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McGILL UNIVERSITY, MONTREAL.

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FROM THE ERIAN AND CARBONIFEROUS,
AND ON
THE CHARACTERS AND AFFINITIES
OF
PALÆOZOIC GYMNASPERMS.

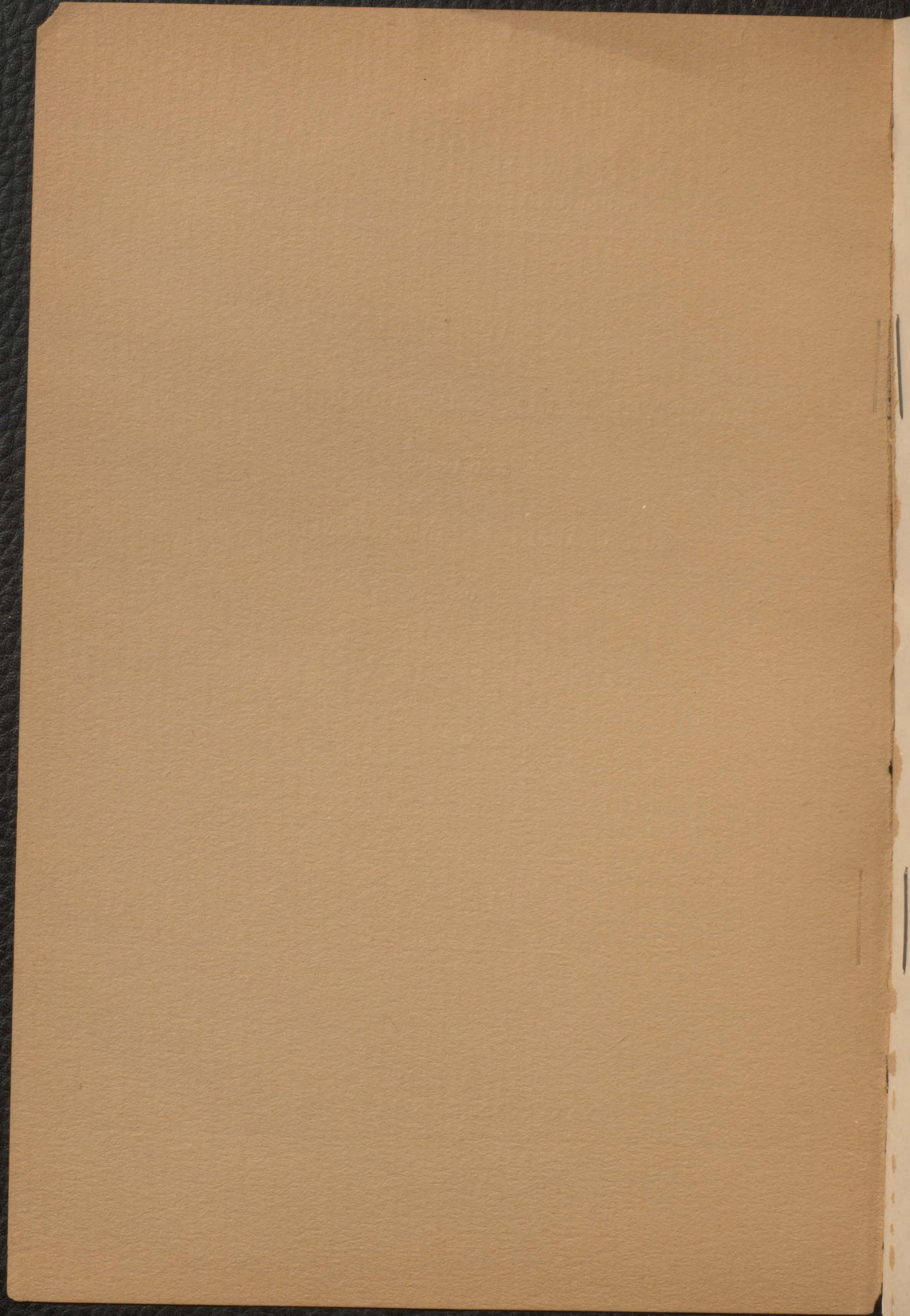
BY

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PETER REDPATH MUSEUM, MCGILL UNIVERSITY, MONTREAL,
NOTES ON SPECIMENS, 1890.

ON NEW PLANTS FROM THE ERIAN AND CARBONIFEROUS,
AND ON THE CHARACTERS AND
AFFINITIES OF PALÆOZOIC GYMNOSPERMS.¹

BY SIR J. WILLIAM DAWSON, L.L.D., F.R.S.

In Palæobotany it often happens that some specimen recently discovered opens up a multitude of new questions respecting former acquisitions. A noteworthy instance of this in my recent experience, has been the kind communication to me by Mr. R. D. Lacey of Pittston, Pennsylvania, of some specimens of Palæozoic Gymnosperms obtained by him in the Catskill and Carboniferous of Pennsylvania. One of these is a large slab containing a leafy and fruit-bearing branch or stem of a new plant allied to *Cordaiteæ* on the one hand and to *Næggerathiæ* on the other, and remarkable for its exhibiting in connection parts usually found separately. Another is a set of specimens of certain peculiar organs of fructification referred by European palæobotanists to the genus *Dolerophyllum*, allied to *Næggerathia*, and which have not, so far as I am aware, been previously found in America. About the same time Mr. Francis Bain, of North River, Prince Edward Island, had placed in my hands some

¹ Reprinted from the CANADIAN RECORD OF SCIENCE, January, 1890.

very interesting examples of the stems known as *Tylo-dendron*, which occur not infrequently in the Permian of that Island, and of which he has found the leaves and probably the fruit along with stems shewing markings and structure.

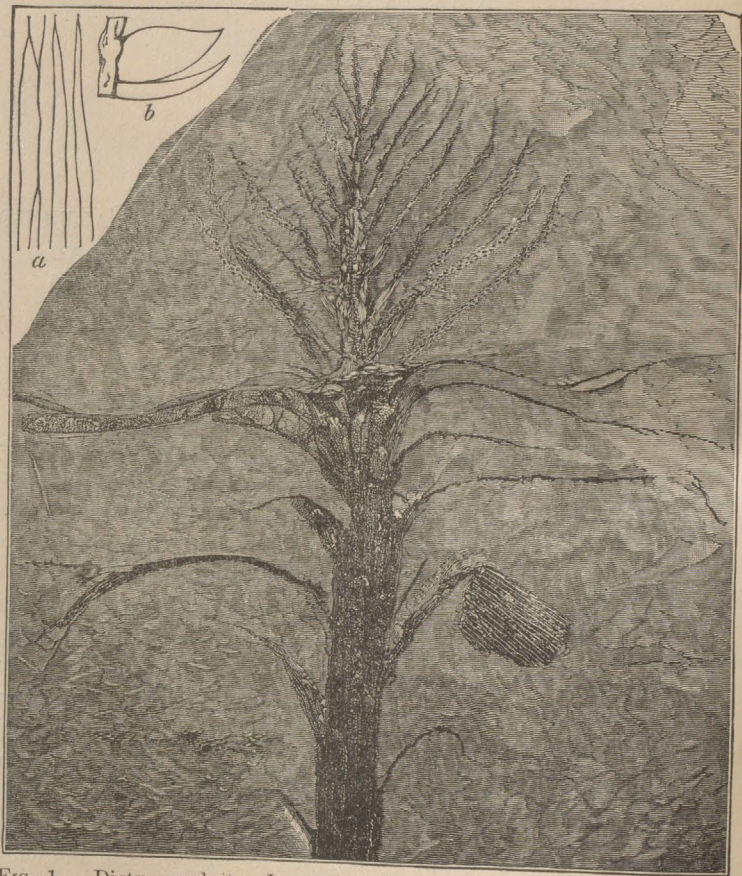


FIG. 1. *Dictyo-cordaites*, Laccoi—much reduced; (a) venation of leaf nat. size; (b) seed and bract, enlarged.

A short notice of Mr. Laccoe's remarkable specimen was sent at once to the *American Journal of Science*,¹ but the

¹ July, 1889.

questions raised by this and the other specimens demanded a more detailed investigation; and I now wish to base on this, and the other specimens above referred to, some general remarks on our present knowledge of Palæozoic Gymnosperms, and more especially on those of North America.

Mr. Lacoë's large specimen, for which I have proposed the generic name *Dictyo-cordaites* in reference to its peculiar netted venation, may be described as follows¹:—

DICTYO-CORDAITES LACOË, Dawson. (Fig. 1)

The specimen is a branch or small stem $2\frac{1}{2}$ cm. in diameter and 46 cm. in total length. It is flattened and pyritised, and shows, under the microscope, only obscure indications of the minute structure, which would seem to have consisted of a pith surrounded by a fibrous envelope and a bark of no great thickness. It would appear, therefore, to be exogenous with a thin woody cylinder and large pith. The stem shows portions of about 15 leaves, which have been at least 16 cm. long and 3 to 4 cm. broad. They are spirally arranged and are decurrent, apparently by a broad base, on the stem. Their distal extremities are seen in a few cases, but in all seem injured by mechanical abrasion or decay. It seems most probable that they were truncate and uneven at their extremities. The stem is terminated by a cluster or compound corymb of spikes of which 20 are seen. They are slender, but seem to have been stiff and woody, and the largest are about 15 cm. in length. The peduncles are knotted and wavy in outline, as if dry and woody in texture when recent. In this they differ from most of the ordinary Antholites, but agree with my *A. Devonicus*,² and also with *A. rhabdocarpi* of the Carboniferous³ which they resemble in the form and arrangement of the fruit. They have short

¹ I am indebted to Professor Penhallow, of McGill University, for his kind aid in the study of the specimen.

² Fossil Plants of Devonian and Upper Silurian, 1871, Plate XIX.

³ Journal London Geological Society, 1867, Plate VII.

pointed bracts, and some of them bear oval fruits, but only a few of these remain, the greater part of them having apparently fallen off before the plant was fossilized. There may have been about 50 to 100 seeds or fruits on each peduncle, and they seem to have been spirally arranged. So far the characters do not differ from those of the genus *Cordaites*, except that in those plants the spikes of fructification are more usually lateral than terminal. Grand'Eury, however, figures¹ one form of *Cordaicladus* in which they are terminal.

The most remarkable peculiarity, however, appears in the leaves, which instead of having the veins parallel, have them forking at a very acute angle, and slightly netted by the spreading branches of the veins uniting with the others near them. This allies the leaves with those of the provisional genus *Næggerathia*, some of which have this peculiarity, as also certain modern Cycads of the genus *Zamia*, which Professor Penhallow has kindly pointed out to me. Leaves with forking veins and even anastomosing to a certain extent, are also known in certain fossils of the genera *Otozamites* and *Næggerathiopsis*, &c., which are referred to Cycads, and the modern Cycadaceous genus *Stangeria* has forking veins. The present plant would seem to be a form of *Cordaites*, tending to *Næggerathia*, which most paleo-botanists believe to have been a gymnospermous genus allied to *Cordaites*. The affinities, however, so far as can be judged, are nearer to the latter; and following the example of Grand'Eury in his nomenclature of the genera, I would propose the name *Dictyo-cordaites* for the present genus, and the specific name *Lacoi*, in honor of its discoverer. I may add here that the general aspect of this plant must have been so near to that of a Carboniferous species of *Cordaites*, as restored many years ago in my Acadian geology,² that I reproduce the figure here.

¹ Flore Carbonifère, Pl. XXV, Fig. 4.

² Second Edition, 1868, Page 458, figure 172.

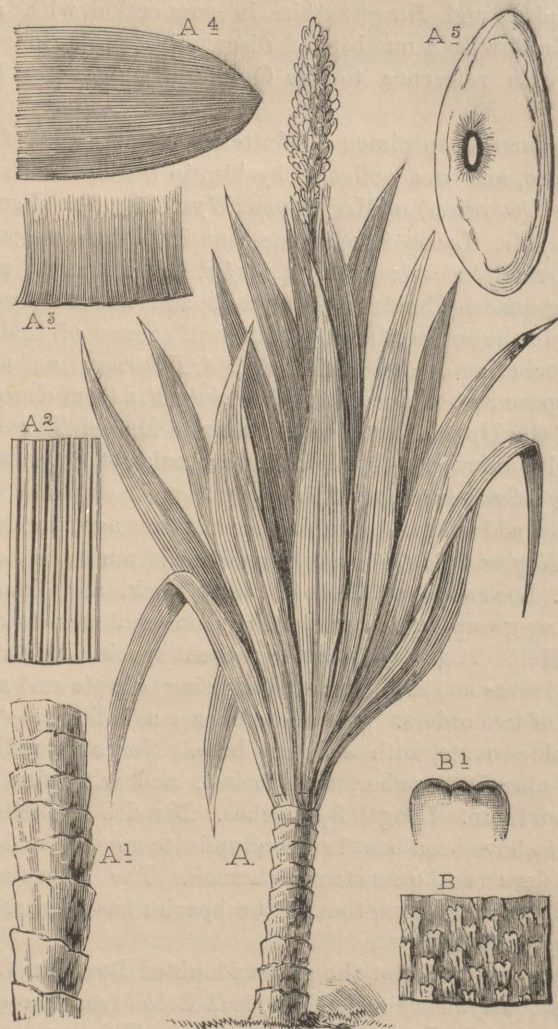


FIG. 2. Restoration of *Cordaites borassifolia*. (1) Stem, (2) leaf, (3, 4) base and point of leaf, (5) section of stem. B. Markings of *Diplotegium*, an allied type (from *Acadian Geology*.)

The specimen thus invites a comparison with the families of Cordaites and Nægerrathia in connection with allied genera and with a number of discoveries made in recent years with reference to the Gymnosperms of the Palæozoic.

Mr. Lacoë's specimen is flattened out on a slab of grey sandstone, and was collected by him in the Lower Catskill (Upper Devonian) of Meshoppen, Wyoming Co., Pennsylvania. Mr. Lacoë informs me that it is there associated with *Archæopteris minor* and *A. major*, Lesqx., and in neighbouring quarries half a mile distant and about fifty feet higher in the series, there are different species of Archæopteris, including one identified with *A. Hibernicus*, and a strobile apparently of *Lycopodites Richardsoni*, a form characteristic of the Upper Devonian of Perry in Maine. These beds have also afforded to Prof. White a species of *Spirifer*, and the *Stylonurus excelsior* of Hall.

I may add that I described, some years ago,¹ under the name *Næggerathia Gilboensis*, a specimen from the collection of Mr. Lockwood of Gilboa, New York, and from the Chemung group, which was kindly communicated to me by Prof. Hall. It differs from the present species in the form of the leaves and also in the veins being simple and apparently of two orders. Its characters are as follows:—"Leaf rhombic-obovate, with a broad base. Nerves or radiating plicæ nine in number, not forked, and with fine striæ between them. Length $3\frac{2}{10}$ inches. Breadth $2\frac{1}{2}$ inches. It seems to have been bent in a conduplicate manner, and clasping or decurrent, on a stem or branch. The form tends to that of *Dolerophyllum*, though the species has been referred to *Næggerathia*."

I may also add that the only undoubted Devonian Cordaites previously in my collections, is *C. Robbii* from the middle Devonian of St. John, New Brunswick. This is a long and broad parallel-sided leaf, pointed at the extremity, and clasping at the base, with parallel veins, and nearly akin to *C. borassifolia* of the Carboniferous. With it are found species

¹ Quarterly Journal Geological Society, 1871.

of *Antholithes*, and of *Cardiocarpon*, which may have belonged to it.¹ It would thus seem that so far as now known in America the typical Cordaites had precedence of the Næggerathiæ, and of Dictyocordaites. My narrow-leaved species *C. angustifolia* is equally ancient with *C. Robbii*, but is of doubtful affinities.

DOLEROPHYLLUM, Saporta.

This genus was established by Saporta for certain densely leaved plants, having rounded leaves with radiating nerves and closely arranged in a spiral manner on the stem. The male inflorescence of these plants consists of a central disk, with cavities for the pollen, and surrounded with radiating fibres, while the seed is of large size and longitudinally striated, being the fruit usually known as *Rhabdocarpus*. It is likely that in America we have usually placed the leaves with ferns, as species of *Cyclopteris*. The fruits are known and have been described as *Rhabdocarpi*. One species, my *Rh. insignis* from Nova Scotia, is an inch and a half in length. Another, *Rh. oblongatus* of Fontaine, from Virginia, is nearly as large. Mr. Lacoë has found separately what is regarded as the male organ of fructification. One of his specimens is a nodule of clay ironstone from Illinois, and exhibits merely the central disk. Two others are flattened in shale and are from the Carboniferous of Pennsylvania. They are of different sizes, but may be of the same species. The larger of the two has a disk three quarters of an inch in diameter, and marked with pits and ridges in an irregularly radiating manner, while the border of radiating fibres is about half an inch in breadth, giving a total diameter of an inch and three quarters.

If we put together the leaves of some of the larger species of *Cyclopteris*, the fruit of *Rhabdocarpus*, and these singular disks, we shall have all the principal parts of *Dolerophyllum* as restored by Saporta from actual specimens found in the

¹ Report on Devonian Plants of Canada, 1871.

coal measures of France.¹ I have not in my own collections any specimens proving this collocation of parts, but give it here on the authority of the French palæo-botanist. The structure of the stem of *Dolerophyllum* does not appear to be known, but its affinities would seem to be Cycadean, and the organs of fructification above described have some resemblance to the remarkable *Carpolithes horridus* of our Cretaceous of the North-west.² The species collected by Mr. Laclef so closely resembles *D. Gossperti* of Saporta, that I hesitate to give it a specific name. It may, however, be distinguished by its longer marginal rays and larger pits on the disk, and may be provisionally named *D. Pennsylvanicum*.

TYLODENDRON, Weiss.

A very important class of fossils in connection with the subject of this paper is that included in the genus *Tylo dendron* of Weiss, which are more characteristic of the upper than the lower members of the later Palæozoic. They are, however, closely allied to some of the forms included in the genus *Knorria*, which goes back to the Devonian. These stems are characterised by elongated ridges spirally arranged, and with a slight groove at one end. Some specimens also show distinct swellings or nodes of larger scars as if giving origin to whorls of smaller branches. They are most frequently sandstone casts, and the surface markings are not those of a true exterior surface, but of an inner cylinder showing the points of exit of bundles of fibres or vessels. These stems have received several names. They constitute the genera *Schizodendron* and *Angiodendron* of Eichwald, and the *Lepidodendron elongatum* of Brongniart is apparently of this nature. It is difficult to distinguish them into good species, and the *T. speciosum* of Weiss covers most of the forms. Weiss has described the structure of the stem as consisting of a cellular pith surrounded with a

¹ Evolution des Plantes, Phænogames, p. 75.

² Trans. R. Socy. of Canada, Vol. I, p. 21, Pl. I., Fig. 3.

cylinder of porous discigerous fibres, with three rows of contiguous pores, and radially arranged. This is of course near to *Dadoxylon*. The stem and fruit have not hitherto been recognised in Europe.

These plants were first recognised in Prince Edward Island by the writer in 1870, and published in his report on the geology of the Island in 1871, under the generic name of *Knorria*. They are there stated to "resemble very closely the Permian stems to which Eichwald has given the name *Schizodendron*." They are also stated to show traces of woody tissue allied to that of Conifers, and are conjectured to have been branches of trees allied to that family. In that Report they are said to occur in the Permo-Carboniferous of Gallas Point, and also in beds referred to the Trias.

Additional specimens were subsequently collected by Mr. Bain of North River, Prince Edward Island, and were sent to me for examination. They are described in a paper published in the Canadian Naturalist in 1885 as follows:—

"Tylodendron was founded by Weiss to include stems with elongate, prominent leaf-bases of the character of those of *Knorria*, but bifurcate at the top. These stems or branches, are very characteristic of the Permian of Russia, Germany and France. They have been found by Weiss to show the character of *Dadoxylon* when the structures are preserved, and are therefore Coniferous; and it is now pretty generally believed that they are decorticated branches of *Walchia*. So far as European evidence extends, they are regarded as strictly Permian, and the species drawn by Mr. Bain is not distinguishable from *T. speciosum* of Weiss. In Prince Edward Island, I have figured (Report, Plate III Fig. 30) what seems to be the same species, though under *Knorria*; but my specimen may have been from the Middle Series, then called Lower Trias, but now regarded by Mr. Bain as Permian.¹

¹ Mr. Bain informs me in a recent letter that he has found specimens of *Tyloedendron* in beds regarded by him as Triassic.

The specimens were associated with branches of *Walchia*, leaves of *Cordaites Simplex*, *Trigonocarpa*, and also with trunks of *Dadoxylon* (*D. materiarium*.)

Since the publication of the paper referred to, Mr. Bain has made additional collections, more especially on St. Peter's Island and other places on the south side of Prince Edward Island, some of which have been sent to the Geological Survey at Ottawa, and others to the writer, along with drawings of specimens still in Mr. Bain's possession. These specimens show the internal structure of the pith and woody cylinder, and varieties in the external markings which may perhaps indicate distinct species; and along with the stems, Mr. Bain has found leafy branchlets and fruits of a peculiar form which, from their association, he regards as belonging to these plants.

The principal external differences in Mr. Bain's specimens, consist in greater or less size and distance apart of the long, projecting, spindle-shaped and furrowed ridges which mark the stems, and in the presence or absence of enlarged nodes marked with whorls of tubercles. This last difference may be specific, and appears to correspond with certain differences in the structure of the wood.

Several of the specimens showing structure, represent the pith-cylinder alone in a silicified state, and these specimens have the external markings as perfectly shown as in the sandstone casts, so that the supposed external markings of *Tyloedendron* may in some cases belong to the outer surface of the pith-cylinders. The internal structure of these medullary cylinders shows, in some cases, the transverse dia-

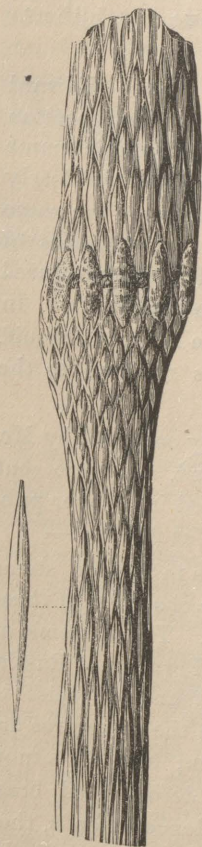


FIG. 3. Portion of stem of *Tyloedendron* (from drawing by Mr. Bain.)

phragms characteristic of Sternbergia. In other examples this is less pronounced or absent. The pith is composed of ordinary parenchymatous tissue, becoming more dense toward the outer surface, and especially in the prominences corresponding to the exterior ridges. In each of these there is also a vacant canal, and similar canals appear in a vertical position in the interior of the pith, as if there had been vessels dispersed through the pith and sending off bundles to the exterior prominences. In some specimens, shreds of woody tissue appear at the surface of the pith, and in others, in which the pith is not preserved, the woody cylinder shows its character somewhat perfectly. In the cross section it presents square meshes in radiating rows, not distinguishable from those of *Dadoxylon*. In the longitudinal section, however, the tissue is seen to be thin-walled, with very indistinct disks, which, so far as observed, appear to be in a single row, in which respect they differ somewhat from those observed by Weiss, which varied from one to three rows, and with frequent medullary rays, simple and composed of few cells superimposed, in which respect,

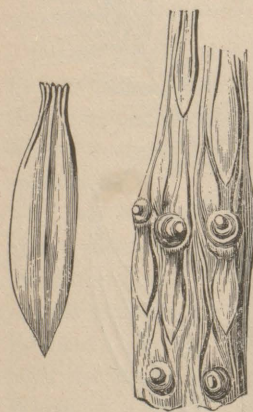


FIG. 4. Leaf-base and outer surface of *Tyloedendron* with fruit scars. (Drawn by Mr. Bain.)

as well as in the disks, they differ from those of *Dadoxylon materialarium* the species found with them in the Permian sandstones of Prince Edward Island. In the nodose specimens, the woody fibres are very small, and in the nodes, become tortuous and interlaced in the manner described by Williamson in the nodes of *Calamites*. In the non-nodose form the tissue is more open and very thin-walled. Nothing is known of the structure of the outer bark except impressions of its form with elongated leaf-bases different from the markings on the internal surfaces.

(Fig. 4.) With reference to the latter it would seem that they

are not limited to the surface of the pith, but occur on the woody cylinder as well. Mr. Bain has observed in one instance, what seems to be an outer envelope which would indicate a thick bark, but its structures are crystalline, and it may be merely a concretionary covering.

The leaves and branchlets in fig. 5 have been found by Mr. Bain in such relation to the debris of *Tyloedendron*, that he regards them as belonging to it. They certainly differ from those of any of the known species of *Walchia*,



FIG. 5. Leafy branch of *Tyloedendron* and leaf enlarged.
(Drawn by Mr. Bain.)

and more resemble those of the genus *Voltzia*. They have apparently three nerves, but the lateral ones may be resin-vessels.

Mr. Bain also finds at St. Peter's Island, with the branches and leaves of *Tyloedendron*, the fruits or seeds represented in Fig. 6. They appear to be wedge-shaped and in fours, and an involucre similar to that in Fig. C. accompanies them, and is supposed to have belonged to them, or possibly to male flowers of the same species. Neither of these organs have been found actually attached to the branches. If these fruits belong to *Tyloedendron* they would indicate taxine affinities, and they somewhat resemble the curious coniferous fruits from the Tertiary of Australia known as *Spondylostrobos*.



FIG. 6. Fruit and bracts of *Tyloedendron*. (a) Fruit. (b) single seed, (c) bracts. (Drawn by Mr. Bain.)

Stems having the markings of *Tyloedendron* occur in the Permo-Carboniferous of Cape John in Nova Scotia, and at that place there are also obscure *Voltzia*-like leaves somewhat resembling those of the Prince Edward Island specimens.

If we connect the trunks, branches, leaves and fruits above referred to, we can now extend the description given by Weiss much beyond that given to his *T. speciosum*, and should perhaps give a new name to the form from Prince Edward Island, more especially as it differs slightly both in markings and structure from that described by Weiss.

TYLODENDRON BAINI, S.N.

Exterior of stem with elongated leaf-bases, truncate above, obtusely pointed below. Pith-cylinder and ligneous surface

with elongate ridges pointed below and bifurcate above, differing in size and form on branches of different sizes. Branches or younger stems with nodes bearing a whorl of prominences projecting beyond the general surface.

Stem consisting of a pith-cylinder somewhat Sternbergian in structure, and formed of cellular tissue denser at the surface and with traces of detached vascular bundles. Woody cylinder with fibres having one row of pores and frequent medullary rays of few rows of cells superimposed.

Foliage borne spirally on pinnate (?) branchlets. Leaves elongate, oblong, acutely pointed, narrowed and decurrent at base, with a midrib and two side nerves, possibly resin ducts. Fruit borne laterally on the branches, and consisting of four large seeds, rounded without, and wedge-shaped within, so that in outline they have a semilunar form. They seem to have been enclosed in an involucre.

Should it prove that the nodose and non-nodose stems are specifically distinct, and that the leaves and fruit above described belong to the latter, the description of the stem will require a slight modification in that sense.

It would appear that in *Tylodendron* we have a gymnospermous type akin to the Taxineæ, and which was characteristic of the Permian, apparently extending also into the Triassic Period.

We may now turn to the consideration of what is known of Palæozoic gymnosperms allied to the forms above noticed, with the view of ascertaining their position in the classification, and clearing up some doubtful points arising from the fragmentary condition of our materials.

In the first part of the "Flore du Monde Primitif" (1820) Sternberg describes and figures, under the names *Flabellaria borassifolia* and *F. palmata*, two groups of leaves from the Coal Formation, both apparently referable to the species now known as *Cordaites borassifolia*. Leaves of this kind have since been found very abundantly in the Carboniferous

in different parts of the world. To separate these plants from others of different type, Unger proposed the name of *Cordaites*, in honour of Corda, who had for the first time figured a somewhat perfect leafy branch (Beitrag 1845). Corda's specimen showed something of the structure of the stem which was described by him as having a ring of scalariform vessels surrounding a cellular pith, having that transversely marked surface known as *Sternbergia*, indicating diaphragms or partitions within. This apparently simple acrogenous structure induced both Unger and myself to regard the plant as allied to Lycopods, and it was placed with these in my *Acadian Geology*, and in my paper on the *Fossil Plants of the Coal Formation of Nova Scotia*.¹ It now appears, however, that Corda's figure must have represented only the inner ligneous zone, and this imperfectly.

The leaves in Sternberg's and Corda's specimens were large, parallel-sided and pointed, with closely placed parallel veins of two orders, and they were attached by a broad base to the stem. The leaves showed bundles of fibres in the veins and stomata in the epidermis.

Brongniart having the same objections with Unger to the name of *Flabellaria*, but acting independently, in 1849 designated the leaves of *Cordaites* by the name *Pychnophyllum*, but was induced by their peculiar form and structure to include them in the Gymnosperms with the allied family of *Neggerathiæ*, and near to the Cycads.² He compares the leaves with those of *Dammara* and *Podocarpus* among the Conifers. Goldenberg and Weiss subsequently corroborated Brongniart's view by the discovery of spikes of fructification known as *Antholites* in association with *Cordaites*. Finally Grand'Eury discovered in the coal field of St. Etienne in France, abundant and well preserved stems, leaves and fruits which have enabled the French palæo-botanists to reconstruct the whole plant and to discriminate several genera and species, constituting a gymnospermous family

¹ Journal of Geological Society.

² Tableaux de Genres.

which they designate *Cordaiteæ*, and which they regard as intermediate between *Cycadeæ* and *Taxineæ*.

As restored on the basis of the French specimens, the typical Cordaites are simple or branching arboreal plants with broad parallel-veined, more or less pointed, leaves attached by a wide base to the stem, and leaving simple transverse scars when removed. They bear spikes of nutlets, or large, naked seeds, each subtended by a bract, and which are usually lateral, though sometimes terminal. The stem has a thick bark, composed of cellular tissue with bundles of bast fibres, and the axis has an outer cylinder of porous tissue, in wedges, with medullary rays, and an inner cylinder of the slit-pored or transversely barred tissue, which I have in previous papers designated by the term pseudo-scalariform, to distinguish it from the true scalariform-tissue, from which it differs in having bars and pores only on two sides, and in the apparent pores being of the nature of transversely elongated discs. It is very common in palæozoic gymnosperms and exists in modern cycads. The pith is cellular with denser tabulæ opposite the nodes of the stem giving it the characters of the casts of pith known as *Sternbergia* or *Artisia*.

Leaves of Cordaites, spikes of fructification known as *Antholites*, now often called *Cordaianthus*, fruits of the kind formerly known as *Cardiocarpum*, but now usually named *Cordaicarpum*, occur somewhat plentifully from the Middle Erian to the Permian. If however, we are to regard, all the *Cardiocarpa* as seeds of Cordaites, it seems remarkable that the species of these fruits should be so numerous in comparison with those of the leaves and stems. In the Middle Erian of New Brunswick, I have recognised five species of *Cardiocarpum*, besides *Antholites* and *Trigonacarpa*, and in the Carboniferous of Nova Scotia, the disproportion, as compared with stems and leaves, is still very great. This might perhaps lead to the inference that many of the species of Cordaites belonged to the higher grounds, and that only waterborne seeds found their way into the aqueous deposits. This would also serve to account for the fact that while leaves of

Cordaites are locally very abundant, they are not so generally diffused geographically as the Sigillaria and Lepidodendra. The oldest species known to me is *C. Robbii* from the Middle Erian of New Brunswick, where it occurs with two species of Antholites—*A. devonicus* and *A. floridus*,—perhaps its male and female flowers, and with the species of *Cardiocarpa* already mentioned. I observe it has been stated that *C. Robbii* has been found in the Upper Silurian of Hainault.¹ The latest species known in Acadia is *C. Simplex* found in the Permian of Prince Edward Island and also in the newer Coal formation of Nova Scotia. *Antholites* and *Trigonocarpa* are found in the same beds, but no *Cardiocarpa*.

Stems of *Cordaites* showing structure have not yet been certainly recognised in this country. This leads, however, to the question whether such stems may not have been referred to other plants. I may mention more particularly those named *Dadoxylon*, (*Araucarioxylon*) and *Sigillaria*.

With a view of settling this question, I obtained through the kindness of the eminent French palæobotanist, M. Renault, specimens of the stems from St. Etienne referred by him to *Cordaites*. These I found to be of two types which may be distinguished as follows:—

(a) Silicified stem, associated with leaves of *Cordaites* proper (*C. borassifolia* or allied). This has a large cellular pith, which has, however, mostly disappeared, leaving a hollow cylinder occupied with structureless silica and vegetable debris. The pith has been nearly an inch in diameter and showed no distinct evidence of *Sternbergia* structure. The woody cylinder surrounding the pith was less than a quarter of an inch in thickness, and consisted of two layers. The inner of no great thickness, shows pseudo-scalariform tissue, while the outer layer, which is radially arranged, is composed of porous woody tissue, the pores or discs being sometimes in one row, and sometimes as many as three

¹ Ward, History of Palæo-botany.

rows, but not contiguous. There are medullary rays which are numerous, simple and of few tiers of cells superimposed. The cortical tissues have perished.

(b) The other stem is of smaller diameter with a strongly marked Sternbergia pith, an inner layer of indistinct pseudo-scalariform or spiral tissue and an outer layer, much thicker in proportion, and with wood-cells having three rows of contiguous hexagonal areoles with central slit pores. The medullary rays are simple. This second stem is not distinguishable from *Dadoxylon* of the type of *D. Brandlingii* or *D. materiarium*. The specimen itself shows no evidence that it belongs to *Cordaites*.

Setting aside, as probably Coniferous, the second specimen and assuming the stem (a) to be truly Cordaitean, it accords with one of the species of *Dadoxylon* described by me from the Erian of New York, namely *D. Clarkii*, which presents similar characters though with a somewhat thicker woody cylinder.¹ *D. Clarkii* was described as follows in 1882.

“The pith cylinder is large and shows ordinary cellular tissue. The medullary sheath or inner fibrous layer consists of pseudo-scalariform and reticulated fibres; but the most remarkable feature of this wood is the structure of the medullary rays, which are very frequent, but short and simple, sometimes having as few as four cells superimposed. This is a character not before observed in coniferous trees of so great age, and allies this Middle Erian form with some Carboniferous woods which have been supposed to belong to *Cordaites* or *Sigillaria*.”

The resemblance of this peculiar stem to those of *Cordaites* and *Tylodendron*, above referred to is obvious.

I have noted and illustrated by characteristic examples, the fact that the erect ribbed trees found in the coal formation section at the South Joggins in Nova Scotia, often contain the remains of their axis, either calcified and standing erect within the tree, or fallen to the bottom in the form of mineral charcoal. The examination of a large number of

¹ Report on Erian Plants of Canada, Part II, 1882.

such axes has led me to the conclusion that there are two types of these erect trees, one with an axis of scalariform tissue only,¹ though with the outer radiating cylinder characteristic of *Diploxyton*, the other with a double axis of pseudo-scalariform tissue internally, and discigerous or multiporous tissue externally, of similar character to the stems of *Cordaitea*. Perhaps in accordance with this is the fact which I have also illustrated, that some so called *Sigillariae* or *Favulariae* of the type of *S. Elegans*, have somewhat broad parallel-veined leaves resembling those of *Poacordaites*.²

As characteristic examples of these trunks, I may refer to two which I have described in the Journal of the Geological Society.

(a) SIGILLARIA (*Diploxyton*.)

The most characteristic example is a trunk rooted in an under-clay in the Joggins section and existing as a sand cast 12 feet in height. This tree was discovered and carefully removed by Mr. Albert J. Hill, who found the interior of the cast a calcified axis extending throughout its length and showing well preserved structure. The structure is described as follows:—³

“The axis is about 6 centimetres in its greatest diameter, and consists of a central pith cylinder and two concentric coats of scalariform tissue. The pith cylinder is replaced by sandstone, and is about one centimetre in diameter. The inner cylinder of scalariform tissue is perfectly continuous, not radiated, and about one millimetre in thickness. Its vessels are somewhat crushed, but have been of large diameter. Its outer surface, which readily separates from that of the outer cylinder, is striated longitudinally. The outer cylinder, which constitutes by much the largest part of the whole, is also composed of scalariform tissue ;

¹ Journal Geological Society of London.

² Acadian Geology.

³ Journal Geological Society of London, Vol. xxxiii., 1877.

but this is radially arranged, with the individual cells quadrangular in cross-section. The cross-bars are similar on all the sides, and usually simple and straight, but sometimes branching or slightly reticulated. The wall intervening between the bars has extremely delicate longitudinal waving lines of ligneous lining, in the manner first described by Williamson,¹ as occurring in the scalariform tissue of certain *Lepidodendra*. (Fig. 4.) A few small radiating spaces, partially occupied with pyrites, obscurely represent the medullary rays, which must have been very feebly developed. The radiating bundles passing to the leaves run nearly horizontally; but their structure is very imperfectly preserved. The stem being old and probably long deprived of its leaves, they may have been partially disorganized before it was fossilized. The outer surface of the axis is striated longitudinally, and in some places marked with impressions of tortuous fibres, apparently those of the inner bark. In the cross-section, where weathered, it shows concentric rings; but under the microscope these appear rather as bands of compressed tissue than as proper lines of growth. They are about twenty in number. Though apparently of very lax tissue, the wood of the outer cylinder may, in consequence of the strength of the vertical rods and transverse bars of ligneous lining, have been of considerable firmness, which would indeed seem to have been implied in the manner of its preservation within the hollow bark."

This stem is evidently that of a *Sigillaria* of the *Diploxylo*n type, with a slender woody axis wholly of scalariform tissue and a thick inner bark, probably mostly of cellular tissue of a lax and easily decomposed character, but probably also with bundles of fibres. This was protected and strengthened externally by an outer bark of sclerenchymatous cells, now converted into coal.

¹ Monthly Microscopical Journal, August, 1860.

(b) SIGILLARIA (Favularia?)

This example was furnished by another erect tree, about a foot in diameter, and which I took down with care and examined its contents. It was described and figured in the journal of the Geological Society of London.¹ It presented the following parts:—

(a.) A coaly outer bark, no doubt originally composed of dense sclerenchyma.

(b.) A cylinder of sandstone, representing the inner bark entirely removed by decay.

(c.) A ligneous axis composed of wood-cells, the inner with two rows of contiguous bordered pores on their radial surfaces, the outer with only one. The medullary rays short, frequent, and of one row of cells or sometimes partly with two rows. Diagonal bundles of pseudo-scalariform tissue traversed this cylinder, no doubt leading to the leaves.

(d.) An inner cylinder of pseudo-scalariform tissue similar to that in the inner cylinder of the axis in *Cordaites* and in *Cycads*.

(e.) A medulla or pith, consisting of a hollow cylinder of cellular tissue sending off at intervals thin diaphragms toward the interior, giving it a *Sternbergia* structure.

This type of *Sigillarian* stem is obviously of far higher grade than the former, and would justify the inference that it belonged to a gymnospermous plant. The structures of the stem correspond with that of others in which the axis exists only as fragments in the base of the once hollow stump. Some of these, however, conform to the type of multiporous wood-cell seen in *Poroxyton*. If the foliage was like that of *Sigillaria elegans*, and the spikes of fructification of the nature of *Antholithes*, these parts might be referred to *Cordaites*, though the stem was ribbed in the manner of *Sigillaria*. I may add here that I have shown² that some *Sigillariae* of the *Favularia* type, divided at top into small

¹ Vols. xxvi. and xxvii., 1870 and 1871.

² Journal Geological Society, Vol. xxii., also *Acadian Geology*.

branches without ribs and with leaf scars very different in form from those of the trunk.

The question now arises whether these different trunks can belong to one genus, or even to one family; whether, in short, we may not have been confounding very different types, of trees under the name of *Sigillariæ*? The first of the above types, that of *Diploxylon*, corresponds with the structure of undoubted *Sigillariæ*, as illustrated by Williamson and other British palæobotanists, and conforms so closely to that of *Lepidodendron* that we can scarcely doubt the close affinity of this particular type with the Lycopodiaceous Acrogens.

On the other hand, so many of the erect ribbed trees at the South Joggins have afforded tissues of a much higher type that we cannot doubt the existence there of trees similar in external characters to the ordinary *Sigillariæ*, yet with internal structures conforming rather to the type of *Cordaitæ*. In these circumstances, while we must admit the Gymnospermous affinities of the latter family, we must wait for further information before being able to define its precise relations to the *Sigillariæ* on the one hand, and the Conifers on the other.

I have referred above to *Sternbergia* piths. These are usually sandstone casts, but in some instances shreds of the enveloping tissues remain. In a few instances the internal structure is preserved. Where the latter occurs it is seen to be cellular, arranged in tubulæ in the manner which I have explained as occurring in the young pith of the Balsam Fir and in the stem of *Cecropia peltata*. Such piths I have described as occurring in large and well preserved stems of *Dadoxylon* of different species from the Middle Devonian to the Permian. The large size of the pith would seem to indicate that the young branches were very thick, in which case they could not have resembled those of *Walchia* or *Araucarites*, which otherwise might be supposed to represent the foliage of these trees, unless, indeed, there were thick branches bearing slender branchlets, or unless, as Williamson has affirmed to have been the case

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in some other Coniferous trees, the pith increased in size with the growth of the stem or branch. There are, however, *Sternbergiæ* which have not belonged to *Dadoxylon*. I have figured¹ specimens which show, attached to them, multiporous tissue like that of *Poroxyton* or *Dictyoxyton*. Others are enveloped with scalariform tissue like that of *Lepidodendron* or *Lepidofoios*. This fact was long ago observed by Corda. Others show pseudo-scalariform and discigerous tissue like those of *Cordaites*, or of the peculiar type of supposed Sigillaroid trees above referred to. Thus it is apparent that the *Sternbergia* piths belonged to a number of trees ranging from Gymnosperms of high type to Acrogens. I may remark here that the true *Calamodendra*, of which *Calamites approximatus* is a type, in so far as the medullary cylinder is concerned, are really internal casts of pith cavities, originally surrounded by a thick woody envelope showing psuedo-scalariform and discigerous tissue, and, therefore, not very dissimilar from that of *Cordaites*. Williamson has shown, however, that the medullary rays and other structures were different, and the stems of *Calamodendra* were jointed in relation to the support of whorls of organs. If these *Calamodendra* were really Acrogens allied to *Calamites*, they present the same curious resemblance to Gymnosperms which we see in another form in one of the types of Sigillaria, and warn us that the structures of stems and the character of fructification may not have been correlated in the Carboniferous in the same manner as in modern stems.

Doubts of this kind are further justified by the consideration of the stems known as *Poroxyton*, *Medullosa*, *Cycadeoxyton*, *Colpoxyton*, *Lyginodendron*, *Kaloxylon* and *Heterangium*, several of which have recently been described in great detail by Williamson and by Renault. These have a true medulla, surrounded by a cylinder of discigerous or reticulated tissue, arranged radially and traversed by medullary rays. Such characteristics would well suit a gymnosper-

¹ Journal Geol. Society, 1871.

mous standing, but, on the other hand, there are specimens which, as Williamson has shown, unite such structures with foliage referred to ferns of the genus *Sphenopteris*.¹ Williamson suggests that inasmuch as the living *Stangeria* among the Cycads combines an exogenous stem with fern-like leaves, the same may have been the case in the Carboniferous. If so, the problem as to their position can be determined in each case only by the discovery of their fructification.

In Bertrand and Renault's recent elaborate memoir on *Poroxyton*, these botanists have shown that this genus possesses an exogenous stem of some complexity. It has a distinct pith, not Sternbergian, with gum canals, an inner or centripetal layer at first in distinct bundles of scalariform and punctated fibres, a true radiating woody zone of multiporous fibres, with numerous medullary rays, and a cambium layer, two layers of inner bark, and an outer suberous bark. The leaves are petiolate and simple, and have a single vascular bundle at base, forking in the blade, in the manner of *Næggerathia*. From these and other more minute characters in the distribution of the tissues, the authors conclude that *Poroxyton* may be placed between the Dyploxyloid *Sigillariae* and the Cycads, as probably a low Gymnospermous type. They refer to three species of *Poroxyton*—*P. Edwardsii*, *P. Boyseti* and *P. Stephanensis*.

Medullosa of Cotta presents several thick woody cylinders twisted together, and with detached star-shaped or radiating bundles of fibres in the pith. The woody tissue of *Medullosa* is said to resemble that of *Palæoxyton*, which is, however, a subgenus of *Dadoxylon*, and allied to the Conifers.

Colpoxyton has a thin woody cylinder and much thicker bark than the preceding, and simple bundles in the pith.

Cycadeoxyton has several concentric circles of fibrous tissue, with cellular tissue between them, somewhat in the manner of Gnetaceæ, and with no fibrous bundles in the

¹ Transactions Royal Society.

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pith. My *Dadoxylon annulatum* shows structures approaching to this last.

Renault has constituted a new genus (May, 1889) under the name *Ptychoxylon*, in which the wedges of the woody cylinder extended inwards, and are then bent so as to simulate internal woody layers.

All these stems are regarded as probably gymnospermous, and with the different types of *Dadoxylon*, the *Cordaites* and *Tylo dendron*, serve to give some account of the trees from which the multiform nutlets and seeds of the Carboniferous and Erian were derived.

The genus *Næggerathia*, like that of *Flabellaria* (*Cordaites*), dates from the time of Sternberg, and his *N. foliosa* is the original type, to which, however, a somewhat miscellaneous group of species has been added by subsequent authors. Some of these, instead of the pinnate leaves of the original species, have simple leaves spirally arranged and decurrent on the stem. This is the case, for example, with *N. flabellata* of Lindley and Hutton, which, on this and other grounds, has been placed with some other species by Schimper¹ in a new genus *Psygmo phyllum*, while Saporta² places them in his genus *Ginkgo phyllum*, supposing them to be akin to the modern Ginkgo or *Salisburia*.

These two types of *Næggerathæ* agree with one another, and differ from *Cordaites* in the flabellate form and forking venation of the leaves. The nearest approach to the *Cordaites* is that of the leaf of *N. flabellata* to that of *C. patulus* Grand Eury.³ Saporta states that the ordinary *Næggerathia* (*N. foliosa*) bear their fructification on the surface of modified leaves, and he is inclined to place them near to the Cycads. On the other hand, he regards the second type (*N. flabellata*, &c.) as more nearly allied to the taxine Conifers, though their fructification is not certainly known. Lacoë's specimen, now under consideration, would, how-

¹ Palæontologie Vegetale.

² Evolution de Monde Vegetal.

³ Saporta *l. c.*

ever, go to show that a plant with Næggerathoid leaves might have a fructification similar to that of *Cordaites*.

It has further become a question with palæobotanists to what extent some of the broad, flabellate and rounded leaves referred to *Cyclopteris* and other genera of ferns, may belong to gymnospermous plants of the nature of Næggerathia. Of these leaves those already referred to of the genus *Dolerophyllum* seem certainly to be Gymnospermous. The peculiar fan-shaped leaves described by Newberry under the name *Whittleseya*,¹ and of which one species occurs in the coal formation of Nova Scotia, belong apparently to the same category. The singular unilateral leaves, or fronds, of which my *Næggerathia dispar* from Nova Scotia was the type, and which Fontaine has recently separated in his genus *Saportea*,² may also be gymnospermous. Less certain is the reference by Saporta to this group of the genus *Cannophyllites* of Brongniart, and of the large and beautiful Erian and Lower Carboniferous fronds of my genus *Megalopteris*.³

I have already referred to the numerous Gymnospermous seeds known in the Palæozoic, and belonging to the genera *Trigonocarpum*, *Cardiocarpum*, *Rhabdocarpus*, etc.

The structure of many of these has been illustrated by Hooker, C. Brongniart, Williamson and myself, and they are unquestionably allied to the seeds of *Cycadææ* and *Taxinææ*. When the vast abundance of these seeds on certain beds is considered, and the fact that Schimper catalogues 67 species, while recent discoveries would nearly double that number, it becomes evident that plants of this grade must have borne a very important part in the palæozoic vegetation, and we have reason to suspect that many stems and leaves now of uncertain affinities will be found to have been of this class.

We may now tabulate as follows the principal Gymnospermous groups which may be represented in the Palæozoic:—

¹ Lesquereux "Coal Flora."

² "Permian Flora."

³ "Evolution du Monde Vegetal."

1. *Sigillariæ* and *Calamodendreæ*.
 Favularia, (in part)?
 Sigillaria proper, (in part)?
 Calamodendron, (in part)?
2. *Cycadææ*.
 Rhizozamites.¹
3. *Næggerathiæ*.
 Næggerathia.
 Poroxyton.
 Dolerophyllum.
 Whittleseya.
 Saportea.
 Medullosa?
 Colpoxyton?
 Ptychoxyton.
4. *Cordaiteæ*.
 Dictyocordaites.
 Cordaites.
 Dorycordaites.
 Poacordaites.
5. *Taxineæ*.
 Psymphyllum.
 Baiera?¹
 Ginkgophyllum.
 Tyloxyton.
 Walchia, Voltzia, etc.
 Dadoxylon.

6. *Coniferæ*.

It would thus appear:

1. That the nearest structural affinities of the Palæozoic gymnosperms with the higher Cryptogams lead toward all the groups of Acrogens, viz.: *Sigillariæ*, *Calamiteæ*, *Lepidodendreæ* and *Ferns*.
2. That the present dominant groups of *Coniferæ* proper and *Cycadaceæ* are absent or slenderly represented in the Palæozoic.
3. That the dominant Palæozoic families are the *Næggerathiæ*, *Cordaiteæ* and *Taxineæ*, and that these occupied a prominent and important place, and culminated in the Palæozoic and early Mesozoic periods.

¹ Permian, of Russia, Schmalhausen.

4. The two former families, did they now exist, would supply connecting links between the Coniferæ and Cycadeæ, and between the latter and the Acrogens.

NOTE TO PAGE 13, SECOND PARAGRAPH.

With reference to the supposed fruit of *Tylodendron*, a comparison may also be suggested with the Eocene fossil fruits from the London clay, of the genus *Selenostrobus*, and with the modern genus *Callitris*. In these, however, the fruit presents a verticil of valves enclosing seeds, rather than of naked seeds. In the case of *Tylodendron*, however, there may have been deciduous scales. The number four appears in some species of *Callitris*. It is five in *Selenostrobus* and *Spondylostrobus*. This subject has been discussed, with reference to the Tertiary and modern fruits, by Bowerbank, Endlicher, Heer, Schimper and Von Mueller.

ADDITIONAL NOTE.

Since writing the description of *Dictyocordaites Lacoii*, I have seen Nothorst's paper on *Dictyozamites* of Oldham, a Cycadean genus with netted venation which occurs in the Mesozoic formations of Japan, India and Sweden.

