FOSSIL PLANTS OF THE GROUP CYCADOFILICES

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Introduction

The group of fossil plants appropriately designated the "Cycadofilices" embraces a number of Paleozoic generic types combining structural characters of the ferns and of the gymnosperms. As originally established by Potonie[1] it was confined chiefly to genera founded on petrified trunks, petioles, and roots, with the provisional reference of several frond types. Subsequent research has established the correlation of the fronds of several of the members, and recently two distinct types of seeds have been definitely identified with two of the Cycadofilic genera, while a third type of fruit has been found united with a genus of fronds not before suspected of belonging to the Cycadofilices. The fact of the discovery of the seeds has been brought to the attention of biologists in this country by several American paleobotanical writers[2] whose brief communications on the subject are confined largely to the nomenclatorial classification of the group, rather than to the characters of the latter. So far-reaching are the paleobotanical findings concerning the members of this group, and so important are they to all evolutionists, that it seems desirable to put American botanists in closer touch with the principal and very interesting features relating to these singular types which appear to stand intermediate to the ferns and the gymnosperms. To do this in brief form is the purpose of this paper.

The number of genera to be included in the Cycadofilices, or Pteridospermeæ, as designated by Oliver and Scott, is necessarily indefinite, since future discovery will doubtless bring to light characters causing the inclusion therein of other genera whose structure or fructification is at present unknown and whose systematic classification is therefore now provisional only. On the other hand, a more complete knowledge of the reproduction in some of the types now included may require their promotion to a higher, gymnospermic, rank. It must be remembered that some of the genera are

[1] *Lehrbuch der Pflanzenpaleontologie*, 1899, p. 160.

[2] Lester F. Ward in *Science*, July 1, 1904, p. 25; Aug. 26, p. 279. E. W. Berry in *Science*, July 8, 1904, p. 56; July 15, p. 86; J. M. Coulter in *Science*, July 29, 1904, p. 149.

known only by the anatomical structure of their stems and petioles; that fronds have been definitely correlated with but four generic types; and that fruits are known in but three. Concerning the microsporangiate organs, we have hardly more information than we have respecting the Cycadofilic fruits.

The group appears to have been confined to the upper Paleozoic, and almost exclusively to the Carboniferous, including, in a broad sense, the Permian. The widely diversified associated or contemporaneous ferns are overwhelmingly eusporangiate, most of them showing closer affinities with the Marattiaceæ than with any other living family, though imperfect rings of various forms several cells in width, or may be in thickness, characterize some of the rarer fern genera. The pteridophytic comparisons are therefore with the Marattiaceæ, the Ophioglossaceæ and, to a less extent, with the Osmundaceæ and the Lygodiaceæ. The gymnospermic characters are principally Cycadean, though Cordaitean, and, in a minor degree, Araucarian characters appear less prominently in a few of the genera.

Types Generally Regarded as Cycadofilic

Cladoxylon.—One of the oldest though less known types with which we have to do is *Cladoxylon* of Unger, from the Lower Carboniferous of Thuringia.[1] The reference of this genus to the Cycadofilices rests on the characters of the stems which are polystelic. The steles, or vascular axes, as seen in transverse section are dilated radially, each stele including a broad central band of primary wood with one or several groups of spiral tracheæ, or primitive xylem elements, at the border. In the earlier stages the stem, even when of considerable size, is typically filicoid; but in most of the older stems each stele develops a zone of secondary wood with more or less numerous medullary rays. The tracheides of both primary and secondary wood are scalariform. The petioles show a structure distinctly characteristic of ferns, and, but for the secondary wood, the pteridophytic nature of the stems would be unquestioned.

The Medulloseæ.—Among the Paleozoic stems longest and best known by their internal structure are those of Cotta's genus *Medullosa.* These stems,[2] sometimes a foot or more in diameter, are polystelic (see plate LIV), the steles being irregular in form and dis-

[1] See Solms-Laubach, *Abh. d. k. Pr. geol. Landesanst.*, Heft, 23, 1896, p. 51.

[2] See Weber and Sterzel, *Beitrage zur Kenntniss der Medulloseæ;* Ber. naturw. Gesell. zu Chemnitz, vol. XIII, 1896, p. 44. See also Solms-Laubach, *Bot. Zeit.*, 1897, p. 175; Scott, *Phil. Trans.*, vol. 191, B, 1899, p. 81; Goeppert and Stenzel, *Palæontographica*, vol. XXVIII, 1881, p. 123.

tantly anastomosing. When numerous the smaller are mostly central, and the larger, more or less ribbon-like and dilated, are concentrically disposed near the periphery. Each stele contains a central axis of parenchymatous conjunctive tissue traversed throughout by anastomosing groups of primary strands. The larger groups, which are peripheral, include pitted tracheides, and are exarch.[1] Each stele is provided with a well-developed zone of secondary wood, loose and spongy in texture, with wide and high medullary rays (see plate LIV, fig. 2). The tracheides are multiserately punctate with bordered pits on their radial walls. The secondary wood is followed by cambium, phloem with phloem rays, and pericycle, while the entire group of steles is enveloped in a periderm surrounded by cortical short-celled parenchyma containing secretory canals suggestive of the gum canals of Cycads. In one species the outer steles are greatly broadened on the peripheral side so as practically to coalesce in a continuous zone or cylinder of normal secondary wood, the secondary wood of the inner side of the steles being inverted with reference to the whole trunk and often forming an inner cylinder of inward-growing exogenous wood. In another form (plate LIV, figs. 3 and 4) the entire stelic zone is surrounded by several successively developed extra-fascicular zones or layers of wood and phloem, an anomalous development which has an analogy in the living *Cycas* and *Encephalartos* also.

The leaf traces of *Medullosa* consist at first of both primary and secondary wood, each derived from its own kind on the peripheral side of the stele, in concentric arrangement; but in passing outward the secondary wood in most cases is lost, and the primary wood separates, while the pitted tracheids disappear, into many small collateral strands, the protoxylem being outward, next the phloem. Several leaf traces originating at different levels furnish large numbers of strands to a single petiole.

The petioles of *Medullosa*, before their final correlation with the parent stems, had been described as *Myeloxylon* and *Myelopteris*.[2] They comprise a ground mass of short-celled tissue including secre-

[1] In describing the arrangement of the woody elements in a bundle collateral in structure the terms "exarch," "mesarch" and "endarch" are used by Williamson and Scott according to the position of the primitive spiral tracheæ (protoxylem) at the outer border of the bundle, in the interior of the bundle, or at the inner border of the bundle.

[2] See Renault, *Mém. Sav. etr. Acad. Sci.*, vol. XXII, no. 10, 1876; Renault, *Cours de botanique fossile*, vol. III, 1883, p. 165; Zeiller, *Fl. Foss. bassin houill. et perm. d. Autun et d'Épinac*, pt. I, Paris, 1890, p. 282; Zeiller, *Éléments de Paléobotanique*, Paris, 1900, p. 131.

tory canals and somewhat concentrically arranged vascular bundles, the whole being surrounded by a thick hypodermal parenchymatous zone containing numerous longitudinal sclerenchymatous strands and secretory canals, and a layer of pallisade tissue. In their general structure they resemble Marattiaceous petioles.

Naturally the Medullosan stems were early regarded by most paleobotanists as more or less distinctly Cycadean; and this view is supported by the structure of the petioles, in which, in some species, a secondary wood accompanies the vascular strands. It must, however, be remembered that collateral primary bundles accompanied by secondary wood also occur in the Ophioglossaceæ.

The researches of Renault[1] have shown that the petioles (*Myeloxylon*) of *Medullosa* bear the large filicoid fronds, often tripinnate and quadripinnate, of the two great frond genera *Neuropteris* and *Alethopteris,* which previously had been generally considered as comprising the most common and characteristic Carboniferous ferns.[2] A portion of a frond of *Neuropteris,* from the Upper Carboniferous of Alabama, is shown in plate LV.

As long ago as 1889 Mr. Robert Kidston[3] described an imperfectly preserved specimen showing what appeared to be stalked synangia or quadrivalvate capsules in union with *Neuropteris heterophylla.* The pteridophytic nature of this fructification has been generally unquestioned, although, on the evidence of the relation of the fronds to *Medullosa,* the genus *Neuropteris* has been put with the Cycadofilices by many authors. The recent discovery by the same distinguished paleobotanist[4] of large solitary Rhabdocarpous seeds attached to the fronds of the same species of *Neuropteris* more than confirms the exclusion of these anomalous types from the ferns.

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[1] *Comptes Rendus,* vol. 94, 1882, p. 1737.

[2] It is of interest to note, in this connection, that in the Lacoe fossil plant collection of the U. S. National Museum one of the rock slabs, about 110 cm. long and 55 cm. in width, contains a fragment from the interior of a frond of *Alethopteris aquilina* in which a rachis 3 cm. or more in width, lying near the border of the slab, gives off 6 alternate primary pinnæ, none of which is small enough to be included in its entirety within the area of the rock, while in the longest fragments of pinnæ, 65 cm. to the broken end, there is no diminution in width. It is impossible to say how high the whole segment may have been above the lowest primary pinnæ; but since none of the pinnules of the secondary pinnæ is even lobed it is evident that the specimen comes from the upper part of the frond. Doctor Scott (*Phil. Trans.,* vol. 191B, 1899, pl. IX) figures a flattened petiolar base of *Medullosa* that is nearly 9 cm. in width.

[3] *Trans. Roy. Soc. Edinb.,* vol. XXXIII, pt. 1, p. 150.

[4] *Proc. Roy. Soc.,* vol. LXXII, Dec. 29, 1903, p. 487; *Trans.,* vol. 197B, 1904, p. 1.

The seeds described by Kidston differ but little in superficial characters, by which alone they are known, from *Rhabdocarpos tunicatus.* The genus *Rhabdocarpos,* which embraces a large number of Carboniferous species, includes generally large oval or oblong, ribbed and sometimes more or less distinctly trigoniate fruits characterized by an outer fleshy and an inner sclerotic test, and by chalaza, micropyle, nucellar membrane and pollenic chamber, while in certain silicified specimens, even pollen grains and archegonia have been observed. It represents one of the simple types of gymnospermous fruit. In these early Paleozoic types the fruit appears to have attained its full size before fertilization, and the pollen grains appear to have rested for some time in the chamber before the release of the antherozoids. No embryo has been observed.

Besides the fronds of *Neuropteris, Alethopteris,* and *Odontopteris,* which have been correlated with *Myelopteris,* and the genera *Callipteris* and *Linopteris* (*Dictyopteris* Gutb.) referred to the Medullosæ by European paleobotanists,[1] it is probable, in the judgment of the writer, that the related genera *Callipteridium,* and *Lesleya* together with *Megalopteris* and its closer relatives are also to be placed within the same enlarged group.

Colpoxylon.—The stem fragments described as *Colpoxylon* by Brongniart,[2] are interesting chiefly from the fact that they are monostelic in one part and polystelic in another, the solitary stele of the lower part of the stem being divided into several steles in passing upward. The structure of the latter, as well as of the petioles, is essentially like that of *Medullosa* to which the genus is evidently closely related.

The Lyginodendreæ.—Passing from the *Medulloseæ,* whose foliage is typified in *Neuropteris,* we will next consider the *Lyginodendreæ,*[3] whose fronds, so far as known, are included in the great frond genus *Sphenopteris.*

Heterangium of Williamson,[4] the most filicoid genus of the family,

[1] The genus *Næggerathia,* originally placed among the Cycadofilices by Potonié on account of the arrangement of the "sporangia" on the ventral surface of the scales in the large strobili, is regarded by most paleobotanists as gymnospermous, though the nature of the reproduction is not definitely determined.

[2] See Renault, *Fl. foss. bassin houill. et perm. d. Autun et d'Épinac,* pt. 2, Paris, 1896, p. 299.

[3] An excellent and succinct description of this family is given by Dr. D. H. Scott, *Studies in Fossil Botany,* London, 1900, p. 307.

[4] Williamson, *Phil. Trans.,* vol. 178B, 1887, p. 289; Williamson and Scott, *Phil. Trans.,* vol. 186B, 1896, p. 703; Renault, *Fl. foss. bassin houill. et perm. d'Autun et d'Épinac,* pt. 2, 1896, p. 248.

resembles a fern in the habit of its delicate quadripinnate frond, the anatomy of its leaf, and its primary wood, while by the structure of the leaf trace bundles and secondary wood, with pitted tracheides, it appears to be related to the Cycadales.

The average *Heterangium* stem is less than 1.5 cm. in diameter, and includes: (1) a large central primary cylinder of anastomosing primary wood strands mingled with conjunctive parenchyma very much as in *Medullosa*, the outer wood strands, of mesarch collateral structure, with spiral, reticulate and pitted (multi-seriate, bordered) tracheides, forming a row, from which the leaf traces originate; (2) a thin zone of secondary wood, with tracheides bordered-pitted on the radial walls, and with broad medullary rays which give it a loose spongy texture; (3) a cambium; (4) phloem; (5) pericycle; (6) an inner cortex of short-celled parenchyma containing vertical rows of transverse sclerotic plates, comparable to the stone cells of living plants; (7) an outer cortex containing vertical strands forming radial and distantly anastomosing hypodermal plates. Adventitious roots spring from the primary wood strands. The petiolar strands, which, in one species, contain traces of secondary wood, are at first collateral, but become concentric on entering the petiole, which contains a single strand. The delicate frond is absolutely filicoid, tripinnate, and finely cuneately dissected, that of *Heterangium Grievii* being indistinguishable from, if not identical with, *Sphenopteris elegans*.[1]

The fructification of *Heterangium* is not definitely known, but it is possible that the male sporangia belong to the type described by Stur[2] as *Calymmatotheca*. The structures of primary stem, thick pericycle, and of petiole also are fern-like and have been compared by Doctor Scott with *Gleichenia*; but the mesarch outer primary strands, and the characters of the secondary wood, with pitted tracheides, strongly suggest the stems and petioles of Cycads.

Lyginopteris.—Very closely related to *Heterangium* is the genus *Lyginopteris* of Potonié[3] (*Lyginodendron* Williamson), for whose beautiful and complete elaboration we are indebted to Williamson[4] and Scott.[5] In the form of its fronds, its microsporangia, and in

[1] *Phil. Trans.*, vol. 163, 1873, p. 377; vol. 164, pt. 2, 1874, p. 675; vol. 166, 1876, p. 1; vol. 178B, 1887, p. 289; vol. 181B, 1890, p. 89.

[2] *Phil. Trans.*, vol. 186B, 1896, p. 703.

[3] *Lehrb. d. Pflanzenpalæont.*, p. 171.

[4] See Stur, *Abh. d. k.-k. geol. Reichsanst.*, vol. VIII, pt. 2, Wien, 1877, p. 130.

[5] Loc. cit., p. 149. See also Kidston, *Trans. Roy. Soc. Edinb.*, vol. XXXII, pt. 1, 1889, p. 137.

the young roots *Lyginopteris* is typically a fern. In its stems, petioles, and seeds it is largely Cycadaceous, though the stems present some analogies with *Osmunda* also.

The stems of *Lyginopteris* (see plate LIII), which are several centimeters in diameter,[1] are monostelic, the center being occupied by a large pith, at the periphery of which occur several (5–8) large, more or less isolated, collateral bundles of small spiral, scalariform, and bordered-pitted tracheides in mesarch structure. Next we have a thick zone of secondary wood consisting of radially and pluriseriately pitted tracheides and broad medullary rays, both direct and secondary. The cambial zone is followed by phloem, which also is rayed. External to this is the pericycle, several cells thick, a thin periderm, a tender, inner, and a resistant outer cortex, which is characterized by radial sclerenchymatous plates longitudinally flexuose-anastomosing so as to form a rhomboidal net in tangential section, the meshes being occupied by parenchyma ("*Dictyoxylon* structure").

The leaf traces, arising from the chief primary strands, break through the secondary wood, and are collateral and twinned while ascending in the pericycle, but they become concentric and V- or W-shaped, without secondary xylem, in the petiole.

The adventitious roots, which were published as *Kaloxylon* by Williamson prior to correlation with the stems, are described by Doctor Scott as exhibiting in their early stages, less than 5 mm. in diameter, 2–8 strands of primary wood in an arrangement closely resembling that of the roots of the Marattiaceæ, or of the Ophioglossaceæ, though when larger they show secondary tissue in a structure "absolutely indistinguishable from that of typical dicotyledons or gymnosperms."

The petioles (originally described as *Rachiopteris aspera* Will.) of *Lyginopteris oldhamia* are found in organic union with the very large, highly compound, finely dissected fronds of *Sphenopteris Hoeninghausii* Brongn.,[2] one of the common species in the Lower Coal Measures of Europe and America. These fronds are so typically filicoid that only anatomical identity in every detail or actual union could suffice to remove them from their previously unquestioned place among the ferns. The reference of the *Calymmatotheca* form of long, sack-like, clustered bodies, regarded as exannulate sporangia, to the *Hoeninghausii* group of Sphenopterids has

[1] *L. robustum* Seward is represented as about 12 cm. in diameter.

[2] Plate LIII, Figure 2. See also Zeiller, *Flore fossile du bassin houill. de Valenciennes,* 1888, p. 82, pl. V, f. 3, pl. VI, f. 1, 2.

recently been supported by Miss Benson,[1] who discussed the connection of these organs with *Lyginopteris* not long before the indisputable correlation, by Oliver and Scott,[2] of seeds (*Lagenostoma* of Williamson) with the same plant, on the basis of the strongly characteristic anatomical features. The fruit described as *L. Lomaxi* is orthotropous, small, only about one-half a centimeter in length, and is borne in pedicellate cupules. The seed, with chalaza, testa, nucellar epidermis, pollenic chamber, etc., is essentially gymnospermic in structure, though exhibiting certain very unique and striking features.

While related to the ferns by its leaves, young roots, and microsporangia, the predominant analogies of *Lyginopteris* are gymnospermous. The mesarch arrangement of the elements in the primary wood strands is to be compared with the structure in the petioles and peduncles of certain living Cycads to which it is almost peculiar. The change in the leaf strand from the collateral to the concentric form while passing to the petiole also finds an analogy in *Osmunda*. The very large pith and the loose spongy secondary wood suggest the Cycads, and the seeds are comparable to those of *Ginkgo*.

Megaloxylon.—The genus *Megaloxylon* of Seward[3] includes stems of considerable size which contain a large primary cylinder of short tracheides mingled with parenchymatous tracts. The thick secondary wood is like that of *Lyginopteris*. The genus is thus closely related by its primary stele and its centrifugal xylem to both *Heterangium* and *Lyginopteris;* but it differs by the exarch structure of the bundle in both the primary xylem and the leaf trace.

Calamopitys.—Closely related to *Lyginopteris* are the slender monostelic stems, from the Lower Carboniferous of Thuringia, described by Unger as *Calamopitys*. This stem[4] has pith, primary and secondary wood like that of *Lyginopteris*. The centripetal tracheides are pitted on all sides; the centrifugal on the radial walls only. *Calamopitys* differs from the genus last mentioned by the change in the leaf strands to a concentric structure on entering the cortex, and by the separation of the strand into several bundles arranged in a ring in the petiole. The structure of the petiole, which accordingly is fern-like, appears to be identical with that of *Kalymma grandis* Ung., which has also been reported from the Middle Devonian Black

[1] *Ann. Bot.*, vol. XVI, 1902, p. 575.

[2] *Proc. Roy. Soc.*, vol. LXXI, no. 474, May 26, 1903, p. 477; *Philos. Trans.*, vol. 197, B, 1904, p. 193.

[3] *Proc. Cambr. Phil. Soc.*, vol. X, 1899, p. 158.

[4] See Solms-Laubach, *Abh. k. Preuss. geol. Landesanst.*, Heft. 23, 1896, pp. 63 and 43; also Dawson and Penhallow, *Can. Rec. Sci.*, vol. IV, 1891, p. 1.

Shale of Kentucky. The fronds and fructification of *Calamopitys* are unknown.

The Cycadoxyleæ.—The stems published by Renault[1] as *Cycadoxylon* are still closer to the Cycads, and their secondary wood is described as distinctly Cycadean. But the *Cycadoxylon* stem presents a strikingly anomalous feature in the occurrence, within the cylinder of outer (normal) secondary wood, of two or more distinct zones of inner crescentic secondary wood, each zone of which with its rays and accompanying broad phloem bands, lies in an inverted position in the body of the pith. The genetic connection with *Lyginopteris* is shown not only in the general characters of the centrifugal wood but also by a slight development of a similar medullary secondary wood in certain specimens of the latter genus.

An important link between the Lyginopterid group and the Cycadales (in a broad sense) is furnished by the stems described by Renault[2] as *Ptychoxylon,* another of the Cycadoxyleæ, which is regarded by both its author and Doctor Scott as essentially Cycadaceous. In this genus (see plate LIV, fig. 1) a very large pith is surrounded by a more or less complete narrow zone of secondary wood similar to that of the other stem genera. But within the cylinder of normal centrifugal wood lie several concentric arcs of fully developed inverted secondary wood, each with its phloem, medullary rays, and phloem rays. At the leaf gaps the edges of the interrupted outer or normal cylinder curve inward to coalesce temporarily with two of the inner arcs of inverted exogenous wood, which are termed "reparatory" arcs. In the relations of the normal and inverted secondary woods *Ptychoxylon* appears to present some analogies with *Colpoxylon* and *Medullosa.* No primary wood appears yet to have been observed in the petrified stems, though the leaf trace is said to be essentially like that of *Lyginopteris.*

Except for the anomalous medullary wood *Ptychoxylon* is Cycadaceous; and this systematic reference is supported by the discovery, in the same beds,[3] of leaves (*Pterophyllum* and *Sphenozamites*) which in form and external characters are distinctly Cycadean, accompanied by a remarkable inflorescence (*Cycadospadix milleryensis* Ren.) provisionally referred to *Ptychoxylon* by Renault.

Protopitys.—In Goeppert's *Protopitys* originally described from the Lower Carboniferous of Silesia and more fully made known by

[1] *Flore fossile du bassin houill. et permien d'Épinac,* pt. 2, 1896, p. 307; Williamson, *Phil. Trans.,* vol. 163, 1873, p. 377; Williamson and Scott, *Phil. Trans.,* vol. 186B, 1896, p. 703; Seward, *Ann. bot.,* vol. XI, 1897, p. 65.

[2] Op. cit., p. 329.

[3] Loc. cit., p. 329.

Count Solms-Laubach[1] we have another unique type of stem combining filical and gymnospermic characters and referred by Doctor Scott to the Cycadofilices, though gymnospermous characters predominate. Its secondary wood, of coniferous structure, contains a large elliptical pith bordered by a continuous zone of primary wood which is thicker and somewhat complex at the ends of the ellipse, whence the leaf strands originate. This genus, on which Count Solms founds a family, appears to the writer to resemble so closely certain of the woods described as *Dadoxylon* (*Cordaites*) as to demand a reëxamination of some of the material showing secondary wood only and referred by authors to the latter genus.

Fossil plants petrified in such a way as to show their microscopical structure are extremely rare in the Carboniferous series of this country, and but few fragments excepting those of *Dadoxylon* and *Psaronius* have come to light. Impressions or carbonized remains are, however, as common in the Coal Measures of America, particularly in the Appalachian trough, as in other parts of the world. Our knowledge of the Cycadofilices, so far as it proceeds from American material, is based almost entirely on these carbonized remains.

Aneimites (*Adiantites* of authors).—The genus *Aneimites* is represented by several species in the basal Coal Measures of both Europe and America, though no petrified specimens (having structure) of that genus are known, and until recently we have had no clue to its fructification. Conclusive data relating to the latter have been furnished by material from the lower Pottsville along New river in southern West Virginia. The fronds, which are commonly known as *Adiantites*, are tripinnate, with slender divisions of the rachis and very deeply dissected cuneate pinnules and lobes, which, as the early name for the genus implies, strongly resemble those of *Adiantum*.[2] The seeds, borne on dichotomous pedicels at the periphery of the somewhat reduced fertile fronds, are small, about .5 cm. long, rhomboidal, and vascularly striate, thinly lenticular in transverse section, the outer envelope being laterally dilated, especially below the middle of the seed, so as to form a wing to the fruit. The seed, seen in all stages of development, is deciduous at maturity by abscission at the broadened apex of the pedicel. The general characters, so far as recorded by the impressions, appear in the main to be conformable to the primitive types of gymnosperms.

[1] *Bot. Zeitung*, 1893, p. 197.

[2] See *Smithsonian Miscell. Colls., Quarterly Issue*, vol. 47, pt. 3, p. 322, pl. XLVIII.

Microsporiferous organs of two forms are intimately associated with the fronds, one of them belonging to the *Calymmatotheca* type. The latter, however, is not found in union with the frond. The discovery of seeds in connection with the *Aneimites* group of supposed ferns necessitates the systematic transfer of this group to the Pteridospermeæ. This reference is based solely on the evidence of the fructification, the anatomical characters of the fronds, whose fern nature had not before been questioned, being still unknown, though the form of the rachis suggests a single petiolar strand like that of *Heterangium*. *Aneimites* is the third Cycadofilic genus in which the seeds are definitely correlated through union with the sterile portions of the frond.

Types Probably Cycadofilic

It has been seen that the reference to the Cycadofilices of the genera individually discussed above is based on (*a*) the anatomical characters of the stems and petioles; and (*b*) on the discovery of seeds still attached to or definitely identified with the fronds, this category being represented by but three types, *Medullosa* (*Neuropteris*), *Lyginopteris*, and *Aneimites* (*Adiantites*). Besides these there is a third category, more indefinite and unsatisfactory, but worthy of mention as *provisionally* referable to the same phylum. It is based (*c*) on their evidently close relationship to one of the above mentioned Cycadofilic genera; on the circumstantial evidence of association; or on the negative evidence of the absence of any recognized filicoid type of fructification.

The third Pteridospermic category includes common genera, not petrified so as to show their internal anatomy, found as impressions or carbonized remains at many hundreds of localities in Europe or America, but whose fructification is not yet known. Some of these genera, which are still placed among the ferns, appear to be habitually associated with certain generic types of seeds in a way to strongly suggest a former union as well as a common source. Thus Grand 'Eury, who more than any other paleobotanist has contributed to our knowledge of the habits of the Paleozoic plants in situ, in two recent papers[1] concludes not only from the absence of rhizomes and connected fructifications, but from the large number of genera of Coal Measures seeds that are unaccounted for and the habitual association of some of the latter with fronds of the Neuropterideæ, that *Pachytesta* is referable to *Alethopteris;* that certain small striate

[1] *Comptes Rendus*, vol. 138, March 7, 1904, p. 607; vol. 139, July 4, 1904, p. 23.

winged seeds (*Odontopterocarpus*) belong to *Odontopteris;* that certain Trigonocarpous seeds, occasionally showing Rhabdocarpous characters also, belong the *Neuropteris* and *Linopteris;*[1] and that some rarely observed minute floral vestiges and smooth capsules, resembling the Arkansas specimens referred by Lesquereux[2] to *Soroclados*, represent the polleniferous organs of *Neuropteris.* Concerning the typical Neuropterids this distinguished savant believes that they "grew from seeds and are primitive Cycads with fern fronds." [3]

Mention has already been made, in the discussion of the Medulloseæ, of the probable Cycadofilic nature of *Callipteridium, Lesleya,* and the Megalopterids, on the basis of what the writer regards as their distinct affinities with the Neuropterid group, and on account of the absence of all traces of fructification in these genera. On the basis of similar strong though negative evidence it becomes not improbable that the supposed fern genera *Mariopteris, Pseudopecopteris* (including the round-lobed Diplothmemæ), *Eremopteris* and *Triphyllopteris* (with *Sphenopteridium*), no trace of whose fructification has yet been found, and whose internal organization is unknown, will eventually be found to belong to the Pteridospermeæ. It is possible, however, that in the cases of some of these genera the identity of the reproductive organs is masked by dimorphism, which seems to have been as prevalent among the ferns of the Paleozoic as it is among those of to-day.

On the other hand, it is far from impossible that some of the types which, solely on the evidence of the anatomical characters of their stems, have been referred to the Cycadofilices may eventually be correlated with some of the isosporous fronds already in hand among the ferns. The lessons learned from *Calamites, Lepidodendron*, and *Sphenophyllum,* which, notwithstanding the development of prominent as well as varied secondary woods, are none the less Equisetales, Lycopodiales, and heterosporous Sphenophyllales respectively, teach us that the accession of secondary wood, even of a structure regarded by many botanists as gymnospermic, should not be accepted as *de facto* proof of an ordinal difference in rank. This important fact should be constantly kept in view, and more particularly when discussing the systematic relations of some of the genera founded

[1] The sporangia approximating the *Crossotheca* type, described by Zeiller (*Fl. foss. bassin houill. d. Commentry,* pt. I, 1888, p. 273) in one of the afore-mentioned genera, *Linopteris,* probably represents, as suggested by Grand 'Eury, only the male sporangia of the genus.

[2] *Coal Flora,* vol. I, p. 328, pl. XLVIII, f. 8.

[3] *Comptes Rendus,* July 4, p. 23.

only on petrified stems, such for example as *Cladoxylon* and *Calamopitys,* which differ essentially from ferns only by the presence of their secondary wood. It must also be remembered that both secondary wood, of a sort, and collateral bundles are found in the Ophioglossaceæ.

Conclusions

The development of secondary xylem in various Cryptogamic families among Carboniferous plants, in various species of the same genus, and at various stages and positions, in the growth of the plant conclusively supports the view, long ago suggested by Williamson in the case of *Calamites,* that secondary wood originated as an engineering feature—a mechanical aid for the support of the gigantic Carboniferous representatives of some of our humble modern families. As such its origin was doubtless polyphyletic and, naturally, since the types appeared in different geological stages, polychronous.

The varied phases in which this secondary wood appeared—in polystelic, inverted intra-medullary, extra-fascicular or accessory, and laterally alternating, as well as modern phases, with their remarkable differences in combination, and in varying degrees of complication—constitute a group of structural anomalies which in themselves offer the evolutionist strong testimony of fortuitous variation. It is as though Nature were at the Carboniferous moment in the midst of a series of amazing engineering experiments, most of which were either buried deep in Paleozoic oblivion, or permitted to survive only as vestigial relics and atavistic ghosts.

Our knowledge of the structures and fructifications of the Cycadofilices (Pteridospermeæ) leaves little room for doubt as to the descent of the Cycads, and perhaps some of the other modern gymnospermous types,[1] from the ferns, though, as Doctor Scott has taken pains to point out, it does not follow that any of the Coal Measure types yet discovered actually represent the *lineal* ancestors of our living gymnospermic genera.

The discovery of seed-bearing members of the Cycadofilices, while answering in part the old question as to the origin of the gymnosperms, injects, at the same time, a new biological problem into the field of inquiry,—viz., the origin of the Cycadofilices. Seeds of so high and so gymnospermoid an organization as *Lagenostoma* or

[1] There is important data in support of the view that a portion, at least, of the conifers were derived from the Paleozoic Lycopodiales through a group of Lycopodineous seed plants whose existence is predicated partly on paleontological indications, partly on theoretical grounds, rather than definitely known or established, and for which Professor Ward (*Science,* Aug. 26, 1904, p. 281) has proposed the class term "Lepidospermæ."

Rhabdocarpos were, on the whole, hardly to be expected in view of the typically filicoid habits of the fronds, the presence of distinctly pteridophytic characters in the stems and petioles, and the antiquity of the seed-bearing types.

Since *Lyginopteris, Calamopitys,* and *Protopitys* are present in rocks of Lower Carboniferous age, it follows that the heterosporous filices, which must have antedated the Cycadofilices, are to be looked for at the very base of the Carboniferous, if not, as is more probable, in the Upper Devonian. *Triphyllopteris,* which the writer believes to be Pteridospermic, occurs near the base of the Lower Carboniferous in America. Concerning the Pteridospermic nature of the specimens reported as *Kalymma grandis* from the Black Shale of Kentucky, there appears to be room for doubt. Should, however, the interpretation of these fossils prove valid, the Cycadofilices will go back to the Middle Devonian (Genessee), or nearly as far as the oldest plant fossils generally recognized as unquestionably ferns. The presence of gymnosperms at this early date is generally accepted on the evidence of the occurrence of fossil woods representing several species of *Dadoxylon,* which includes the trunks of Cordaites. Some of these early species have, as has already been suggested, very much in common with *Protopitys.*

In a discussion of the recent discoveries relating to the Cycadofilices, which he seems inclined to regard as gymnosperms, Professor Zeiller remarks that it may become necessary to refer to the Carboniferous as the epoch of the gymnosperms, rather than of the Cryptogams. Whatever the limits and final interpretations of the Cycadofilices, they constitute a well-marked filicoid group preëminently characteristic of the Carboniferous, which may appropriately be paleobotanically designated as the epoch of the Pteridosperms—the seed-bearing ferns.

Explanation of Plate LIII

Fig. 1. Cross-section of a stem of *Lyginopteris oldhamia,* about 4½ times the natural size. At the margin of the large central pith area, which contains numerous sclerotic nests, are the primary wood strands (*x*), eight in number; external to these is the broad zone of secondary wood (with cambium and secondary phloem), interrupted by the passage of the leaf traces; *ph,* a primary phloem group; *pd,* periderm, limiting the pericycle which contains other sclerotic groups; *lt* 1–*lt* 5, leaf traces (numbered in the order of their phyllotaxy) becoming twined while ascending in the pericycle; the periderm is followed by the inner cortex and the outer cortex, the latter with its radial plates, the longitudinal anastomoses of which are not seen in the cross-section. From the Lower Coal Measures at Oldham. After Williamson and Scott.

Fig. 2. Fragment, in natural size, from a portion of the frond of *Sphenopteris Hœninghausii,* the leaf of *Lyginopteris.* From the Pottsville near Quinnimont, West Virginia.

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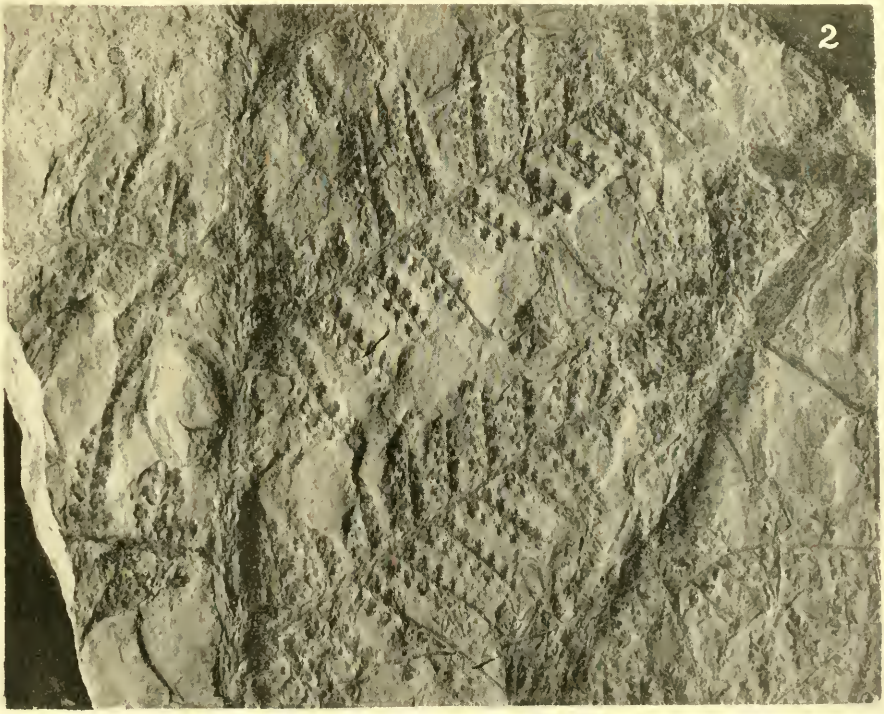


STEMS OF CYCADOFILICES

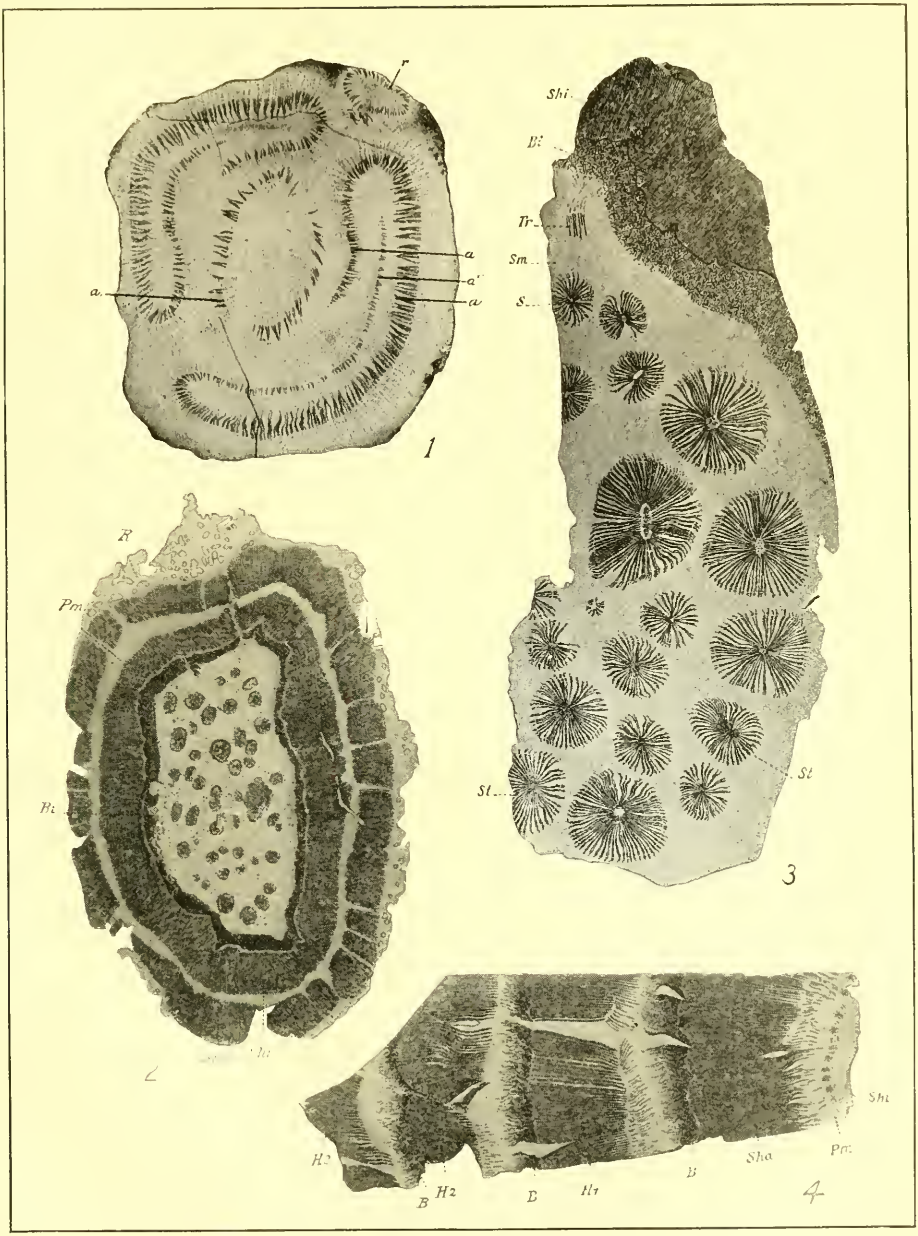
Explanation of Plate LIV

Fig. 1. Cross-section of stem, *Ptychoxylon Levyi*, enlarged a little more than one-half. *a*, outer zone of secondary wood, bordered with an equally wide zone of rayed phloem, the whole being normal or centrifugal in growth; *a′* and *a″*, zones of inverted secondary wood in bands temporarily continuous with the outer zone at the openings where branches have broken through, one of the latter, *r*, being still included in the section; a_1 inner zone or cylinder of inverted or centripetal wood with medullary rays, and rayed phloem; *r* branch with secondary wood. In this specimen the pith cells and primary wood are not shown, while the cortical tissues were lost before petrification. From the Permian of Autun. After Renault.

Fig. 2. Cross-section of stem of *Medullosa stellata* var. *typica*, slightly reduced. Small steles, each with its centrifugally developed secondary wood, are scattered in the central (principal) medullary area; *sha*, outer, normal, secondary wood; *shi*, zone of inner and inverted secondary wood, the medullary elements not appearing in the illustration; *Bi*, zone of inner phloem or bast of the inverted exogenous wood; the white line indicates the cambial zone; *R*, portion of cortex. From the Permian of Chemnitz. After Weber and Sterzel.

Fig. 3. Portion of the section of the interior of a trunk 48 cm. in diameter. of *Medullosa stellata* var. *gigantea*, about 9/10 the natural size. *Sm*, ground mass of central pith containing a number of small steles, *st*, with their radiate secondary wood, the primary elements being shown in the centers of some of the larger medullary steles; *Shi*, portion of inner zone of the enveloping cylinder of inverted or centripetal secondary wood with its thick phloem. *Bi*. *Bi*.

Fig. 4. Cross-section of a fragment of the same specimen and just external in position to that seen in figure 3. *Shi*, small fragment of the inner, inverted, zone of secondary wood seen in the previous figure; *Pm*, partial pith, including bundles, probably of primary wood; *Sha*, normal or centrifugal secondary wood, with phloem, *B*, and phloem rays; H_1B, and H_2B, succeeding zones of secondary wood with rayed phloem zones. From the Permian of Chemnitz. After Weber and Sterzel.



STEMS OF CYCADOFILICES

Explanation of Plate LV

Fragment of a frond of *Neuropteris* cf. *Smithii,* about 2/5 the natural size. The fronds early described as *Neuropteris* are now recognized as merely the foliage of *Medullosa.* From the Pottsville at Warrior, Alabama. Collection of Alabama State Geological Survey.

NEUROPTERIS, A CYCADOFILIC FROND