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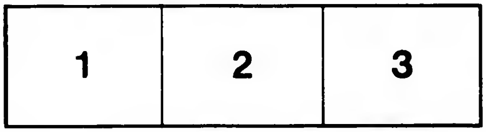
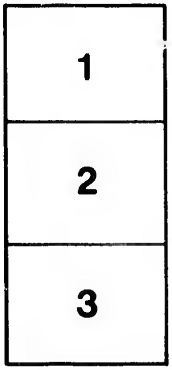
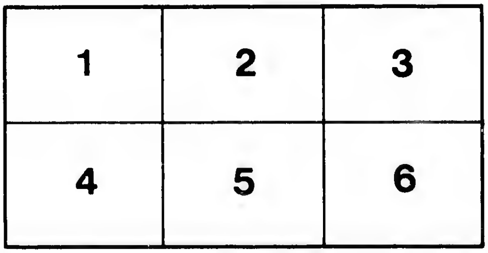






[*From the* Quarterly Journal *of the* Geological Society *for May* 1871.]

On the Structure *and* Affinities *of* Sigillaria, Calamites *and* Calamodendron. By J. W. Dawson, LL.D., F.R.S., F.G.S., Principal of McGill University.

(Read May 11, 1870*.)

[Plates VII.-X.]

1. Sigillaria.

The difficulty of arriving at a correct knowledge of the structure of these curious trees is caused principally by the unequal durability of the different parts of the stem. It arises from this that some portions have usually perished, while others were in process of mineralization, and the portions which remain have in a great degree lost their original form and arrangement. The outer bark, while extremely durable, was too impenetrable to be preserved in any other way than as compact coal. The fibres of the bark and of the woody axis are often mineralized or imperfectly preserved as mineral charcoal. The cellular portions of the bark and of the axis have usually entirely disappeared. Still, imperfectly preserved stems can be obtained in great abundance in any coal-field by those who are content to work on such unpromising material.

Probably the finest specimen of a *Sigillaria* hitherto described is that of *S. elegans*, so admirably figured by Brongniart, and which has long served to give to the student of palæobotany his ideas of the structure of the genus. Unfortunately, however, Brongniart's specimen represents a small or young stem belonging to the somewhat aberrant subgenus *Favularia*; so that it fails to give an adequate idea of the structure of the typical fossil *Sigillariæ*, which are much more common and important, at least in the coal-fields of Nova Scotia. The structure of these last, as observed in specimens obtained at the South Joggins, was, I believe, first described by me in my paper on the Vegetable Structures in Coal, published in the 'Journal' of this Society in 1859. The specimens subsequently figured in the 'Journal' of this Society, and in the 'Transactions' of the Royal Society, by Mr. Binney, under the name of *S. vascularis*, belong, in part at least, to types of structure quite distinct from that of the true *Sigillariæ*†.

My own results as to the typical *Sigillariæ* are thus shortly summed up in my paper on the "Conditions of Deposition of Coal"‡:—"In the restricted genus *Sigillaria* the ribs are strongly developed, except at the base of the stem; they are usually much

* For the discussion on this paper see Quart. Journ. Geol. Soc. vol. xxvi. p. 490.

† It would seem that the specimens figured by Mr. Binney as *Sigillaria vascularis* (Philos. Trans. vol. clv.) belong in part to the *axis* of a remarkable Sigillarioid tree, of which specimens have been kindly shown to me by Prof. Williamson, and in part (especially pl. xxxv. figs. 5 & 6) to the *whole stem* of a *Lepidodendron*. The latter plant has been described by Mr. Carruthers as *Lepidodendron selaginoides*.

‡ Quart. Journ. Geol. Soc. vol. xxii. p. 129.

broader than the oval or elliptical tripunctate areoles, and are striated longitudinally. The woody axis has both discigerous and scalariform tissues, arranged in wedges, with medullary rays as in exogens; the pith is transversely partitioned in the manner of *Sternbergia*; and the inner bark contains great quantities of long and apparently very durable fibres, which I have, in my descriptions of the structures in the coal, named 'bast-tissue.' The outer bark was usually thick, of dense and almost indestructible cellular tissue. The trunk, when old, lost its regular ribs and scars, owing to expansion, and became furrowed like that of an old exogenous tree."

It will be understood that this statement refers to the main stems of the ribbed *Sigillariæ* of the type of *S. reniformis* and *S. Brownii*, so abundant in the coal-formation of Nova Scotia, and that it is made with especial reference to the conditions of the accumulation of coal in that province. The evidence on which it is based may be stated under the following heads:—

Erect Trunks.—The numerous erect stumps of *Sigillariæ* occurring at the South Joggins, and at Sydney, Cape Breton, are usually preserved as casts in sandstone, the only part of their organic substance remaining being the outer bark, which exists in the state of compact coal. Still the interior structures have not altogether perished, but may be recognized as a layer of mineral charcoal in the bottom of the stony column, under the sand and other foreign matters subsequently introduced. Occasionally the bark of the tree has collapsed before it could be filled with sediment, and the only remains of the trunk consist of the little mound of carbonaceous matter derived from the tree itself. Cases of this kind are mentioned in my paper on the South Joggins*. In addition to the coaly matter showing structure, we can also occasionally find in the interior of such erect trees a transversely striated sandstone cast (*Sternbergia*) representing the medullary cylinder. In one instance only have I found the medullary cylinder calcified in such a manner as to show its structure, and surrounded by the woody cylinder also in a calcified state. This specimen was that described, but not adequately figured, in my paper on the Structures in Coal, and I now propose to figure it more in detail (Plate X.). Ordinarily the coaly mass consists of confused fragments of mineral charcoal derived from the wood and the fibrous tissues of the bark; but these often retain their structure very perfectly.

After collecting and examining the woody matter thus remaining in twenty or more of these erect trees, I have found that, with one exception, it consists of tissues of a uniform character, presenting only such differences as might be expected in trees generically allied. The tissues observed are discigerous or porous wood-cells with from one to four rows of pores, pseudo-scalariform tissue, and elongated structureless cells of the bark (the "bast-tissue" of my former papers). These structures indicate that the woody parts of these trees were identical in character with those of the calcified axis above mentioned.

* Quart. Journ. Geol. Soc. vol. x. p. 1.

The exception above referred to is, that in one tree, which from its markings I supposed to be a *Sigillaria*, the woody tissue was composed of large cells, with many rows of pores ("multiporous tissue" of my former papers) of the type of that to which Prof. Williamson has given the name of *Dictyoxylon**. Since, however, as Prof. Williamson has well shown, such tissue may be regarded as a modification of the discigerous variety, and since Corda long ago found it in the axis of a species of *Stigmaria*†, there is nothing improbable in the supposition that we have here merely an indication of a specific or subgeneric difference coming within the limits of the genus *Sigillaria*, as at present understood.

It is to be observed that most of the erect trunks in the coal-formation have not preserved their external markings with sufficient distinctness to allow the species to be determined by the leaf-scars; but they show in most cases the characteristic ribs and rows of punctures or areoles, modified in the manner which is usual in the case of old trunks of these plants near their bases‡.

In Plate VIII. figs. 12, 14, 15, 16, I have represented some of the more usual forms of tissue in the erect *Sigillariæ*.

In Plate X. I have represented the best-preserved axis in my possession. Fig. 23 shows the structures in the entire stem, except the portions of cellular bark lost by decay. In the centre is a *Sternbergia*-pith (*a*). This is surrounded by a woody cylinder (*b*), the inner part of which (fig. 24, *b* 1) consists of scalariform tissue passing towards the outer surface into pseudo-scalariform (*b* 2), reticulated with pores (*b* 3), and discigerous (*b* 4). This woody axis has medullary rays (figs. 25, 26, 27), and is traversed by bundles of scalariform tissue proceeding from the inner part of the cylinder. The outer portion of the inner bark, not seen in this specimen, but in similar prostrate stems, is composed of elongated thin-walled bast-cells, with somewhat obtuse ends, and of larger diameter than the woody fibres of the axis (fig. 29). The tissues of the woody axis are all arranged in radial series (fig. 28).

Prostrate Trunks.—In the coarse shaly coals, and in the roof-shales of the ordinary seams, there are often flattened stems of *Sigillaria*, having the tissues partially infiltrated with carbonate of lime or carbonate and sulphate of iron. The tissues usually preserved in these flattened trunks are those of the bark, and more especially its large bundles of elongated or prosenchymatous cells ("bast-tissue"). Of this I have been enabled to obtain very perfect specimens from these flattened trunks. In a few instances only the woody structure of the axis remains, showing the same descriptions of wood-cells already referred to as characteristic of the erect trees. Plate VIII. fig. 11 is an example of the structures in one of these prostrate stems.

* Trans. Royal Micro. Soc., Aug. 1869.

† Beiträge zur Flora &c. 1845, pl. xiii. Corda regards this as the structure of *S. ficoides*, and the more ordinary variety as that of *S. ana hra*.

‡ The species which I have described as *S. Brownii*, Acad. Geol. 2nd edition, may be regarded as a representative of these trees.

Sternbergiæ.—The fine specimen of the axis of an erect *Sigillaria* already referred to shows that the pith of these trees was of that transversely laminated character which gives rise to the fossils known as *Sternbergiæ.* Hence we may suppose that some at least of the numerous casts of *Sternbergiæ* found in the Coal-formation have been derived from *Sigillariæ*; but this can be ascertained only by a careful microscopic examination of the remains of woody matter clinging to the casts. The results of the study of a considerable number of specimens may be stated as follows:—

(*a*) As Prof. Williamson and the writer have shown, some of these *Sternbergia*-piths belong to coniferous trees of the genus *Dadoxylon.* Plate VII. fig. 1 represents a beautifully preserved cylinder of this kind enclosed in the wood of *Dadoxylon materiarum.*

(*b*) A few specimens present multiporous tissue, of the type of *Dictyoxylon*, which, according to Williamson, has a *Sternbergia*-pith. Plate VII. fig. 4 affords an instance of this.

(*c*) Other examples show a true scalariform tissue, comparable with that of *Lepidophloios* or *Lepidodendron*, but of finer texture. Corda has shown that plants of the type of the former genus (his *Lomatophloios*) had *Sternbergia*-piths. Some plants of this group are by external characters loosely reckoned by botanists as ribless *Sigillariæ* (*Clathraria*); but I believe that they are not related even ordinally to that genus. Plate VII. fig. 5 represents a *Sternbergia*, with tissue partly reticulated and partly scalariform. Plate VIII. fig. 7 represents a specimen with true scalariform tissue. Plate VII. fig. 6 is a scalariform vessel of *Lepidophloios* drawn to the same scale for comparison. It will be seen that it is of much coarser texture.

(*d*). The majority of carboniferous *Sternbergiæ* show structures identical with those described above as occurring in erect *Sigillariæ.* Such *Sternbergiæ* and their structures are represented in Plate VII. figs. 2 and 3, and Plate VIII. figs. 8, 9, 13. Fig. 8 is a reduced section of a large flattened tree, apparently a *Sigillaria* with *Sternbergia*-pith (fig. 9), of great beauty, and not dissimilar from those sometimes found in the erect *Sigillariæ.* The tissue enclosing it was unfortunately imperfectly preserved, but had three rows of pores (fig. 9 *a*).

Structures in Coal.—The constant association of *Sigillaria* with the beds of coal, in the underclays, in the roof-shales, and in the coal itself, is too well known to require any detailed reference; and the inevitable conclusion that the *Sigillariæ* were the principal plants concerned in the accumulation of the mineral fuel of the true coal-measures is generally accepted by geologists. It would naturally follow from this that tissues of *Sigillaria* should be more abundant in the coal than those of other plants. Accordingly, as I have shown in my paper on the "Structures in Coal," and on the "Conditions of Coal-deposition," tissues similar to those above described are those which actually occur most abundantly in the mineral charcoal of the coal-seams. That of the liber or fibrous bark is perhaps the most abundant of all, and that of the woody axis the next in frequency of occurrence.

It has been held to be an objection to the identification of the discigerous tissues above mentioned with those of *Sigillaria*, that the *Stigmariæ*, when their structure happens to be preserved, show merely scalariform tissue. To this it may be answered:—(1.) That, as Corda has shown*, some *Stigmariæ* have reticulated or multiporous tissues. (2.) The tissue of *Stigmaria* is not essentially different from the pseudo-scalariform fibres of the stem, and is arranged in a similar manner, showing that it is homologous rather with woody than with vascular tissue. (3.) Many *Stigmariæ* probably belong to *Favularia* and similar forms, or possibly even to Lepidodendroid plants†. In either case the structure would be unlike that of the stems of *Sigillaria* proper. (4.) Inasmuch as the proportions of pseudo-vascular and discigerous tissue may differ greatly in the stems of *Sigillariæ*, it would not be unreasonable to suppose that the tissue, which is more particularly important for the strengthening of the stem, should be absent, or in a feeble state of development, in the root. Something of this kind occurs in the roots of Cycads, and perhaps, if detailed examinations were made, might be found to be more general than is commonly supposed. (5.) The outer part of the axis, being left exposed by the decay of the loose cellular matter of the inner bark, may, in most cases, have perished. In my specimen of the axis of *Sigillaria*, above described, it is in parts much disorganized, and has disappeared, or been converted into coal, on one side.

The evidence included under the above heads is sufficient to show that the ordinary ribbed *Sigillariæ* referred to in my previous papers, possessed in their main trunks the following kinds of tissue, in proceeding from the circumference to the centre:—

(*a*) A dense cellular outer bark, usually in the state of compact coal—but when its structure is preserved, showing a tissue of thickened parenchymatous cells.

(*b*) A very thick inner bark, which has usually in great part perished, or been converted into coal, but which, in old trunks, contained a large quantity of prosenchymatous tissue, very tough and of great durability. This "bast-tissue" is comparable with that of the inner bark of modern Conifers, and constitutes much of the mineral charcoal of the coal-seams.

(*c*) An outer ligneous cylinder, composed of wood-cells, either with a single row of large bordered pores‡, in the manner of Pines

* Beiträge zur Flora der Vorwelt.

† Brown, in 1847, described, in the 'Proceedings' of this Society, Stigmaria-roots of *Lepidodendron*. Baily seems to have shown that such roots belong to the singular Lepidodendroid *Cyclostigma* of the Devonian of Ireland; and Schimper asserts a connexion of Stigmaria roots with trees which he refers to *Knorria*.

‡ These are the same with the wood-cells elsewhere called discigerous tissue, and to which I have applied the terms uniporous and multiporous. The markings on the walls are caused by an unlined portion of the cell-wall placed in a disk or depression, and this often surrounded by an hexagonal rim of thickened wall; but in all cases these structures are less pronounced than in *Dadoxylon*, and less regular in the walls of the same cell, as well as in different layers of the tissues of the axis.

and Cycads, or with two, three, or four rows of such pores sometimes inscribed in hexagonal areoles in the manner of *Dadoxylon*. This woody cylinder is traversed by medullary rays, which are short, and composed of few rows of cells superimposed. It is also traversed by oblique radiating bundles of pseudo-scalariform tissue proceeding to the leaves. In some *Sigillariæ* this outer cylinder was itself in part composed of pseudo-scalariform tissue, as in Brongniart's specimen of *S. elegans*; and in others its place may have been taken by multiporous tissue, as in a case above referred to; but I have no reason to believe that either of these variations occurred in the typical ribbed species now in question. The woody fibres of the outer cylinder may be distinguished most readily from those of Conifers, as already mentioned, by the thinness of their walls, and the more irregular distribution of the pores. Additional characters are furnished by the medullary rays and the radiating bundles of scalariform tissue when these can be observed.

(*d*) An inner cylinder of pseudo-scalariform tissue. I have adopted the term pseudo-scalariform for this tissue, from the conviction that it is not homologous with the scalariform ducts of Ferns and other Acrogens, but that is merely a modification of the discigerous wood-cells, with pores elongated transversely, and sometimes separated by thickened bars, corresponding to the hexagonal areolation of the ordinary wood-cells. A similar tissue exists in Cycads, and is a substitute for the spiral vessels existing in ordinary Exogens.

(*e*) A large medulla, or pith, consisting of a hollow cylinder of cellular tissue, from which proceed numerous thin diaphragms toward the centre of the stem.

The structures above referred to may undoubtedly exist in different proportions in different species, and also in the same species in different parts, and at different stages of growth. In the woody axis more particularly, there is evidence that in such forms as *S.* (*Favularia*) *elegans*, the scalariform, or pseudo-scalariform, tissues were predominant. In young stems also, and in roots, this would probably be the case; and in the latter the texture was much coarser than in the stem; and, further, Prof. Williamson has shown me specimens from the Lancashire coal-field, which I have no doubt are Sigillarioid trees of the type of *S. vascularis* of Binney, and which, instead of a *Sternbergia* pith, have scalariform cells and vessels in the centre, and in which the bundles of scalariform vessels traversing the wood are included in considerable masses of cellular tissue, elongated vertically, like medullary rays. This plant presents external markings of the *Clathraria*-type. Mr. Carruthers has also shown me a specimen ribbed externally, and apparently a *Sigillaria* or *Syringodendron*, which shows only a cylinder of large scalariform fibres similar to those of *Stigmaria*. These facts show how wide differences may exist in the structures of stems referred by their superficial markings to *Sigillaria*.

In the case of specimens showing structure merely, it will undoubtedly require much further investigation to enable us always to distinguish the structures characteristic of the subgenera of *Sigillaria*, or absolutely to separate these from those of certain peculiar conifers on the one hand and from those of the higher acrogens on the other. Young and succulent stems of *Dadoxylon* may have much resembled *Sigillaria* in their structure. Young stems of *Sigillaria* proper may have approached closely to those of *Favularia*; and since I have shown* that the branches of *Favularia* resemble *Clathraria* in their scars, this last may have presented a still feebler type of internal organization. Further, there is, as I have already stated, reason to believe that some of the species referred by palæobotanists to the *Clathraria*-division are really forms of *Lepidophloios*. These difficulties, in connexion with the defective state of preservation of specimens, may excuse many differences of opinion, though I think the facts already stated in this paper are sufficient to put all students of the subject on the right track in regard to at least one leading type of these plants, and to remove some of the more fruitful sources of error.

We may now proceed to inquire what light the structures of *Sigillaria* throw on its affinities. On this question, taken in its most general aspect, there have, I believe, in modern times been only two opinions, the views as to alliance with *Euphorbiæ* and *Cacti* held by some older botanists having been given up. Some botanists, conspicuous among whom is Brongniart, hold that *Sigillariæ* were gymnospermous plants, allied to Cycadaceæ. Others are disposed to regard them as acrogens, and as closely related to Lycopodiaceæ.

In favour of the latter view may be urged the apparent association with *Sigillaria* of certain strobiles resembling those of *Lepidophloios*, the points of resemblance between the tissues of *Favularia elegans* and those of *Lepidodendron*, and the resemblance of certain *Sigillariæ*, or supposed *Sigillariæ*, of the *Clathraria*-type to *Lepidophloios*.

In favour of the former view, we may adduce the exogenous structure of the stem of *Sigillaria*, and the obvious affinity of its tissues to those of Conifers and Cycads, as well as the constant association with trees of this genus of the evidently phanerogamous fruits known as *Trigonocarpum* and *Cardiocarpum*. On the other hand, the resemblance to *Lepidodendron* may be shown to depend merely on comparisons of a part of the tissues of *Sigillaria* with those of that genus. Grave doubts may also be entertained as to whether strobiles of *Lepidophloios*, and even stems of that genus have not been improperly mixed up with *Sigillaria*.

It is probable that all botanists who have studied these plants, might agree that, if not Gymnosperms, they at least present points of affinity with them, and might be regarded as in some sense a link connecting them with Acrogens. Supposing this much to be admitted, important questions remain as to their possible relations to the modern Conifers and Cycads. The higher *Sigillariæ* unquestion-

* "Conditions of Deposition of Coal," Quart. Journ. Geol. Soc. vol. xxii. p. 130.

ably resemble Cycads in the structure of their stems. Their long rigid narrow leaves may be compared to single pinnæ of the leaves of Cycads. Their cord-like rootlets, as I have ascertained by actual comparison, are similar to those of Cycads. If their fruit was of the nature of *Cardiocarpum* or *Trigonocarpum*, this also would correspond. They differed principally in the division of the stem below into those remarkable underground branches, the *Stigmariæ*, and in the great upward extension and, in some instances at least, ramification of the stem. The former may be regarded as a special modification connected with their peculiar habitat. The latter may be interpreted as a modification either tending backward to the Lycopodiaceæ or forward to the Coniferæ. Since, so far as we at present know, the ramification prevails chiefly in the lower forms, the former may be the more correct view. It is even possible that the *Sigillariæ* may include forms bridging over the space between the higher Acrogens and the Gymnosperms. Viewed in this way, the typical ribbed *Sigillariæ* point downwards through *Calamodendron* and *Calamites* to the Equisetaceæ, and the *Favularia*- and *Clathraria*-types point through *Lepidophloios* and *Lepidodendron* to Lycopodiaceæ. In the upward direction their affinities point both towards Conifers and Cycads. As our knowledge of the structure of individual species of *Sigillaria* increases, we may hope more certainly to trace the links of these affinities. It is, however, to be observed here, by way of caution, (1) that, of the plants reckoned among the several genera or subgenera of *Sigillariæ*, some may eventually prove to be gymnospermous and some cryptogamous, and (2) that, as we shall find in the next group to have been actually the case, some of these plants may, with a cryptogamous fructification, have presented a structure of stem more complex than that found in modern plants of similar grade.

2. Calamodendron and Calamites.

Calamites are among the most abundant fossils of the Carboniferous period, and occur also in the Devonian; and from their peculiar habitat and mode of growth, they are not only preserved as flattened stems, but also occur in immense numbers standing on the beds on which they grew.

They have naturally been regarded from the first as allied to Equisetaceæ; and this opinion is ably and, indeed, conclusively maintained by Schimper in his recent work*, and has been illustrated by the recent description of the fruit by Mr. Carruthers. Difficulties have, however, arisen from the fact that some stems regarded as Calamites have been found to be surrounded by a thick woody cylinder composed of discigerous and pseudo-scalariform tissue, similar to that of the type of *Sigillaria* above described. Some botanists have regarded these last as distinct from the true *Calamites*, and have placed them in the genus *Calamitea*, Cotta, or *Calamodendron*, Brongniart; and Williamson has recently proposed

* Paléontologie Végétale.

the name *Calamopitus** for a group believed to be intermediate between *Calamodendron* and true *Calamites*. On still other grounds, *Bornia* and other genera or subgenera have been separated from *Calamites* proper. Latterly Schimper has endeavoured to combine the view of the Equisetaceous affinities and annual growth of the stems of *Calamites* with what, at first sight, seems the totally irreconcilable woody character of the stem of *Calamodendron* as described by Cotta, Dawes, and Binney.

In all my own publications on this subject, from the date of my first paper on *Calamites* published in the Journal of this Society†, I have held that Calamites proper are Equisetaceous plants, having the external characters of their stems preserved, and that in the last respect they differ from the internal casts which belong to *Calamodendron*. All my subsequent observations have served to confirm these conclusions, which I would now illustrate by the following considerations.

1. The true *Calamites* (e. g. *C. Suckovii*, *C. cannæformis*, *C. Cistii*, &c.), when well preserved, present, externally, somewhat flat smooth striated ribs, with distinct nodes, and having, at the upper end of each rib, a rounded areole with a central dot or scar, marking the disarticulation of a leaf, branchlet, or root, or, in some cases, the extremity of one of those radial prolongations of the pith which have been described by Williamson. In one specimen in my possession there is a double set of marks—smaller ones on the node, apparently belonging to the appendages, and larger marks below the node, which may represent the radial prolongations of the pith (Pl. X. fig. 22). The cortical investment is very thin and dense, and presents externally the characters of an epidermis, not showing, as in the case of *Sternbergia* or *Calamodendron*, a coating of woody fibres externally, and therefore cannot be regarded as a mere medullary sheath or, as Schimper supposes, the membrane lining the hollow interior of the stem. I may remark here, that erect Calamites are sometimes surrounded by a calcareous or ferruginous concretionary coating which must not be confounded with the true surface of the stem.

2. The ordinary Calamites are seen to stand erect, rooted *in situ*, and attached together at the bases, or arising from rhizomata. The stems can be seen to bud from each other; and the roots can be traced proceeding from their bases and lower nodes. Figures of erect specimens were given in my paper on Erect Calamites, and also in that on the South Joggins‡. Abundant specimens may be obtained in the magnificent petrified Calamite brakes at the last-mentioned locality, and, I venture to say, cannot be studied by any geologist without producing the conviction that the erect cylindrical casts imbedded in groups in the sandstone must represent the true external form of the plant. I have also shown, in the paper above cited, that these erect stems are crushed by lateral pressure, and broken down

* Preoccupied by Unger for certain Devonian plants.

† On the Occurrence of Upright Calamites near Pictou, Nova Scotia, Quart. Journ. Geol. Soc. vol. vii. p. 194.

‡ Quart. Journ. Geol. Soc. vol. vii. p. 194, and vol. x. p. 1.

and flattened at the top, exactly as somewhat strong fistulous stems would be. It is obviously impossible that casts of medullary cavities could be preserved in this manner. Neither *Sternbergiæ* nor casts of the pith of *Calamodendra* ever occur under such circumstances.

3. The stems of *Calamites* may be seen to have produced leaves and branchlets in such a manner as to prove that they are complete stems preserving their external surface. In my paper on the South Joggins, I figured and described the leaves of *C. Cistii* as seen attached to the erect stems. I have since, in 'Acadian Geology,' figured those of *C. Suckovii*, found under similar circumstances; and I have specimens which appear to me to verify the figure given by Lindley and Hutton of the leaves of *C. nodosus*. I have also obtained beautifully preserved specimens of the leaves of *C. transitionis*, a species common to the Devonian and Lower Carboniferous. It has been supposed that the scars on the nodes of *Calamites* are merely the marks of bundles of vessels passing from the interior towards the surface; but it is obvious that, in the case of stems actually producing leaves and branchlets, this cannot be the true explanation, though after seeing the very instructive slices of Prof. Williamson's *Calamopitus*, kindly shown to me by him, I am prepared to admit that in some specimens, at least, they may represent the "medullary radii," which, as already stated, sometimes appear *in addition to* the true vascular scars.

4. The leaves of *Calamites* were not, as is often stated, identical with those of *Asterophyllites*; and the genus *Calamocladus*, in which Schimper has placed many plants of the latter genus, is therefore altogether unnecessary. A careful microscopic examination of the leaves which I have found attached to Calamites convinces me that they have distinct characters, and affords an additional link of connexion with Equisetaceæ. The leaves of *Asterophyllites* proper are flat, expanded in the middle, and with a distict midrib. Those of *Calamites* are strictly linear, thick, and angled, and are besides marked with transverse lines or striæ. Similar transverse lines occur on the branchlets of some modern *Equiseta*, and are produced by lines of minute stomata. Well-preserved specimens of Calamite-leaves have precisely the same appearance, so that they may be compared to branchlets of *Equiseta* deprived of their sheath. Flattened leaves of *Calamites*, it is true, sometimes present the appearance of a midrib; but this arises either from the prominence of the upper angle, or the appearance of an internal axis through the substance of the leaf. Unless very badly preserved, they can always be distinguished from *Asterophyllites* or *Annularia*. The connexion supposed, by Ettingshausen and others, to obtain between *Calamites* and *Asterophyllites* has arisen either from accidental association, or from failure to distinguish leaves and stems of *Calamites* from the corresponding parts of *Asterophyllites**. The conjecture of Brongniart that some, at least, of the *Asterophyllites* may be leaves, not of

* The species *Asterophyllites comosus*, L. v. H., appears to consist of, or to include, leaves of *Calamites*; and there is reason to doubt whether the proper *Asterophyllites* should be separated from *Annularia*.

Calamites, but of *Calamodendron*, rests on different grounds, and is supported by the fact that some of the larger stems which may be supposed to represent the external surface of *Calamodendron*, have tumid nodes similar to those of the branches of *Asterophyllites*. Stems of this kind are sometimes found in an erect position in the Coal-measures of Nova Scotia, and are manifestly distinct from those of ordinary Calamites.

5. The microscopic structure of *Calamites* is not precisely identical with that of *Calamodendron*, though the latter may be regarded as a more advanced type of the former. The Calamites have a thin outer coat with lacunæ, or air-cells, like those of modern *Equiseta*; and the tissue intervening between these contains large vasiform tubes marked on the surface with numerous rows of small pores ("multiporous tissue" of my papers on the Structures in Coal, &c.), and which bear some resemblance to the fibres of *Dictyoxylon* as described by Williamson (Pl. IX. fig. 19). This structure has been illustrated by Goeppert, Unger, Schimper, and others; and I have verified it by the microscopic examination of numerous flattened Calamite-stems in the shales and coarse coals. Facts of this kind kind were mentioned in my paper on the 'Structures in Coal.'

The *Calamodendra*, on the other hand, are casts of the medullary cavities of stems having a thick woody envelope disposed in wedges separated by intervening tracts of cellular tissue, which, according to Williamson, are of the nature of large medullary rays, while smaller medullary rays occur in the intervening wedges, and presenting the same discigerous and pseudo-scalariform tissues observed in *Sigillaria*. I have represented in Plate IX. two forms of *Calamodendron* with the tissues found attached to them. These stems, no doubt, have lacunæ like those of Calamites, and resemble them in general arrangement of parts, but differ in the much greater development of the woody tissue, and, in some species at least, in the character of this tissue.

6. The fructification of Calamites I have not found in connexion with the stems. I have no doubt, however, that some of the spikes of fructification described by authors as the fruit of *Calamites*, really belong to these plants. There has, however, been some confusion between the fruit of *Calamites* and *Asterophyllites*, which demands attention from those who have access to the specimens.

It results from the facts above stated that the true equisetaceous Calamites are well known to us by their external forms, habit of growth, and foliage, as well as by their internal structure; and on all these grounds no reasonable doubt can be entertained as to their affinities. Whether, as Schimper supposes, they were merely annual stems like those of modern *Equiseta*, admits of more doubt. In the equable climate of the Coal-period such stems may have continued growing from year to year. Nor do I think that their rhizomata were relatively so important as those of *Equiseta*. In some of the species, at least, the erect stem itself, fortified by adventitious roots, and partly buried by increasing deposits of sediment, seems to have served the purpose of a rhizoma*. The best example that I have seen of the rhizoma of a Calamite is that figured in Plate IX. (fig. 21), from a specimen presented by me to the Geological Society many years ago.

With regard to *Calamodendron* the difficulties are greater, and have been well stated by Prof. Williamson in a recent paper in the 'Memoirs of the Literary and Philosophical Society of Manchester'†, in which he describes under the generic name *Calamopitus* a peculiar stem, which, while he identifies it in its general characters with *Calamites*, he justly regards as being in internal structure distinct from the *Calamodendra* described by Cotta and Binney.

The characters of *Calamodendron* as distinguished from ordinary *Calamites* may be summed up as follows:—

(*a*) The part usually preserved is the internal axis, corresponding to a *Sternbergia*. It presents ribs similar to those of *Calamites*, but more angular, and almost always having traces of woody fibres capable of showing the structure on some part of their surface. I have not seen on these casts any distinct traces of scars or areoles. These casts of the pith of *Calamodendron* constitute the greater part, if not the whole of the specimens referred to *C. approximatus*.

(*b*) More complete specimens are invested with woody matter, arranged in wedges, and consisting of elongated cells and porous, discigerous, or pseudo-scalariform tissue. My specimens do not show distinctly the arrangement of these; but this has been well described by other observers. Williamson describes medullary rays in the woody bundles in addition to the large cellular tracts intervening between them.

(*c*) The actual external surface of *Calamodendron* is not certainly known; but I have been disposed to regard as of this kind those ribbed stems, found in the coal-formation, which have swollen nodes as if caused by the emission of whorls of small branches. I have specimens of these in my collection, which I have hesitated to name or describe until they could be better understood. Prof. Williamson's description of *Calamopitus* now inclines me to suppose that they belong to that genus or to allied forms.

With regard to the affinities of the *Calamodendra*, the structure of the stem raises them above the Calamites and modern *Equiseta*, and justifies the conjecture of Brongniart that they may have been gymnosperms. Williamson, Carruthers, and Binney, however, attribute to them a cryptogamous fructification. In this case they may, as the former suggests, be a connecting link between Acrogens and Gymnosperms. Should subsequent investigations confirm this view, it will throw an interesting light on the possible affinities of *Sigillaria*. *Calamites*, on the one hand, and *Lepidodendron* on the other, are distinctly cryptogamous and are related to, or included in, the modern families of Equisetaceæ and Lycopodiaceæ. But *Calamodendron* seems to form a connecting link between *Calamites* and the ribbed *Sigillariæ*; and in like manner *Lepidophloios* seems to connect the

* See my description in Quart. Journ. Geol. Soc. vol. x.
† Vol. iv. 3rd Series.

Lepidodendra with the *Sigillariæ* of the *Favularia*-type. On the other hand, as already stated under *Sigillaria*, the ribbed *Sigillariæ* may be related through *Ormoxylon* and *Dadoxylon* to the modern Conifers, and the *Favulariæ* may be related to the Cycads. This relationship may be expressed as follows:—

Cycadaceæ.   *Coniferæ.*
Dadoxylon.
Favularia?   Palæoxylon.
Ormoxylon †.
Dictyoxylon.

SIGILLARIA.

Rhytidolepis.   Calamodendron.
Favularia?   Calamopitus.
Clathraria.   Bornia.
Syringodendron.   Calamites.
Lepidophloios.   *Equisetaceæ.*
Lepidodendron*.
Lycopodiaceæ.

I do not give this Table with any view to theories of derivation, but merely as an expression of probable affinities among these very curious and ancient types of vegetation.

I may add here a few words with reference to *Sphenophyllum*, a genus which some authors unite with *Calamites*. The verticillate, cuneate, veiny leaves of this plant, and its spikes of fructification have long been known; and in 1865 I was enabled by a specimen in the collection of Sir W. E. Logan to determine the structure of its stem, which contains a slender axis of reticulato-scalariform vessels of the type of those in *Tmesipteris*‡. These plants obviously had no connexion with *Calamites* or *Calamodendron*, but constitute a peculiar synthetic type, presenting points of resemblance to Ferns and Marsiliaceæ.

In conclusion, and with reference to my former papers on the "Structures in Coal," I would repeat the statement made in those papers, that the tissues of *Sigillaria*, as defined in this paper, and of *Calamodendron* enter more largely than any others into the composition of the mineral charcoal, and other parts retaining structure, of the coal of Nova Scotia; and I have reason to believe that similar tissues are at least very abundant in the coal of this country.

Supplementary Note.—Owing to the delay in the publication of the above paper, it is necessary to add the following statements:—

(1) Prof. Williamson has described another type of Calamitean stem, which he regards as intermediate between his *Calamopitus* and *Calamodendron* §, but which has the *reticulated* or *multiporous* vessels of the former. To Prof. Williamson is due the credit of recognizing this structure for the first time in English specimens, though, as above

* Including *Sagenaria*. † Dawson, MS.

‡ Quart. Journ. Geol. Society, May 1866.

§ Manchester Lit. and Phil. Soc. Proceedings, 1870.

stated, it had previously been well known elsewhere. I regard these plants, so well described by Williamson, as true *Calamites*, in the sense in which that word is used above.

(2) The same palæobotanist has independently expressed the belief above stated, that the leaves of *Calamites* are distinct from those of *Asterophyllites*, and has also stated a distinction between those so-called *Volkmanniæ* which may be regarded as fruits of *Calamites* and those which belonged to *Asterophyllites* *. He has also described a specimen of *Stigmaria* showing the medullary rays, and otherwise approaching to the structures which should be found in the roots of the typical *Sigillariæ* above described.

(3) Schimper, in his 'Paléontologie Végétale,' vol. xi., has treated the *Sigillariæ* very slightly. He adds no new facts of importance to their history, does not separate them from the plants of the genus *Lepidophloios*, usually mixed with them, refers the whole to one genus, and places them with the Lycopodiaceæ.

(4) Binney, in the Palæontographical Society's Publications, vol. xxiv., has described, under the name of *Bowmanites cambrensis*, a very interesting plant, which I regard as a typical member of the group *Asterophylliteæ*, as distinguished from *Calamiteæ*.

(5) Attention having been directed by Prof. Huxley to the presence of *spore-cases* in Coal, I have endeavoured to show, in a paper in the 'American Journal of Science' for April, that these bodies are not a large constituent of ordinary Coal, and that any importance which they possess in this respect is due to their identity in chemical composition with those *cortical* and *epidermal* tissues which, like the *suberin* of cork, are more nearly allied in composition to Coal than any other recent vegetable matters, and better fitted, by their chemical and mechanical properties, for its production.

EXPLANATION OF THE PLATES.

Plate VII.

Fig. 1. *Sternbergia*, pith of *Dadoxylon*; 1 *a*, section of one side, showing diaphragms; 1 *b*, section of a diaphragm and three wood-cells, magnified; 1 *c*, two wood-cells, highly magnified, showing reticulated walls.

2. *Sternbergia*, pith of *Sigillaria*, natural size; 2 *a*, 2 *b*, discigerous tissue investing the same.

3. *Sternbergia*, pith of *Sigillaria*, natural size; 3 *a*, discigerous and scalariform tissue.

4. *Sternbergia*, natural size; 4 *a*, reticulato-scalariform tissue.

5. *Sternbergia*, natural size; 5 *a*, 5 *b*, scalariform and reticulato-scalariform tissue.

6. Scalariform vessel of *Lepidophloios*.

Plate VIII.

Fig. 7. *Sternbergia*, of Lepidodendroid tree?, natural size; 7 *a*, scalariform tissue.

8. Section of a flattened stem (*Sigillaria*?) 1 foot in diameter, converted into coal, with *Sternbergia*-pith.

* Manchester Lit. and Phil. Soc. Proceedings, Feb. 1871.

Fig. 9. *Sternbergia*, pith of the same, natural size; 9 *a*, discigerous tissue of the same.

10. Another stem, probably Coniferous, with *Sternbergia* pith.

11. Woody tissue of prostrate *Sigillaria*: 11 *a*, bast-tissue of the same.

12. Woody tissue of a *Sigillaria*; 12 *a*, medullary ray.

13. Tissue of a *Sternbergia* similar to fig. 9.

14, 15, 16. Discigerous tissue of erect trees (*Sigillariæ*) in mineral charcoal.

PLATE IX.

Fig. 17. *Calamodendron approximatum*, cast of pith; 17 *a*, 17 *b*, discigerous and scalariform tissue of the same.

18. *Calamodendron* invested with woody tissue: A, pith; B, woody cylinder; 18 *a*, cross section; 18 *b*, cross section, magnified, showing compression of the tissue; 18 *c*, discigerous and pseudo-scalariform tissue of the same.

19. Portion of a multiporous vessel of a true *Calamites*, magnified to the same scale with figs. 17 *a* & 17 *b*.

20. Stem of erect *Calamodendron* (S. Joggins, Nova Scotia), showing its external surface, one-third nat. size.

21. Base of stem of *Calamites* (S. Joggins), showing rhizoma, reduced.

22. Node of *Calamites*, showing scars of verticillate branchlets and of radial processes.

PLATE X.

Fig. 23. Radial section of stem of *Sigillaria* of the type of *S. Brownii*, Dawson, restored, natural size: *a*, pith; *b*, woody cylinder; *c*, cellular inner bark; *d*, fibrous bark; *e*, outer cortical layer.

24. Radial section of the woody cylinder, magnified (letters as above); and portions of the tissues more highly magnified below: *b* 1, inner pseudo-scalariform cylinder; *b* 2, 3, 4, discigerous outer cylinder.

25. Radial section, more highly magnified, showing one of the radiating bundles of vessels (this section has been inverted); 25 *a*, single pseudo-scalariform vessel from radiating bundle.

26. Tangential section of the same stem, showing the woody fibres and one of the radial bundles, and the medullary rays.

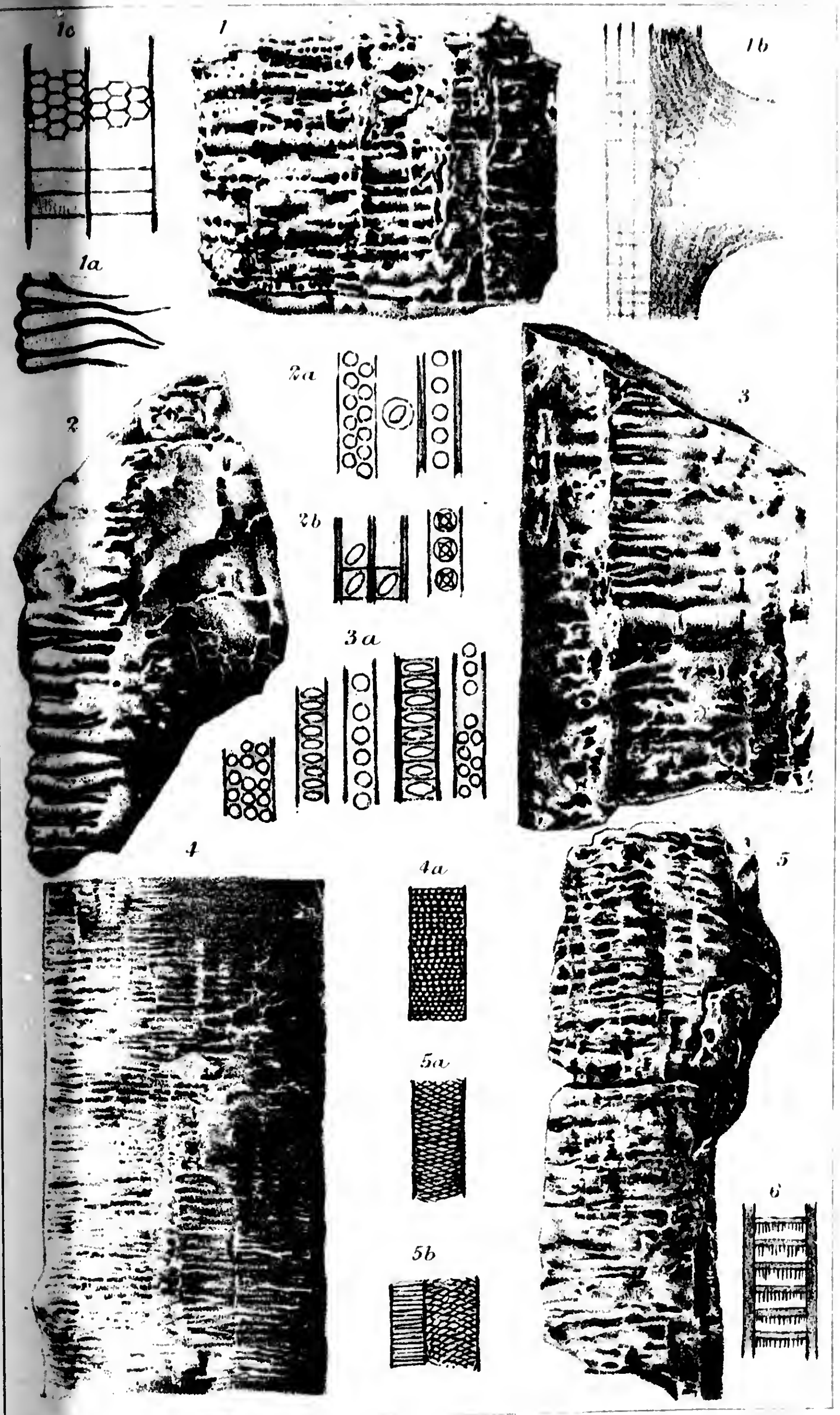
27. Tangential section showing woody fibres and medullary rays, more highly magnified.

28. Radial arrangement of woody fibres, magnified.

29. Fibres or elongated cells of the bark (*d*).

Note.—All the drawings of *separate fibres and vessels* in the above figures are on one scale.

W.G.Smi



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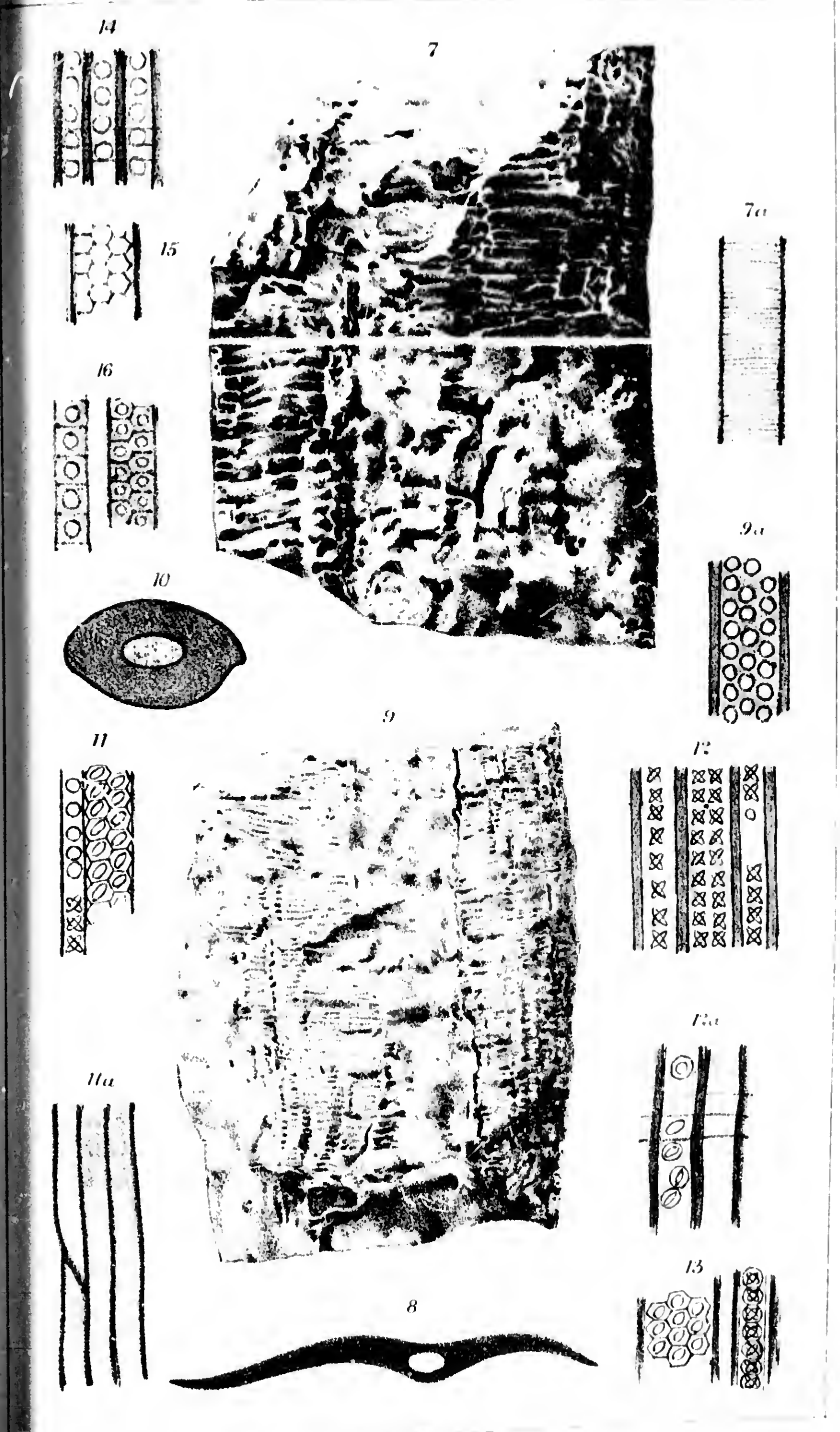

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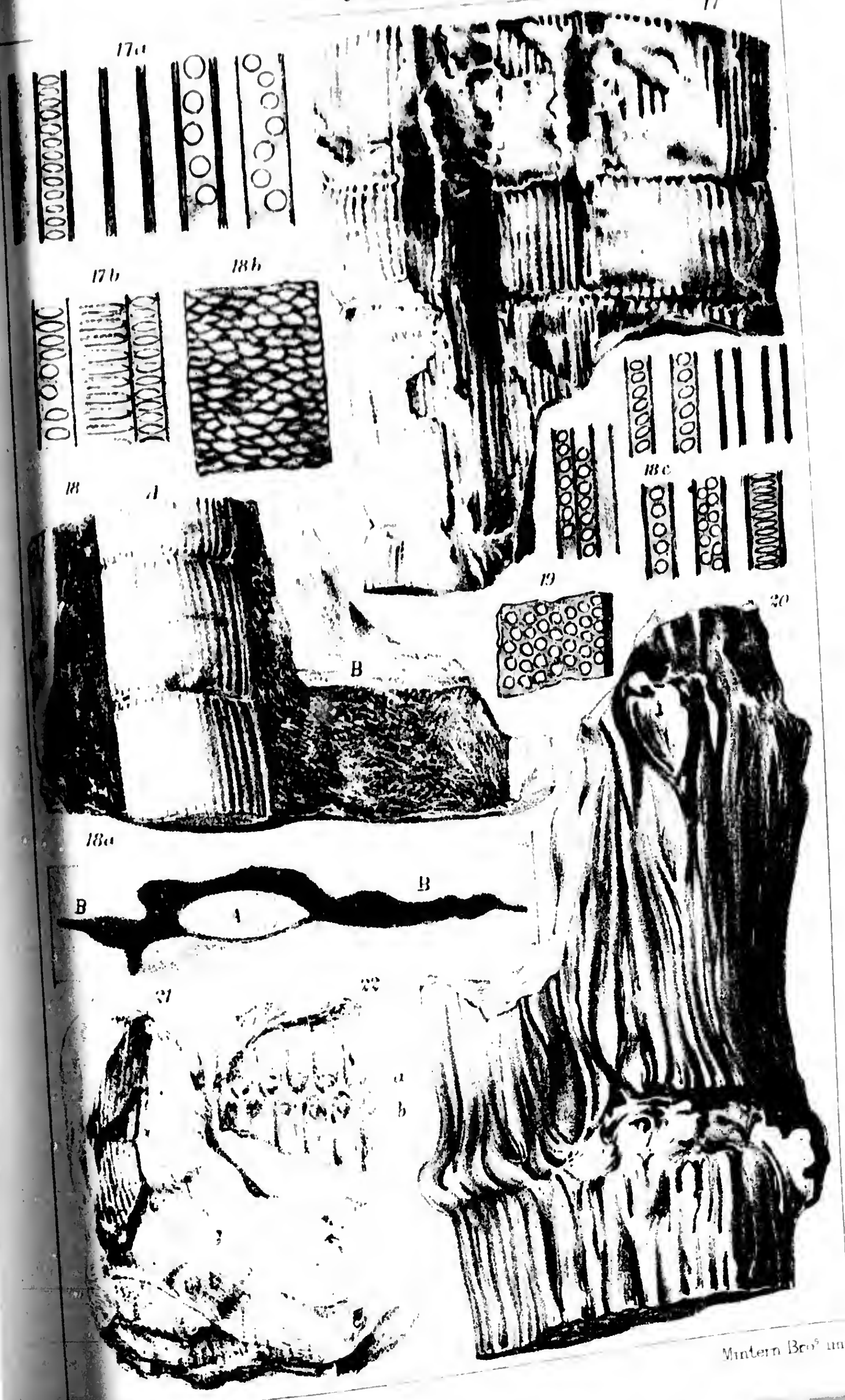

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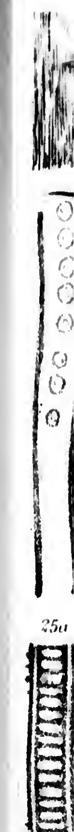
CALAMODENDRON & CALAMITES.



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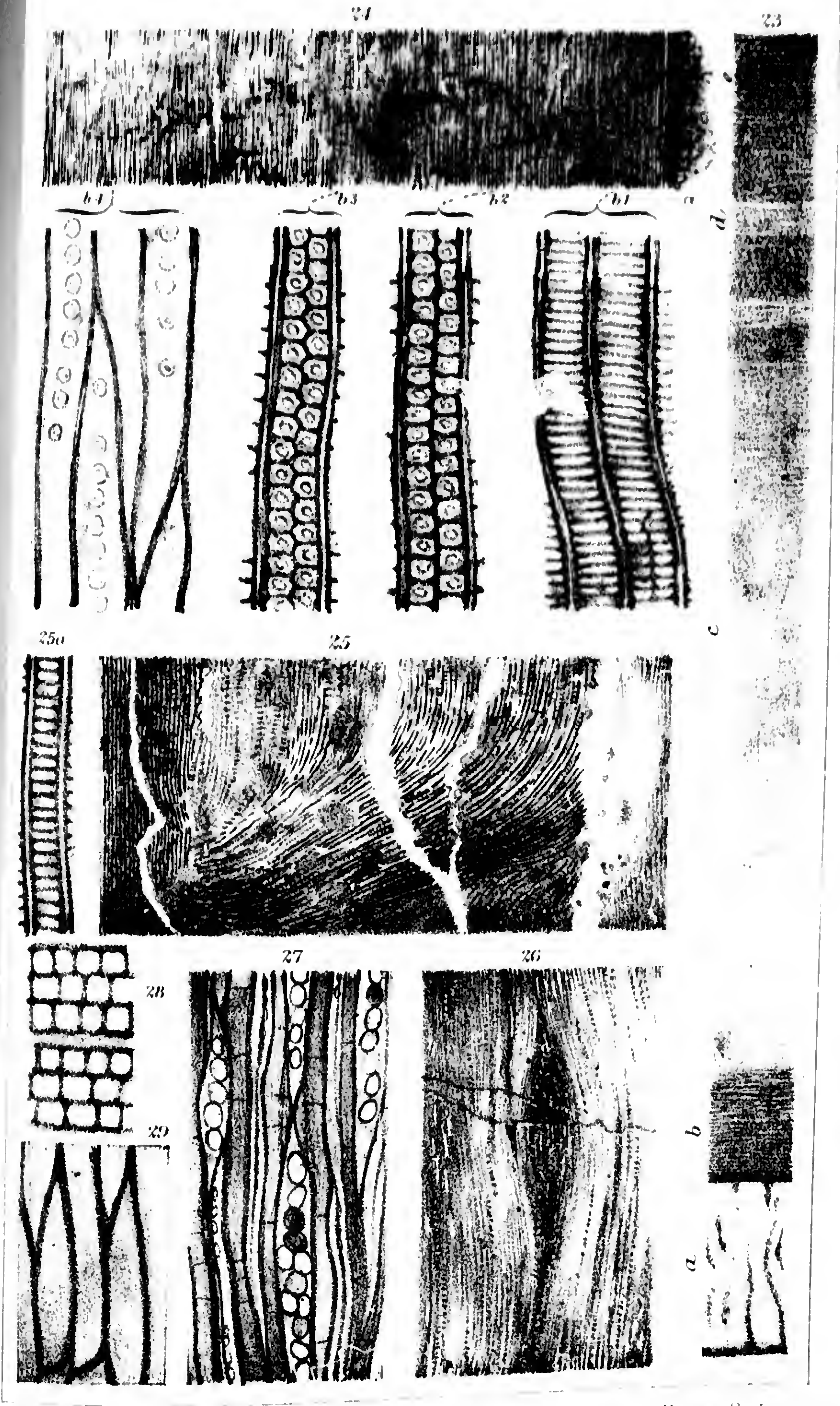

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SIGILLARIA.