaceae or else we must believe that its nodal structure has been so modified by its aquatic habitat, which has caused its leaves to become sheathing, that evidence from this region should be disregarded.

In the Ericales, Ebenales and Contortae the single leaf-trace shows no indication of being three-lobed, a fact which may be taken to indicate that the unilacunar condition in these orders has been produced by the loss of the two lateral traces rather than by the approximation of the original three.

Tubiflorae

This immense order is characterized almost without exception by a nodal structure which is unilacunar (*figs.* 25 and 26). In the many genera from the sixteen families of this order investigated only Cyrtandra, one of the Gesneraceae, displayed other than this single-gapped condition. Three or five strands and gaps is typical for this genus. Such an exception may be regarded as merely one of the cases where the anatomy of the node is not conservative; or it may be taken as an indication that the Gesneraceae are relatively primitive among the Tubiflorae and connect such families as the Bignoniaceae and Scrophulariaceae with the Rubiales.

The leaf-trace in the Tubiflorae is very often three-lobed or tripartite (*fig.* 25) indicating that it has had its origin as a fusion of the three bundles of the ancestral trilacunar type. On evidence from nodal anatomy the Tubiflorae as defined by Engler appear to be a very natural order.

Plantaginales

Plantago is trilacunar.

Rubiales

All families in this order save the Adoxaceae were investigated. The Caprifoliaceae, Valerianaceae and Dipsacaceae are entirely trilacunar except for a few instances (Sambucus and others) where they may be five bundles and gaps. The Rubiaceae, however, are overwhelmingly unilacunar, the only exception observed being the genus

Sarcocephalus where the presumably ancient trilacunar condition persists.

Cucurbitales

The Cucurbitaceae are entirely trilacunar, apparently. The petiole in most members of the family is large, especially at the base, and contains a ring of many strands. Just as these enter the stem, however, they become grouped into three bundles, each of which is inserted separately.

Campanulatae

In this order the Campanulaceae are entirely unilacunar. The Goodeniaceae and Compositae, however, are trilacunar (*fig.* 28) or in rather rare cases multilacunar. The theory so generally held and maintained in the recent classifications of Engler and Hallier that the Compositae have been derived from the Campanulaceae or their near allies therefore receives no support from nodal anatomy for if our general hypothesis as to the origin of the different types of nodal structure in the angiosperms is correct, we should certainly not expect the trilacunar condition of the Compositae to have been derived from the unilacunar (and hence reduced) one which characterizes the Campanulaceae. We should more naturally look to the trilacunar Goodeniaceae, Dipsacaceae or Caprifoliaceae for the ancestors of the Compositae. Evidence from nodal anatomy seems to indicate that the Campanulatae ought perhaps to be divided into more than one order.

The following table presents a more condensed summary of the occurrence of the various types of nodal anatomy throughout the dicotyledons. Numbers refer to number of gaps. Those in parenthesis indicate rare conditions for the family.

This tabular review of the nodal anatomy of the dicotyledons makes it evident that we are here dealing with a character which is almost always very constant within any particular family. It will be noted that a trilacunar condition may frequently become expanded into a multilacunar one in the same family or even in the same genus, but that it is rarely contracted into the unilacunar condition in nearly related forms. The two main types are really the unilacunar and the multilacunar and it is only in comparatively few cases, such as the Magnoliaceae, Cruciferae and Dilleniaceae that these both occur in any considerable number in the same family.

VERTICILLATAE
Casuarinaceae, 1.

PIPERALES
Piperaceae, 3 and 7.
Chloranthaceae, 3 and many.

SALICALES
Salicaceae, 3.

GARRYALES
Garryaceae, 3.

MYRICALES
Myricaceae, 3 and (1).

LEITNERIALES
Leitneriaceae, 3.

JUGLANDALES
Juglandaceae, 3 and (5).

JULIANALES
Julianaceae, 3.

FAGALES
Betulaceae, 3.
Fagaceae, 3.

URTICALES
Ulmaceae, 3.
Urticaceae, 3.
Moraceae, 3 and 5.

PROTEALES
Proteaceae, 3.

SANTALALES
Santalaceae, 1.
Olacaceae, 3.
Loranthaceae, 1.

ARISTOLOCHIALES
Aristolochiaceae, 3.

POLYGONALES
Polygonaceae, many.

CENTROSPERMAE
Chenopodiaceae, 1.
Amarantaceae, 1.
Nyctaginaceae, 1.
Phytolaccaceae, 1.
Aizoaceae, 1.
Portulacaceae, 1.
Caryophyllaceae, 1.

RANALES
Trochodendraceae, 1, 3, and 5.
Cercidiphyllaceae, 3.
Ranunculaceae, 3 and many.
Lardizabalaceae, 3.
Berberidaceae, 3 and many.
Menispermaceae, 3.
Magnoliaceae, 1, 3, and many.
Calycanthaceae, 3.
Anonaceae, 1.
Myristicaceae, 1.
Monimiaceae, 1.
Lauraceae, 1.
Hernandiaceae, 1.

RHOEDALES
Papaveraceae, 3.
Capparidaceae, 1.
Cruciferae, 3 and 1.
Resedaceae, 1.

ROSALES
Crassulaceae, 3 and 1.
Saxifragaceae, 3 and (5).
Pittosporaceae, 3.
Brunelliaceae, 3 and 5.
Cunoniaceae, 3.
Hamamelidaceae, 3.
Eucommiaceae, 1.
Platanaceae, 7.
Crossosomataceae, 3.
Rosaceae, 3 and (1) and (5).
Connaraceae, 3.
Leguminosae, 3 and (5).

GERANIALES
Geraniaceae, 3.
Oxalidaceae, 3.
Tropaeolaceae, 3.
Linaceae, 3.
Erythroxylaceae, 1.
Zygophyllaceae, 3.
Rutaceae, 3.
Simarubaceae, 7.
Burseraceae, 5.
Meliaceae, 5.
Mapighiaceae, 3 and (1).
Vochysiaceae, 1.
Tremandraceae, 1.
Polygalaceae, 1.
Euphorbiaceae, 3 and (1).

SAPINDALES
Buxaceae, 1.
Empetraceae, 1.
Coriariaceae, 1.
Anacardiaceae, 3.
Cyrillaceae, 1.
Aquifoliaceae, 1 and (3).
Celastraceae, 1.

Staphyleaceae, 3.
Aceraceae, 3.
Hippocastanaceae, 3 and (5).
Sapindaceae, 3.
Balsaminaceae, 1.

RHAMNALES
Rhamnaceae, 3.
Vitaceae, 3, 5, and 7.

MALVALES
Elaeocarpaceae, 3.
Tiliaceae, 3.
Malvaceae, 3 and (many).
Sterculiaceae, 3.

PARIETALES
Dilleniaceae, 3 and 1.
Eucryphiaceae, 3.
Ochnaceae, 3.
Marcgraviaceae, 1.
Theaceae, 1.
Guttiferae, 1.
Dipterocarpaceae, 3 and 5.
Cistaceae, 1.
Bixaceae, 3.
Violaceae, 3.
Flacourtiaceae, 3.
Stachyuraceae, 3.
Passifloraceae, 3.
Caricaceae, 3 and many.
Begoniaceae, 5.

MYRTIFLORAE
Peneaceae, 1.
Oliniaceae, 1.
Thymeleaceae, 1.
Eleagnaceae, 1.
Lythraceae, 1.
Punicaceae, 1.
Lecythidaceae, 1.
Rhizophoraceae, 3.
Nyssaceae, 3.
Alangiaceae, 3.
Combretaceae, 1.
Myrtaceae, 1.
Melastomataceae, 1.
Oenotheraceae, 1.

UMBELLIFLORAE
Araliaceae, many.
Umbelliferae, many.
Cornaceae, 3.

ERICALES
Clethraceae, 1.
Pirolaceae, 1.
Ericaceae, 1.
Epacridaceae, many.
Diapensiaceae, 1.

PRIMULALES
Theophrastaceae, 1.
Myrsinaceae, 1.
Primulaceae, 1.

PLUMBAGINALES
Plumbaginaceae, 3.

EBENALES
Sapotaceae, 1.
Ebenaceae, 1.
Symplocaceae, 1.
Styracaceae, 1.

CONTORTAE
Oleaceae, 1.
Loganiaceae, 1.
Gentianaceae, 1 and (many).
Apocynaceae, 1.
Asclepiadaceae, 1.

TUBIFLORAE
Convolvulaceae, 1.
Polemoniaceae, 1.
Hydrophyllaceae, 1.
Borraginaceae, 1.
Verbenaceae, 1.
Labiatae, 1.
Solanaceae, 1.
Scrophulariaceae, 1.
Bignoniaceae, 1.
Orobanchaceae, 1.
Gesneraceae, 1, (3) and (5).
Columelliaceae, 1.
Lentibulariaceae, 1.
Globulariaceae, 1.
Acanthaceae, 1.
Myoporaceae, 1.

PLANTAGINALES
Plantaginaceae, 3.

RUBIALES
Rubiaceae, 1 and (3).
Caprifoliaceae, 3 and (5).
Valerianaceae, 3.
Dipsacaceae, 3.

CUCURBITALES
Cucurbitaceae, 3.

CAMPANULATAE
Campanulaceae, 1.
Goodeniaceae, 3 and 5.
Compositae, 3 and (many).

The chief importance of a comparative study of the node will consist in providing us with evidence whereby we may group related families together into orders which shall be more natural than the present ones. No one character is, of course, sufficiently constant to be made the sole basis of such a reclassification. The structure of the node is not always invariable, by any means, and further study will doubtless reveal numerous exceptions to the foregoing brief outline and make necessary many changes in it. The value of such a character as this, however, is that, compared with many others, it is extremely constant and very simple.

The present paper, which is based on a study of only about four hundred genera, is but a brief indication of what are some of the main facts which a comparative study of the node brings forth. A very much more thorough and extensive investigation will be necessary before we shall be able to say to just what extent nodal anatomy may be made useful in classification. That it will assume an important position in the final construction of the phylogeny of the angiosperms appears to be reasonably certain.

The writer wishes to express his thanks to the authorities of the Harvard Botanical Garden and of the Arnold Arboretum for use of material in their collections.

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Harvard University.

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DESCRIPTION OF FIGURES OF PLATES XXX–XXXIV

Figures are drawn from transverse sections cut just below the node. Xylem of stem cross-lined, of departing leaf-trace bundles solid black.

FIG. 1. PINACEAE, Picea.
FIG. 2. PINACEAE, Agathis (vigorous twig).
FIG. 3. GNETACEAE, Ephedra.
FIG. 4. FAGACEAE, Quercus.
FIG. 5. POLYGONACEAE, *Rumex Acetosa.*
FIG. 6. POLYGONACEAE, *Rumex obtusifolius.*
FIG. 7. CHENOPODIACEAE, *Chenopodium album* (young plant).
FIG. 8. CHENOPODIACEAE, *Chenopodium album* (mature plant).
FIG. 9. AMARANTACEAE, Gomphrena.
FIG. 10. AMARANTACEAE, Amaranthus.
FIG. 11. RANUNCULACEAE, Paeonia.
FIG. 12. RANUNCULACEAE, Xanthorrhiza.
FIG. 13. CRUCIFERAE, *Sisymbrium leiocarpum.*
FIG. 14. CRUCIFERAE, Barbarea.
FIG. 15. ROSACEAE, Physocarpus.
FIG. 16. ROSACEAE, Spiraea.
FIG. 17. LEGUMINOSAE, Cladrastis.
FIG. 18. CELASTRACEAE, Evonymus.
FIG. 19. AQUIFOLIACEAE, *Ilex opaca.*
FIG. 20. AQUIFOLIACEAE, *Ilex verticillata.*
FIG. 21. GUTTIFERAE, Hypericum.
FIG. 22. MYRTACEAE, Eucalyptus.
FIG. 23. ARALIACEAE, Acanthopanax.
FIG. 24. ERICACEAE, Vaccinium.
FIG. 25. SOLANACEAE, Solanum.
FIG. 26. POLEMONIACEAE, Phlox.
FIG. 27. EBENACEAE, Diospyros.
FIG. 28. COMPOSITAE, Solidago.
FIG. 29. POTAMOGETONACEAE, *Potamogeton pulcher* (after Chrysler).
FIG. 30. ARACEAE, Acorus, young plant (after Chrysler).

DESCRIPTION OF PHOTOGRAPHS OF PLATE XXXV

All sections are transverse, in the region just below the departure of the traces.

PHOTO. 1. *Betula*, trilacunar type. × 20.

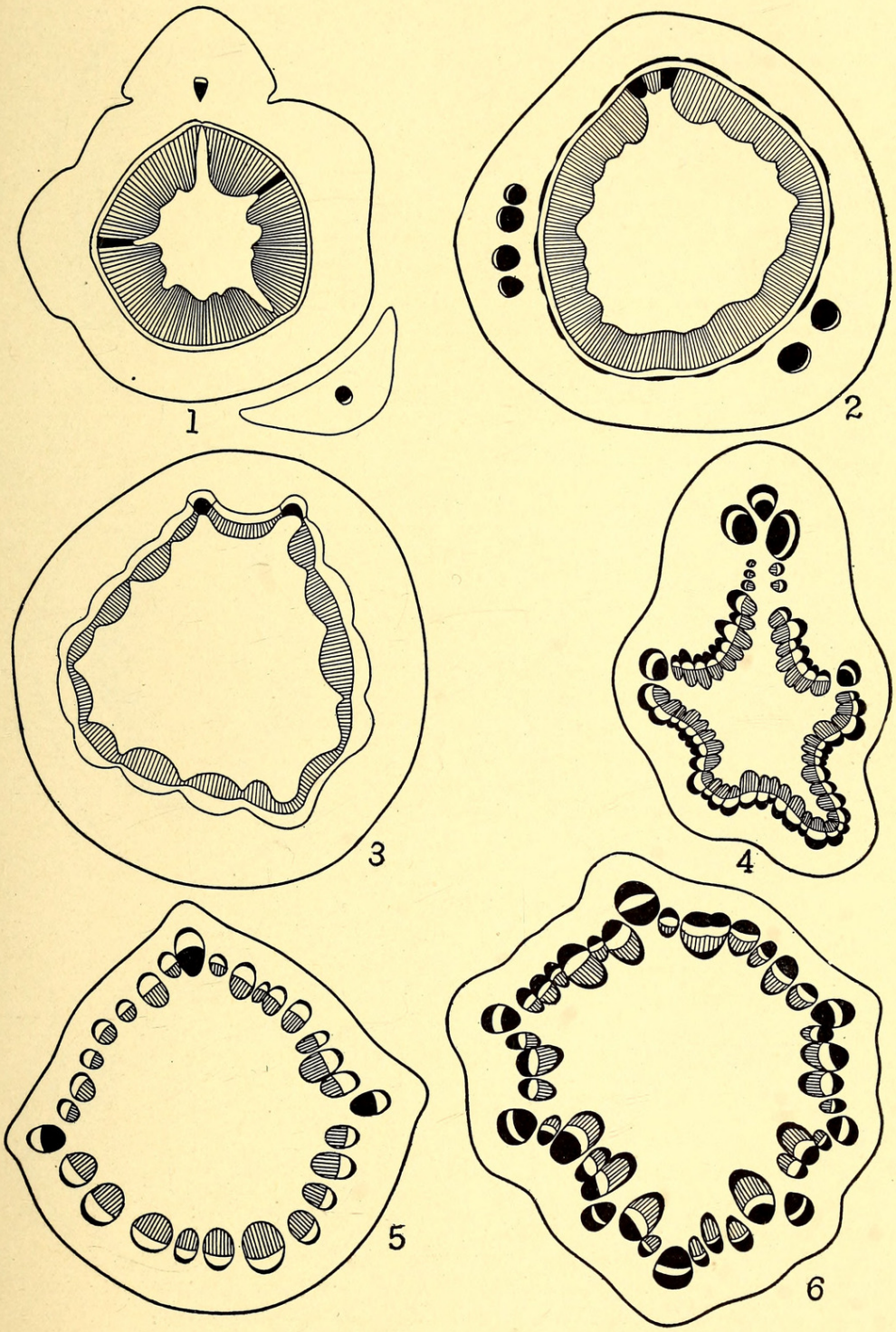
PHOTO. 2. *Cornus*, trilacunar type. × 12.

PHOTO. 3. *Lindera*, unilacunar type. Although the gap is single, there are three bundles in the trace, indicating that the unilacunar condition in this instance has probably arisen by the approximation of three originally distant strands. × 25.

PHOTO. 4. *Eucalyptus*, unilacunar type. In this case the trace is single. × 20.

PHOTO. 5. *Xanthorrhiza*, multilacunar type. × 20.

PHOTO. 6. *Acanthopanax*, multilacunar type. × 9.



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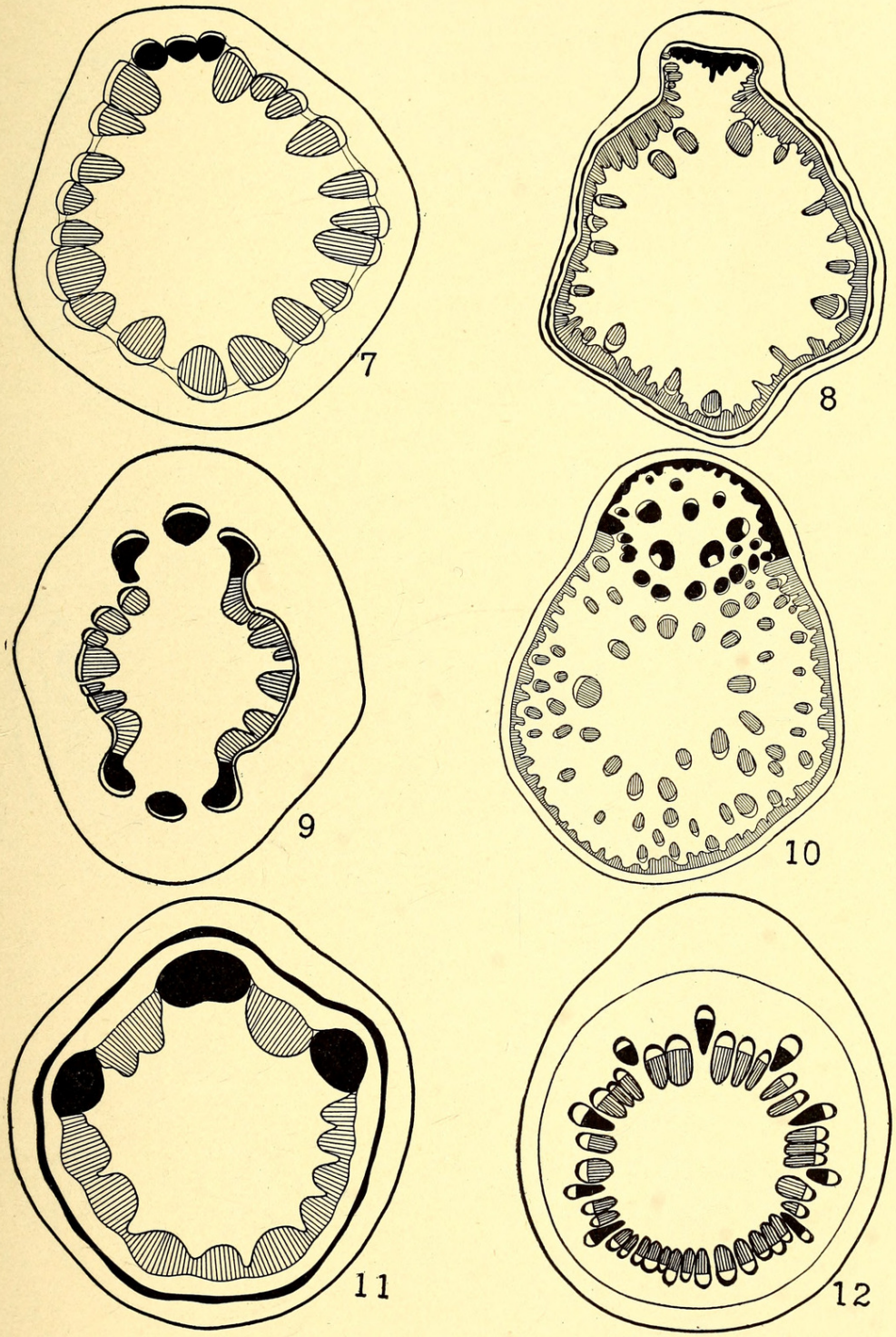

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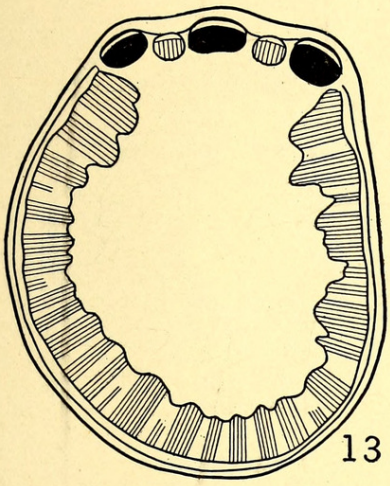

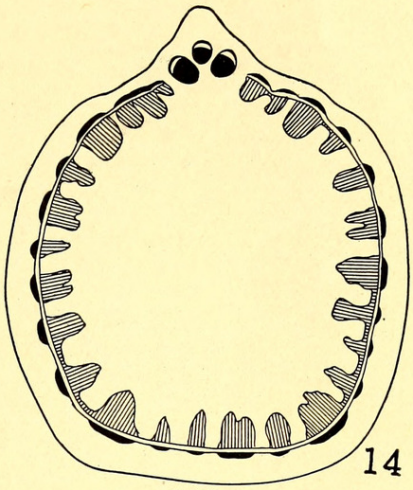

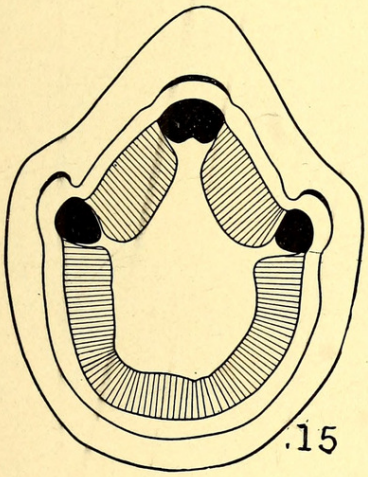

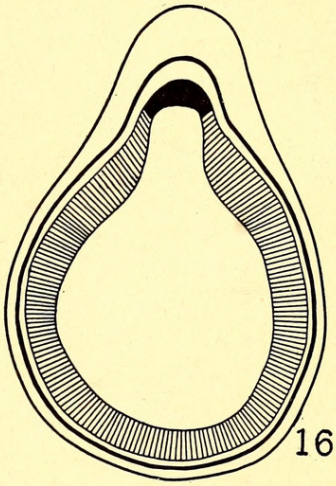

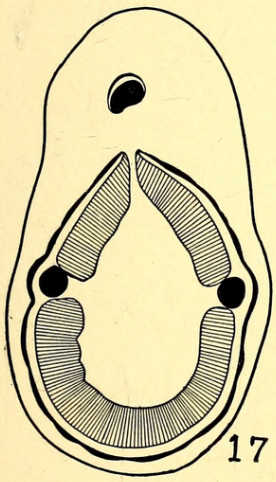

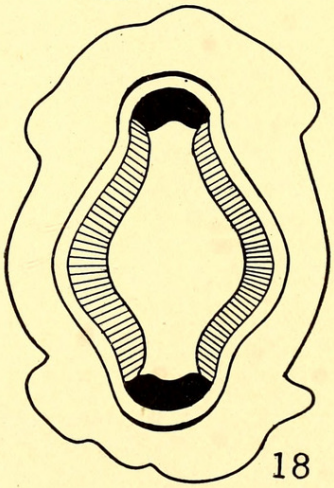

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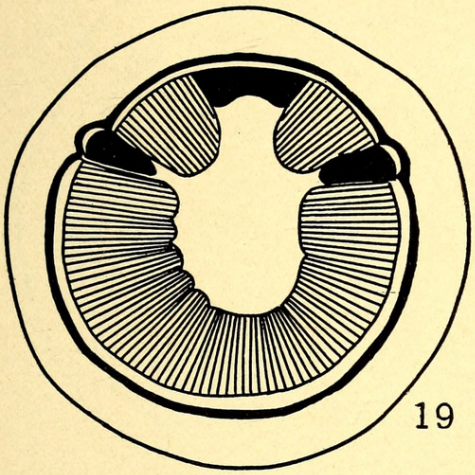

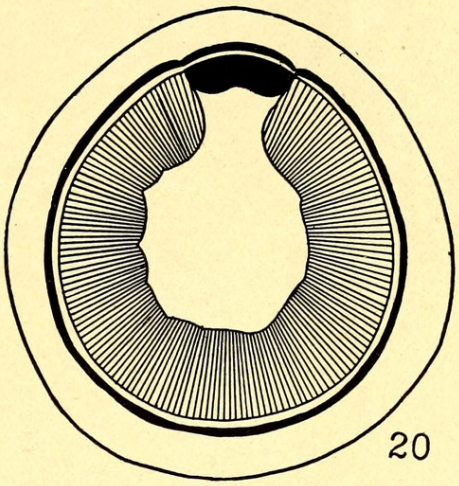

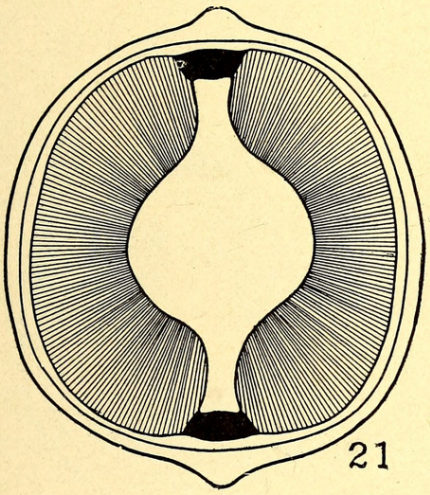

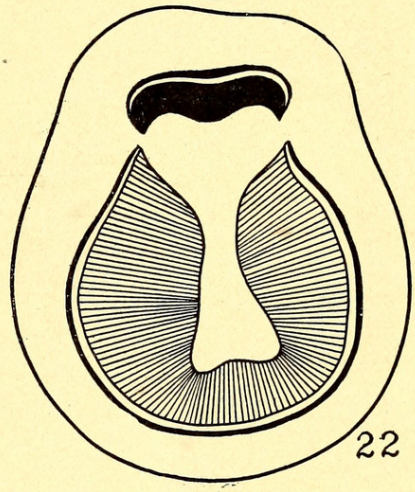

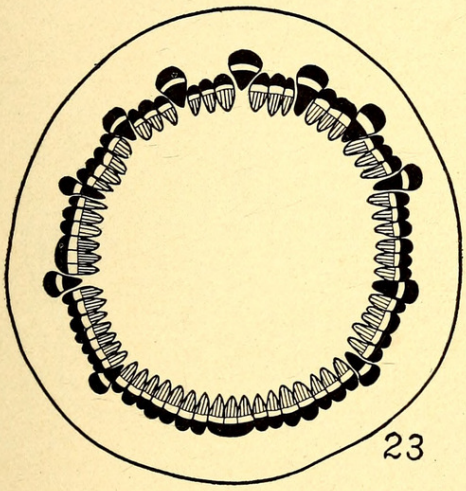

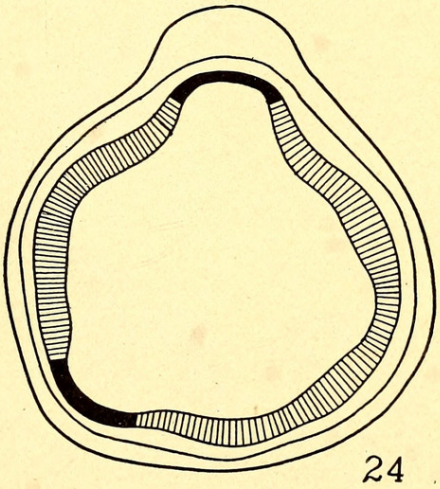

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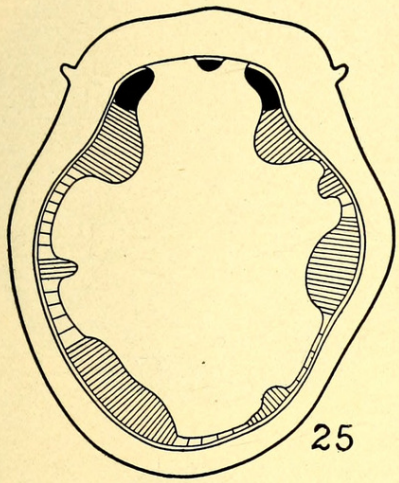

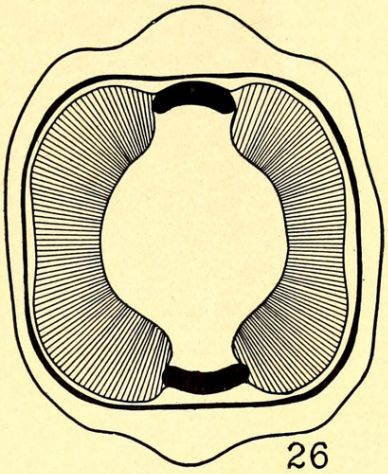

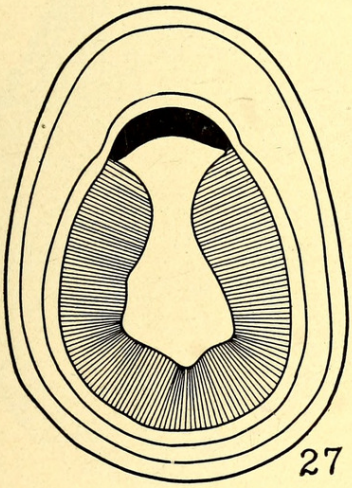

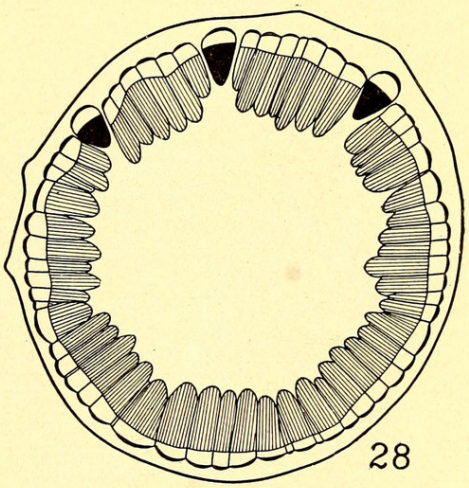

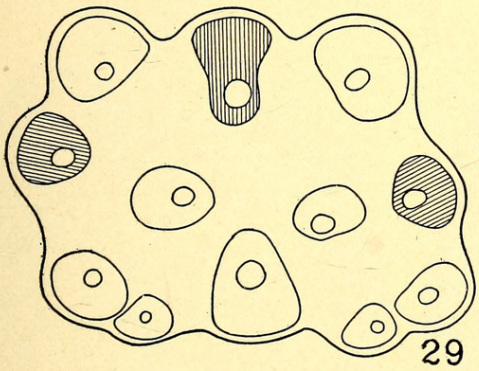

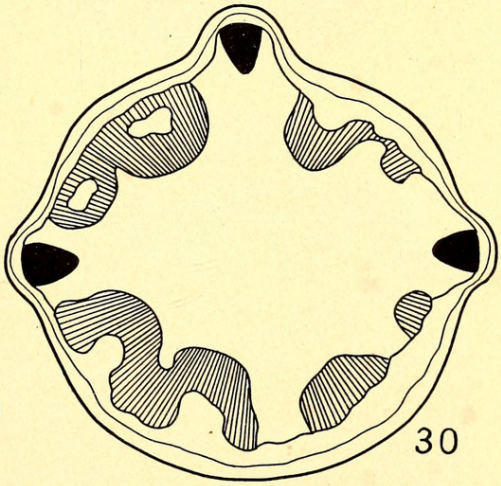

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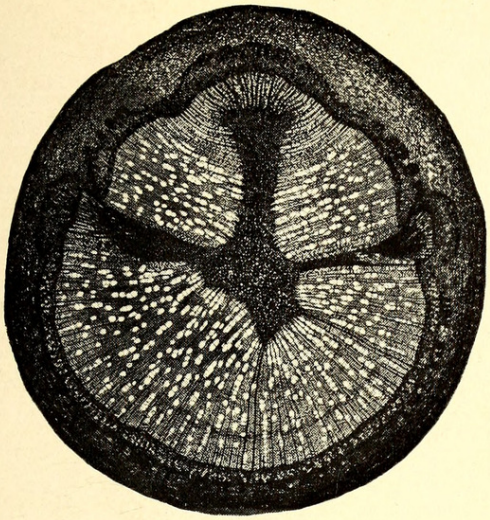

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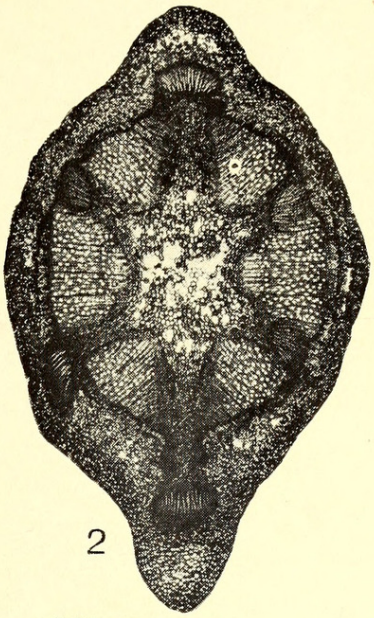

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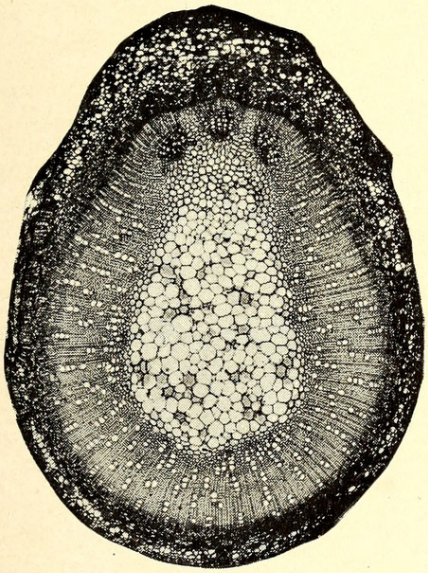

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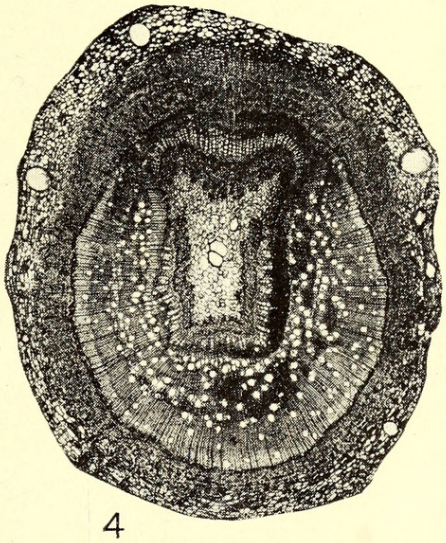

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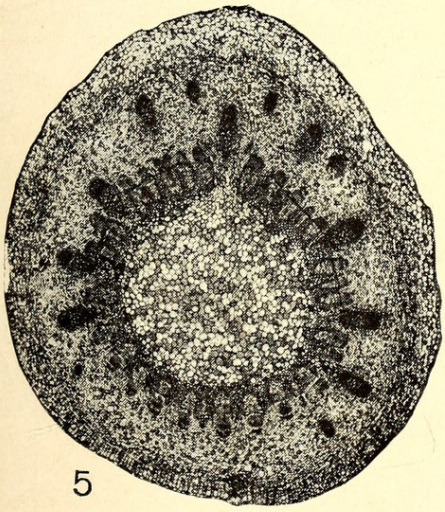

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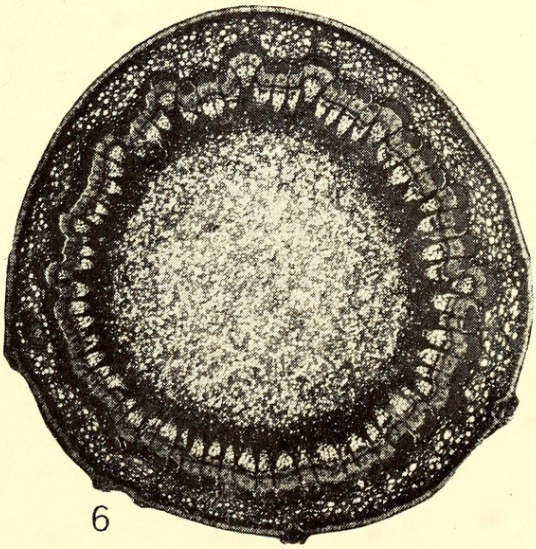

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