

X. *On the Microsporangia of the Pteridospermæ, with Remarks on their Relationship to Existing Groups.*

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[PLATES 25—28.]

IN the month of June last, I communicated to this Society a "Preliminary Note on the Occurrence of Microsporangia in Organic Connection with the Foliage of *Lyginodendron*."* In the present paper I propose to deal more fully with the subject and to describe and figure the specimens in detail which formed the subject of the preliminary note. There will also be included in this communication the description of a new species of *Crossotheca* (*C. Hughesiana*), the structure of whose microsporangia is identical with that of *Crossotheca Höninghausi*, BRONGT. sp., and which confirms the observations made on the structure of the microsporangia of that species.

Before proceeding it is necessary to make perfectly clear that the plant named *Sphenopteris Höninghausi* by BRONGNIART† is identical with the *Lyginodendron Oldhamium* of WILLIAMSON.‡ This view is, I believe, generally accepted, but it seems desirable to give the evidence on which I think this relationship is clearly proved.

In 1874, WILLIAMSON pointed out, when describing *Rachiopteris aspera*, the similarity of the foliage of that plant with the pinnules of *Sphenopteris Höninghausi*. He says: "The pinnules of this plant (*Sphenopteris Höninghausi*) exhibit aspects which resemble those of figs. 13 and 14 (*Rachiopteris aspera*) in the closest manner, rendering the conclusion that our Oldham fossil is generically, if not specifically, identical with the above plant an exceedingly probable one."§ He further suggested that *Rachiopteris aspera* was the petiole of *Lyginodendron Oldhamium*,|| though it was not till some time later that the organic connection of *Rachiopteris aspera* with *Lyginodendron Oldhamium* was proved.¶

In 1891, from the study of certain specimens of *Sphenopteris Höninghausi*, I was

* 'Roy. Soc. Proc.,' B, vol. 76, p. 358, Plate 6, 1905.

† BRONGNIART, 'Hist. d. Végét. Foss.,' vol. 1, p. 199, Plate 52, 1829.

‡ *Dadoxylon Oldhamium*, BINNEY, 'Proc. Lit. and Phil. Soc. Manchester,' 1866; WILLIAMSON, "On the Organisation of the Fossil Plants of the Coal Measures," Part IV, 'Phil. Trans.,' 1873, p. 377; WILLIAMSON and SCOTT, "Further Observations on the Organisation of the Fossil Plants of the Coal Measures," Part III, *Lyginodendron* and *Heterangium*, 'Phil. Trans.,' B, vol. 186, p. 703, 1896 (plates).

§ 'Phil. Trans.,' vol. 164, Mem. VI, pp. 684, 685, 1874.

|| 'Phil. Trans.' (1873), Mem. IV, p. 403, and Mem. XII, vol. 178, B, p. 298, 1887.

¶ 'Phil. Trans.,' B, vol. 181, 1890, Mem. XVII, p. 91.

strongly of opinion that WILLIAMSON'S suggested relationship of *Lyginodendron Oldhamium* was correct,* and that such is the case I am now fully persuaded. The evidence on which this conclusion is based must, however, be briefly stated, as it is necessary for me to prove that the specimens about to be described are really the *Lyginodendron Oldhamium* of WILLIAMSON as well as the *Sphenopteris Höninghausi*, BRONGT.

The foliage of *Lyginodendron Oldhamium* (which for the present will be referred to as if it were an independent species) occurs in two conditions of preservation in the "coal balls" of the Lanarkian Series† of Lancashire and Yorkshire. In one of these the segments of the pinnules are more or less distinctly convex, so that sections passing through the pinnules parallel with the surface show a series of disconnected segments as at *a*, fig. 1, A. Under these conditions it is difficult to form a true idea of the shape and form of the pinnules. More rarely the pinnules are found flattened when a fortunate section parallel with their surface shows their true form, as at *b*, fig. 1, A, or better, at *a*, fig. 1, B. In the "coal balls" the specimens have been subjected to comparatively little pressure, and even small stems and branchlets, in transverse section, are seen to be preserved "in the round." Hence in the "coal balls," in the great majority of cases, the pinnules of *Lyginodendron Oldhamium* occur in the convex condition, whereas flattened examples of pinnules are much more rare.

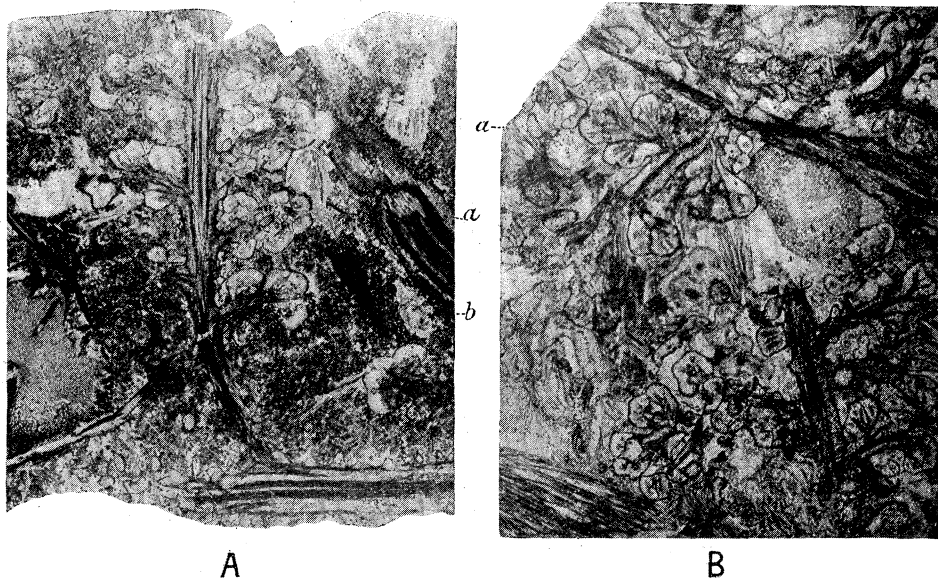


FIG. 1.—*Crossothea Höninghausi*, BRONGT. sp. (*Lyginodendron Oldhamium*, WILLIAMSON).

- A. Form of sterile pinnules, with convex segments. Halifax. *Horizon*.—Halifax Hard Bed, Lanarkian Series. $\times 6$. (K/632.) B. Form of sterile pinnules, with flattened segments. Dulesgate. *Horizon*.—Halifax Hard Bed, Lanarkian Series. $\times 6$. (K/664c.)

* KIDSTON, 'Geol. Soc. of Glasgow Trans.,' vol. 9, pp. 46 and 48, Plate 4, fig. 44.

† "Lower Coal Measures of certain Districts," see KIDSTON, 'Quart. Journ. Geol. Soc.,' vol. 61, p. 320, 1905.

In transverse section the convexity of the cup-shaped form of pinnule is well seen at fig. 2, A. It would therefore appear that the convex form of pinnule is the normal condition and that when the pinnules appear as flat expansions, this is due to pressure.

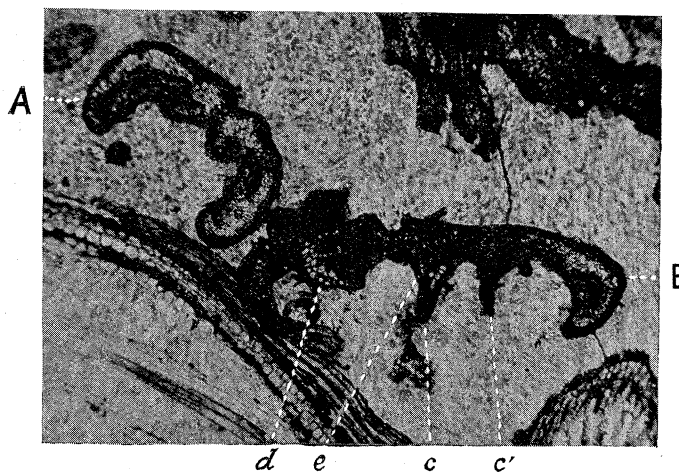


FIG. 2.—*Crossothea Höninghausi*, BRONGT. sp. (*Lyginodendron Oldhamium*, WILL.).

Transverse section of foliage, showing convex form of pinnule at A, and spines springing from the surface of fragment of another pinnule, B, at *c, c'*; at *d* is seen the midrib of the pinnule, and at *e* one of the lateral veinlets. Dulesgate. *Horizon*.—Halifax Hard Bed. $\times 22$. (K/664A.)

Among impressions on shale of *Crossothea Höninghausi*, BRONGT., the same two conditions of preservation occur. The convex pinnuled form is seen natural size at



FIG. 3.—*Crossothea Höninghausi*, BRONGT. sp.

Form of sterile pinnules with convex segments. From pit sinking, Tullygarth Pit, near Clackmannan. *Horizon*.—Lanarkian Series. Natural size. (K/938.)

fig. 3 and the flattened condition enlarged four times at fig. 4. In the ordinary impressions, specimens showing convex pinnules are very rare; the compressed and

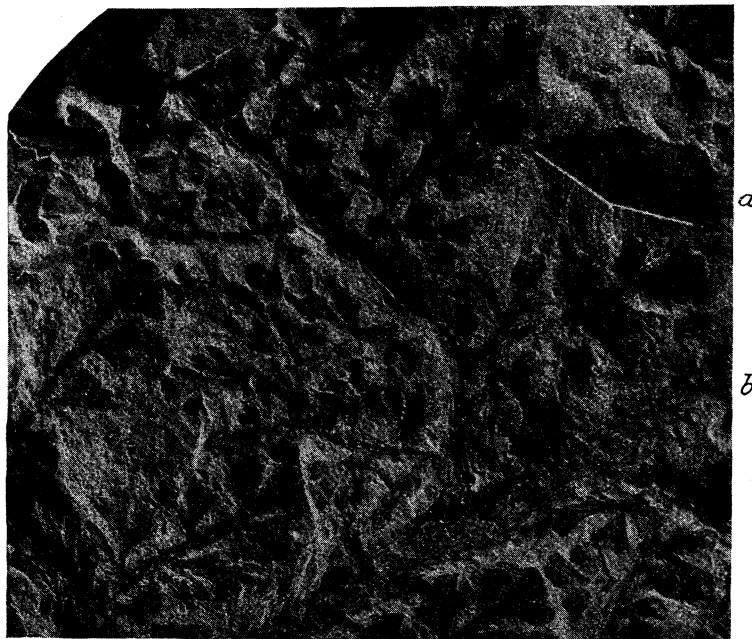


FIG. 4.—*Crossothea Höninghausi*, BRONGT. sp.

Form of sterile pinnules with flattened segments, showing the spines attached to the foliage, *a*, and the spiny rachis, *b*. $\times 4$. DOULTON'S marl quarry, Netherton, South Staffordshire. *Horizon*.—Between Fireclay Coal and Bottom Coal, Westphalian Series. Collected by Mr. H. W. HUGHES, F.G.S. (K/940.)

flattened condition being the common state in which the plant occurs as an impression, and this is the condition of nearly all the specimens I have seen preserved in the clay band ironstone nodules of the Dudley Coal Measures, as shown on Plate 25, figs. 1, 2, 3, where three small specimens from the roof of the Thick Coal, Coseley (Westphalian Series), are shown enlarged two times, in illustration of slight variation in the form of the sterile pinnules of this species. The dark points of the sterile pinnules shown on the fertile example, Plate 25, figs. 4 and 5, are caused partly by shadow (as the points of the pinnule segments are slightly bent into the stone), and partly from some carbonaceous material adhering to the impressions.

A longitudinal section of the outer cortex of *Lyginodendron Oldhamium* is given at fig. 5, B, enlarged two times. The sclerenchymatous bands which run longitudinally through the outer cortex form a series of meshes, from near the centre of which, on the outer surface, arises a short spine-like outgrowth. The bases of two of these are seen at *a*, fig. 5, B.

The impression of the outer surface of a stem of *Sphenopteris Höninghausi*, BRONGT., is given at fig. 5, natural size. Here are seen the rhomboidal meshes formed by the sclerenchymatous bands in the outer layer of the cortex *a*, in which is also seen the little cicatrice of the spine-like outgrowth. These spines are

frequently found attached to the impressions, and have been described by several authors.

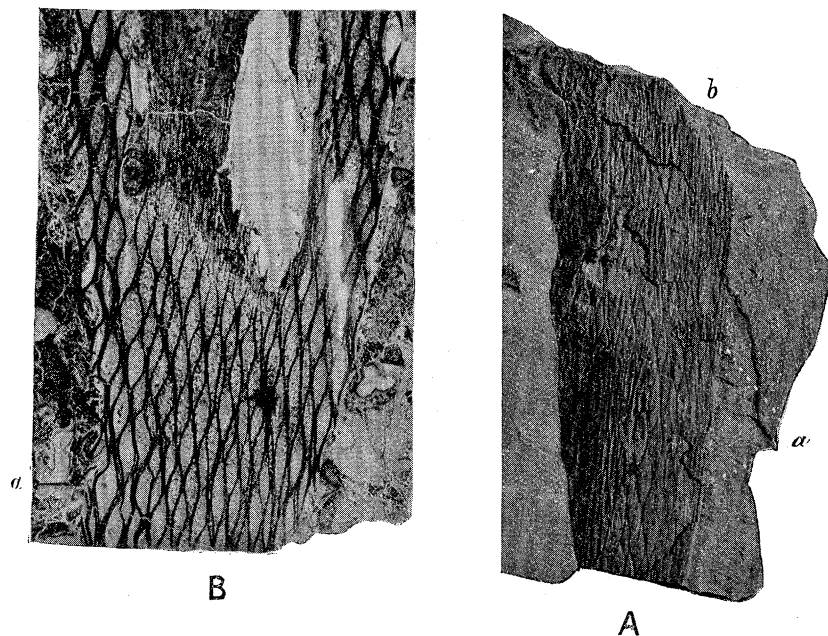


FIG. 5.—*Crossotheca Höninghausi*, BRONGT. sp. (*Lyginodendron Oldhamium*, WILL.).

- A. Impression of outer surface of stem, showing at *a* and other portions of the fossil the rhomboidal areas formed by the sclerenchymatous bands, in the centres of some of which the scars of the spines are seen. Compressed and carbonised portions of the sclerenchymatous outer cortex are seen adhering to the impression, as at *b*. Whitehall Colliery, Rosewell, Midlothian. *Horizon*.—Lanarkian Series. Natural size. (K/3218.) B. Tangential section through the outer cortex of stem, showing the net-like structure of the sclerenchymatous bands. At *a* the punctiform remains of two spines are seen. Dulesgate. *Horizon*.—Halifax Hard Bed. Lanarkian Series. $\times 2$. (K/592G.)

One of the characteristics of *Lyginodendron Oldhamium* is the occurrence of these spines (or glandular spines) on the stems, rachis, and even on the limb of the pinnules, though they are not equally present on all specimens; still their presence is one of the outstanding features of *Lyginodendron Oldhamium* and, as far as at present known, among plants occurring in the “coal balls” of Lancashire and Yorkshire, “no other fossil plant is known which bears glands at all comparable to those”* of *Lyginodendron Oldhamium*.

A transverse section of a pinnule of *Lyginodendron Oldhamium*, enlarged 22 times, is given at fig. 2, B, where two of these spines are exhibited at *c*, *c'*, and they are frequent on sections of petioles and stems.

Turning now to *Sphenopteris Höninghausi*, the occurrence of spine-like outgrowths is one of its distinctive characters. They are frequently seen on impressions, and even when the spines have been removed from the stems and petioles their position is generally indicated by a scar, as seen in figs. 4, *b*, and 5, A. Among fern-like plants occurring as impressions in the Lanarkian Series of the British Coal Measures,

* OLIVER and SCOTT, ‘Phil. Trans.’ B, vol. 197, p. 228, 1904.

Sphenopteris Höninghausi is the only one known to me which possesses these spine-like outgrowths, and they occur not only on the stems and petioles, but also on the pinnules, as seen on fig. 4, *a*.

These spines vary in their frequency of occurrence, but generally they are present in greater or less numbers. It is, of course, only on exceptional and very rare occasions that the spines on the pinnules are shown on impressions of the plant preserved in ordinary coal shale.

It is therefore seen that all the characters available for a comparison between *Sphenopteris Höninghausi* and *Lyginodendron Oldhamium* are absolutely identical, and these are not unimportant :

1. Form and shape of the sterile pinnules.
2. Stems having net-like meshes formed of sclerenchymatous bands in the outer cortex.
3. Stems, petioles, and pinnules bear spine-like emergences.
4. That among the plants showing structure from the Lanarkian Series, *Lyginodendron Oldhamium* is the only one known to possess all the characters mentioned above and that of the impressions of fern-like plants from the same horizon, *Sphenopteris Höninghausi* is also the only one known to possess all these characters.

The identity of *Lyginodendron Oldhamium* with *Sphenopteris Höninghausi* seems therefore to be proved beyond all doubt.*

Crossotheca Höninghausi, BRONGT. sp.

PLATE 25, FIGS. 1–16, PLATE 26, FIGS. 17–32, AND PLATE 27, FIG. 60.

1829. *Sphenopteris Höninghausi*, BRONGT., 'Hist. d. Végét. foss.,' vol. 1, p. 199, Plate 52.
1903. *Sphenopteris Höninghausi*, KIDSTON, 'Trans. Roy. Soc. Edin.,' vol. 40, p. 785.†
1877. *Calymmotheca Hæninghausi*, STUR, 'Culm Flora,' Part 2, p. 266.
1905. *Crossotheca Höninghausi*, KIDSTON, 'Proc. Roy. Soc. London,' B, vol. 76, p. 358, Plate 6.

Structure.

1866. *Dadoxylon Oldhamium*, BINNEY, 'Proc. Lit. and Phil. Soc. Manchester,' vol. 5, p. 115. (Stem.)

* *Sphenopteris Höninghausi* also occurs in the overlying Westphalian Series. Some Lower Carboniferous (Culm) species possess such spine-like outgrowths, but none of these occur so high up as the Lanarkian Series. I cannot accept the proposed union of some of the Culm species with *Sphenopteris Höninghausi*, from which they seem to be specifically distinct (POTONIÉ, "Ueber einige Carbonfarne," II. Theil, 'Jahrb. d. König. Preuss. Geol. Landesanstalt für 1890,' p. 16, Plates 7–9, 1891; 'Zeitsch. d. deut. geol. Gesell.,' Jahrg. 1891, p. 291).

† List of references and synonymy will be found here.

1869. *Dictyoxyylon Oldhamium*, WILL., 'Monthly Mic. Journ.,' vol. 2, p. 66, Plate 20, figs. 3 and 4. (Stem.)
1873. *Lyginodendron Oldhamium*, WILL., Mem. IV, 'Phil. Trans.,' p. 404. (Plates.) Mem. XVII, 'Phil. Trans.,' B, vol. 181 (1890), p. 89. (Plates.) WILLIAMSON and SCOTT, "Further Observations on the Organisation of the Fossil Plants of the Coal Measures," 'Phil. Trans.,' B, vol. 186 (1895), p. 703. (Plates.)
1899. *Lyginopteris Oldhamia*, POTONIE, 'Lehrb. d. Pflanzen-Palæontologie,' p. 170.
1872. *Edraxyylon*, WILL., 'Proc. Roy. Soc. London,' No. 136, p. 438. (Petiole.)
1874. *Rachiopteris aspera*, WILL., 'Phil. Trans.,' Mem. VI, p. 684. (Plates.) (Petiole.)
1876. *Kaloxylon Hookeri*, WILL., Mem. VII, 'Phil. Trans.,' vol. 166, p. 23. (Plates.) Mem. XIII, 'Phil. Trans.,' B, vol. 178 (1887), p. 293. (Plates.) (Root.)
1904. *Lagenostoma Lomaxi*, WILL. M.S., in OLIVER and SCOTT, "On the Structure of the Palæozoic Seed *Lagenostoma Lomaxi*," 'Phil. Trans,' B, vol. 197, pp. 193-247, Plates 4-10. (Seed.)

Sterile Pinnules.—These have been already referred to and illustrated in figs. 1-4 and are further shown on Plate 25, figs. 1-3 ($\times 2$). Normally the pinnules appear to have been more or less convex, but this condition is much more rarely met with in the coal shales than that in which they are flattened by pressure as shown in figs. 1, B, and 4, and Plate 25, figs. 1-3. When the specimens are uncompressed the segments of the pinnules seem more rounded than when flattened, their form then appearing more truncate at the apex.

Irrespective of the presence or absence of pressure, the form of the pinnule cutting varies somewhat from having more or less rounded lobes as figured by BRONGNIART, with which fig. 3 and Plate 25, fig. 1, agree, to the more cuneate pinnuled form given by ANDRÆ,* with which Plate 25, fig. 2, corresponds. Still more narrow pinnuled forms than these occur, as seen on Plate 25, fig. 3. When a large series of specimens is examined, and this is especially noticeable when the specimens all come from the same locality and horizon, it will be found that they show a very considerable variation in the form of the ultimate segments of the pinnules—a character well brought out in the figures of the sterile condition of *Crossothea Höninghausi* which have been given by the various writers who have figured this plant.

The young fronds of *Crossothea Höninghausi* were circinately coiled, and a partially developed specimen is given on Plate 26, fig. 30, which is enlarged two

* 'Vorweltliche Pflanzen,' Plate 4.

times. This fossil bears very obviously the marks of having been somewhat "withered" before mineralisation took place.

Fertile Pinnules.—The fertile pinnules of *Crossotheca Höninghausi* occur on the fronds in association with sterile pinnules, and this seems to be characteristic of the genus *Crossotheca*,* as the fructification of almost all the described species has been found in association with sterile pinnules, when the specimens were of a fair size.

Unfortunately the specimens from Coseley are usually contained in small nodules and only show fragments of pinnæ, but some of these have shown the organic connection of sterile and fertile pinnules. Three such examples are given on Plate 25, figs. 4 and 5, 6 and 7, 9 and 10, and another on Plate 26, fig. 32, but the barren pinnules do not show very clearly on this last figure. All these figures are enlarged two times, and the barren pinnules are indicated by the letter *b*.

The greater number of the fertile specimens bear no sterile pinnules, but they agree entirely in form and structure with the fertile pinnules of those specimens where both sterile and fertile pinnules occur in organic union. No doubt can therefore exist as to these fertile examples belonging to *Crossotheca Höninghausi*. Several of these fertile specimens showing different states of development are figured on Plates 25 and 26.

Before describing the specimens, reference may be made to their mode of preservation. The majority of the specimens are preserved as casts, but the casts in some cases still contain the almost indestructible microspores; in other cases the cavities of the impressions (which in many cases are uncompressed) have been infiltrated with carbonate of lime, and such a specimen is shown on Plate 26, fig. 23. Before infiltration the greater part of the more delicate tissue had decayed, but some of the denser or firmer tissue has remained in however a disorganised condition, and it is in such specimens, where the structure has been partially preserved, that the bilocular nature of the microsporangia is seen.

In the case of the other fertile specimens the outer surface of the sporangia almost invariably adheres to the matrix, and as the specimens are preserved somewhat "in the round," one almost invariably sees on one exposed surface the inside of the inner half of the sporangia. The fracture appears to pass longitudinally through what must in many cases have been uncompressed hollow sporangia. This is well seen on Plate 26, fig. 19, *a*, *a'*, *a''*.

Pedicle.—The fertile pinnules were attached to a very stout pedicel, which at the point of union with the pinnule is suddenly bent and remains united for some distance to the upper surface of the pinnule, Plate 25, fig. 11, *m*. The pinnule must, therefore, have been somewhat peltate in relation to its pedicel.

Limb of the Fertile Pinnule.—The limb of the fertile pinnule is oval, and is seen enlarged two times on Plate 25, figs. 6 and 7, and on Plate 26, fig. 32. Fig. 7 is

* ZELLER, 'Ann. d. Sciences Nat.,' 6e Sér., Bot., vol. 16, p. 180, 1883.

shown in text-fig. 6, with matrix unrepresented, to illustrate more clearly the form of the limb. On Plate 25, fig. 8, they are enlarged four times. In each case the limb is indicated by the letter *c*. Perhaps they are best seen at fig. 8, shown also at text-fig. 7, which is an enlarged view of the part lettered *c* on fig. 7. These specimens show the upper surface of the pinnules, which has a striated appearance, entirely due, I believe, to shrinkage, for it will be seen that they must have possessed considerable substance and seem almost to have been turgid. This opinion is based on the cavity they leave in the matrix, which is well seen on Plate 25, figs. 11 and 12, Plate 26, figs. 19, 21, and 31, *d*. The limb is from 2–2.50 mm. long on the specimen given on Plate 25, fig. 6.

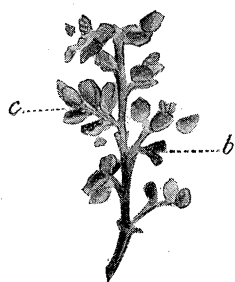


FIG. 6.—*Crossotheca Höninghausi*, BRONGT. sp.

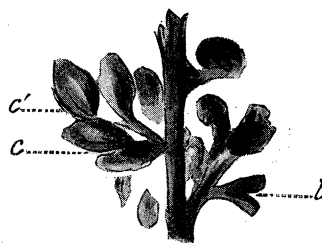


FIG. 7.—*Crossotheca Höninghausi*, BRONGT. sp.

Specimen given on Plate 25, fig. 7, drawn without surrounding matrix to show upper surface and form of the fertile pinules. × 2.

Portion of specimen shown on Plate 25, fig. 7, and at text-fig. 6, enlarged 4 times.

Nervation.—The nervation is not clearly seen. A strong vein seems to enter the pinnule from the pedicel some little distance from the margin, where it divides at an acute angle into two main branches. This is observable on the specimen given on Plate 25, fig. 11, but is hidden in the figure by the shadow of the cavity. It can be faintly seen, however, on Plate 25, fig. 8, *c'*.*

Microsporangia.—Each fertile pinnule usually bore six, rarely seven, bilocular microsporangia. They are fusiform and end in a sharp point. The upper portion of the microsporangium was attached to the under surface of the limb and probably seated on a lateral veinlet.

The sporangia do not seem to have been united among themselves, and though their upper extremities approach each other, they do not seem to have been attached to a common point. The centre around which they radiate is always a solid piece of the matrix. This is occasionally seen through the decay of the limb, and the removal of the other half of the “nodule.” This is seen in fig. 18, and enlarged four times in fig. 19, at *e*, *e'*. There is in this specimen a natural dissection preserved in stone.†

* Probably lateral veinlets sprang from the veins, as seen in *Crossotheca Hughesiana*, Plate 28, fig. 59.

† This is beautifully seen in *Crossotheca Hughesiana*, Plate 28, figs. 49, *i*, 50, *i*, about to be described.

The sporangia are about 1.5 mm. wide in their broadest part, which appears to be where they become free from the limb, and are about 3 mm. long.

In the immature condition the free portion of the microsporangia is bent inwards and their apices form the apex of a hemispherical sorus. This is clearly seen on Plate 26, fig. 17, where several of the sori exhibit the outer surface of the sporangia. On the sorus marked *f*, the individual sporangia can easily be seen and appear to be seven in number. They are separated by little ridges that are made by the mud which originally filled the hollow hemisphere formed by the inward arching sporangia being subjected to pressure before complete solidification of the rock took place, when the mud would be pressed out between the free portions of the sporangia, and thus form the little ridges which separate the individual microsporangia.

The small specimen shown enlarged two times on Plate 25, figs. 9 and 10 (which show the two halves of the nodule), is in the same stage of development as that given on Plate 26, fig. 17, and the dark marks which appear on figs. 9 and 10, *h*, are deep impressions of uncompressed sori in shadow, and which show the impress of the sporangia on the sides of the hollow. This was the first specimen on which the microsporangia were observed in connection with the sterile pinnules, *b*, and which also yielded microspores.

At maturity the sporangia spread out, and their free portions extend past the margin of the limb, when the sorus has very much the appearance of an epaulet. Plate 25, figs. 11, 12, *d*, 5, *g*; Plate 26, figs. 19, *d*, 21, *d*, 22, *g*. Their outer surface appears to be smooth.

It has been already mentioned, that owing to the fracture of the stone frequently passing longitudinally through the centre of the sporangia, which seem to have been empty and uncompressed, one often gets a view of the *inner surface* of the wall of the sporangium which faces towards the centre of the sorus. This very frequently exhibits the slit by which dehiscence has taken place--and it is clearly seen, enlarged two times, on Plate 25, fig. 12, and enlarged four times on Plate 26, figs. 19, *h*, and 22, *h*, but is especially well exhibited at fig. 19, *h'*, where it appears as an open slit.

It has already been remarked that some of the specimens have been infiltrated with carbonate of lime, and one of these is shown enlarged two times on Plate 26, fig. 23. In the specimens preserved in this manner the structure of parts of the microsporangia has in a few cases been preserved.

In fig. 23, the white matter is the carbonate of lime, the darker parts are the remains of the sporangia. This example has also been in an immature condition, for at *f* the impression of an unopened sorus is clearly seen, the state of development of this example corresponding to that of fig. 17.

At Plate 26, fig. 24, the sorus marked *k*, fig. 23, is shown enlarged six times. The greater part of the structure has disappeared, but the walls of the two loculi of the microsporangia have in several cases been preserved. The tissue composing these walls must have been very dense and firm, for almost all the other tissues have

disappeared. Fig. 25 shows the two loculi, lettered α on fig. 24, in slightly oblique transverse section. When seen truly transversely, they are circular in section. Fig. 26 shows another pair of loculi whose plane of section is more longitudinal, where the narrow wall dividing the loculi is very clearly seen. Fig. 27 illustrates a somewhat similar condition. This union of the two loculi is so frequent in some of the specimens that the geminate nature of the loculi within the microsporangia is placed beyond doubt.

All these loculi still contain the microspores, and their bright orange colour, with clearly defined dark margins, makes them very conspicuous objects when seen under a hand lens.

Each of the loculi measures about 0.50 mm. in diameter, the pair occupying about 1 mm., while the microsporangium is about 1.50 mm. wide. Even the size of the loculi in relation to the width of the microsporangium confirms what actual observation has shown, that the sporangia are bilocular.

The cleft by which dehiscence took place passed longitudinally down the centre of the inner face of the microsporangium, as shown on Plate 26, fig. 19, h' , and Plate 25, fig. 12, d , and thus the microspores of both loculi would be liberated simultaneously.

Some of the microspores are shown enlarged 500 diameters on Plate 25, figs. 13-16, and on Plate 26, figs. 28 and 29. As a rule they are very much contracted and folded or crumpled, and I believe that all have been derived from microsporangia which had not arrived at complete maturity. Had they been quite mature it is improbable that the microspores would have been so much crumpled. This crumpling is represented at figs. 13 and 14. The other specimens figured were more free from wrinkles, but on none of them were they perhaps entirely absent, though not represented on the figures.

The microspores, which are easily removable for microscopical examination, are circular or slightly oval, and measure $50\ \mu$ to $70\ \mu$ in diameter. Their outer surface is roughened by numerous closely placed, very minute, blunt points. These are placed on an outer hyaline layer (the extine), which is sometimes seen extending as a colourless band beyond the underlying denser yellow layer (the intine). The spores are provided with a distinct triradiate ridge, Plate 25, figs. 15 and 16, Plate 26, figs. 28 and 29, though this is often difficult to see on account of the crumpling of the spore wall. Its presence indicates that the microspores are tetrahedrally developed.

It will be seen from the foregoing description of the microsporangia of *Crossotheca Höninghausi*—the *Lyginodendron Oldhamium* of WILLIAMSON—that they differ from the microsporangia, described by Miss BENSON under the name of *Telangium Scotti*,* and which some have thought were the microsporangia of *Lyginodendron*. I cannot help thinking that this opinion has been somewhat supported by the fact

* *Telangium Scotti*, a new species of *Telangium (Calymmatotheca)* showing structure ('Ann. of Bot.', vol. 18, p. 161, Plate 11, 1904).

that STUR placed *Sphenopteris Höninghausi* in his genus *Calymmotheca*, but he did so without the slightest knowledge of its fructification.

The microsporangia of *Crossotheca Höninghausi* are distinguished from those of *Telangium Scotti* by the following differences, which are shown underneath in tabular form :—

<i>Crossotheca Höninghausi.</i>	<i>Telangium Scotti.</i>
Microsporangia free, borne upon a fertile limb and united to its lower surface for a distance of about one-third of its diameter.	Microsporangia terminate a pedicel deprived of a limb and united to each other in their basal portion.
Free portion of microsporangia hangs down as a fringe beyond the margin of the limb.	Microsporangia upright and united at their base around a common point of attachment.
Microsporangia bilocular.	Microsporangia with a single loculus.

That *Telangium Scotti* is the microsporangium of another member of the *Pteridospermeæ* is more than probable, but it is clearly not the microsporangium of *Lyginodendron*. The structural points shown by *Telangium Scotti* do not seem to afford any remarkable agreement with *Lyginodendron*, and are such as will probably be found to be in great part common to the microsporangia of some of the *Pteridospermeæ*.

The morphology of the fertile lobe of *Crossotheca Höninghausi* will be considered after *Crossotheca Hughesiana* has been described.

Crossotheca Hughesiana, KIDSTON, n. sp.

(Plate 27, figs. 33 to 43 ; Plate 28, figs. 44 to 59.)

Only the fertile condition of this species is known, as, unfortunately, none of the specimens show any organic connection with sterile pinnules.

All the specimens occur in clay band ironstone nodules of the "10-foot Ironstone Measures," which form the roof of the "Thick Coal," Coseley, near Dudley (Westphalian Series). The specimens were communicated to me for examination, along with other plants from the same locality, by Mr. H. W. HUGHES, F.G.S., to whom I take this opportunity of recording my indebtedness, in the specific name adopted for the species.

In all the chief structural characters, *Crossotheca Hughesiana* agrees entirely with *Crossotheca Höninghausi*, and the two species have, as far as their microsporangia are concerned, a very close affinity.

Fertile Pinnules and Nervation.—The most perfect specimen in some respects is shown on Plate 27, figs. 33 and 35, the two figures giving the two halves of the same nodule. Fig. 35 shows the surface of the limbs of the pinnules, this half of the specimen having, as it were, lifted off the other half shown at fig. 33, where the

impression of the immature sporangia is seen. The fossil itself has disappeared, and when these two halves are placed in position on one another, under the impression of each pinnule limb there is a little hollow from which the limb and the microsporangia have decayed and been removed.

On fig. 33 (and fig. 34, which is a portion of the same specimen enlarged two times), the sori appear as if they were hemispheres, but this appearance of elevation which they seem to possess is due entirely to the illumination, as nothing now remains but their hollow impress in the stone.

The pinnules are stalked, obtusely cordate in form (figs. 35, *a*, 36, *a*), and placed alternately on the ultimate pinnæ. The stalk of the pedicel was suddenly bent immediately before joining the pinnule to whose dorsal surface it was adnate for a short distance (Plate 27, fig. 37, *b*; Plate 28, fig. 46, *b*).

The vascular bundle which enters the limb from the termination of the pedicel seems to divide into two or more branches immediately on entering the limb—probably on its upper surface—for on the lower surface of the limb they appear to spread out as separate veinlets. Two of these are specially prominent and are shown in several cases, as on Plate 27, figs. 35, *c*, 36, *c*, and on Plate 28, fig. 47, *c*, but in only a single pinnule have I seen clearly the lateral veinlets. This pinnule is shown enlarged six times on Plate 28, fig. 59. Here one of the more prominent veins gives off a short lateral veinlet at its upper end, and a little further down a second veinlet is given off. A third veinlet seems to have arisen directly from the main vein, for even at the small cavity which marks the entrance of the vein from the pedicel it seems to be free.

This small glimpse of the nervation of the fertile pinnules is of considerable importance, for if we fill in with dotted lines the probable veinlets which are missing, there cannot have been more than eight or nine veinlets at most in this pinnule, and this corresponding with the number of sporangia in the larger sori, makes it certain that each microsporangium was situated on a veinlet.

What one might think were traces of lateral veinlets on figs. 35, *a*, and 36, *a*, are due to encrustations of oxide of iron, but whether occupying the position of veinlets or not I am unable to say.

The apex of the limb of the fertile pinnule given at fig. 59 is broken off, which accounts for its rounded appearance as shown in the drawing. The limb of the pinnule is about 5 mm. long and 5 mm. broad at its widest part.

Microsporangia.—In the immature condition the microsporangia have their free portions bent inwards with their apices meeting in the centre. The specimens figured on Plate 27, figs. 33, 34, 40, and 41, represent this condition, also that given on Plate 28, fig. 58, *f*, where six microsporangia can be counted. The greatest number of sporangia observed in any sorus is nine.

The earliest stage of development which has been met with is seen on Plate 27, fig. 40, where the lower part of a pinna is given, natural size. The principal rachis

is very stout—4 mm. wide—and is longitudinally striated. It gives off alternate ultimate pinnæ with proportionally thick rachis, which in turn bear stalked fertile pinnules (figs. 40, *g*, and 41, *g*). The sporangia are immature and curved inwards, forming small globular, “apple-like” bodies, which are seen enlarged two times at fig. 41. The loculi of the sporangia, through the disappearance of part of the outer wall, are distinctly seen in many cases in this specimen and reveal the yellow microspores with which they are filled.

An upper portion of a pinna is seen on Plate 27, fig. 42, which, taken in connection with the basal portion given at fig. 40, illustrates well the general growth of the plant. The sori are here on longer pedicels (*g*) than on the example given at fig. 40, and its state of development seems more advanced.

The infolded sporangia are well seen at fig. 33, *h*, and in the enlargement, fig. 34, *h*, where the lines limiting the sporangia are clearly observable. The infolding of the sporangia is also well seen at fig. 51. On the specimen given on Plate 27, fig. 33, eight microsporangia enter into the composition of this sorus, while at fig. 58, *f*, six appear to be the number, although elsewhere nine have been observed. The number of *microsporangia* forming a sorus appears to vary according to the position of the pinnule on the frond.

At maturity the sporangia spread outwards and their free portions extend past the margin of the limb like a fringe.

As already mentioned in describing *Crossotheca Höninghausi*, when the nodules containing the specimens are split open, the sporangia are sometimes shown on one-half of the nodule and the impression of the limb on the other. On Plate 28, fig. 49, a sorus is thus exhibited. It contains eight sporangia which appear to be free from each other, though their upper extremities surround a small central inorganic boss as at *i*. The same is seen at fig. 50, *i*, where the microsporangia are seven in number. Both these figures are enlarged two times.* The example given on Plate 28, fig. 44, illustrates the general appearance of the sori and this example is enlarged two times at fig. 45. Other specimens showing the same general characteristics, also enlarged two times, are given on Plate 28, figs. 52, 53, 56 and 57. Further reference will be made to these figures.

The microsporangia are bilocular, curved, lanceolate, and terminate in a sharp point. Their form is well seen in the natural dissection, given enlarged two times on Plate 28, fig. 53, where the side view of a microsporangium is clearly defined at *k*, the part between the lines *k*, *l* is that which would be attached to the limb of the pinnule, the portion beyond *k* would form the fringe. The shape of the microsporangia is also seen at figs. 46, *k*, 56, *k*, and 57, *h*. In fig. 56 the flexuous vascular strand is seen in the rachis as a dark stain.

The microsporangia are bilocular as in *Crossotheca Höninghausi*, and the two *loculi* of a sporangium are drawn enlarged 10 times on Plate 27, fig. 38. The two

* These specimens are more fully described on a subsequent page.

loculi, *m*, *m*, separated by a common wall, *n*, are clearly seen, the whole being embedded in carbonate of lime.

Dehiscence took place by a longitudinal cleft running down the inner side of the sporangium and in line with the dividing wall of the two loculi. This is clearly seen at *o*, on Plate 28, figs. 45, 52, 56, and 57. In all these cases *the fracture of the stone* has passed more or less longitudinally through the sporangium, and in the figures the view given is that of the inner surface of the wall of the sporangia which faces towards the centre of the sorus.

The sporangia of several of the specimens contain the microspores. These when unshrunk are globular and possess a well marked triradiate ridge which shows that they have been tetrahedrally developed. Their outer surface is roughened with minute apiculi. Most of the spores are considerably crumpled and have probably been more or less immature. All my microspores have been taken from sporangia embedded in carbonate of lime and preserved in the manner already described.

The microspores are circular or slightly oval and measure on an average 50 μ to 55 μ in diameter. On Plate 27, fig. 39, a specimen is seen in which the three ridges are represented by three clefts; the wall of the microspore is also crumpled at its periphery. Fig. 43 shows the other surface and is also crushed at the edges. Plate 28, figs. 54 and 55, shows two other microspores, all of which are enlarged 500 times. Any slight wrinkling that these microspores showed is not represented in the figures.

Morphology of the Fertile Segments of Crossotheca.

From the position of the fertile segments on the frond of *Crossotheca* there can be no doubt that the fruiting segments are pinnules modified for the purpose of fructification. The limb of the fertile pinnules is much altered in form from that of the sterile pinnules, being entire in *Crossotheca Höninghausi* and some other species, but lobed in *Crossotheca sagittata*, LX. sp., and *Crossotheca trisecta*, SELLARDS.*

Restricting our remarks more specially to the two species described in this paper, the limb of the fertile pinnules must have been of considerable thickness from the hollow it leaves in the stone on its decay (Plate 25, fig. 11, *d*; Plate 26, fig. 31, *d*; Plate 28, fig. 51, *e*). The pedicel of the fertile pinnule is also attached to it in a manner different from its attachment to the sterile pinnule. In the sterile condition the pinnules of *Crossotheca Höninghausi* are gradually contracted into the stalk; in the fertile pinnules the stout pedicel suddenly bends before joining the pinnule, where it extends over the upper surface, to which it becomes adnate for a distance equal to about one-third of the diameter of the pinnule, where the vein from the pedicel enters it. (Plate 28, figs. 48, *d*, 46, *b*; Plate 25, fig. 11, *m*; Plate 27, fig. 37, *b*.) This peculiar attachment of the pedicel has been well shown by ZEILLER.*

It has usually been understood that the sporangia of *Crossotheca* hang from the

* *Crossotheca Crepini*, ZEILLER, 'Flore foss. Bassin houil. de Valen.,' Plate 13, figs. 1, c, 1, d.

under surface or margin of the pinnules.* Such is, however, in the specimens here described, not the case. On Plate 28, figs. 49, 50, 50A, two natural dissections of the sori are shown. Fig. 50A shows the impression of the smooth surface of the limb, which has lifted off the sorus shown at fig. 50, exposing seven hollows left by the seven microsporangia which have composed this sorus. The raised ridges uniting with a central boss of matrix are specially well seen in fig. 49, *i*. The sorus shown at fig. 60, Plate 27, shows very clearly that the hollows are formed by the sporangia, *g*, into the insides of which one looks in this specimen, and that the ridges separating the sporangia and uniting in a central boss are formed by the rock in which the specimen is embedded. On the right and left sorus of fig. 52, *o*, a small portion of the limb seems to have adhered to the microsporangia and thus obscures their terminations.

The restoration of a sorus given in radial section at text-fig. 8 and in transverse section at fig. 9 explains the mode of preservation of the figures just described. At fig. 8, *a*, is seen the limb, at *b, b'*, two of the sporangia. The part of the matrix lettered *c* is the central boss with which the ridges unite in figs. 49, 50, Plate 28, and fig. 60, Plate 27. The rays in these figures represent the space between the sporangia and cannot be shown in a radial section, but if a transverse section be made in the line of *d, d'*, fig. 8, as shown at text-fig. 9, we have represented the condition shown in some of the specimens. Here *c* represents the boss of rock, *e* the rays and *b* the bilocular sporangia. This figure represents the condition shown at figs. 49, *i*, 50, *i*, Plate 28, and fig. 60, Plate 27. The sporangia therefore appear to have been quite free from each other or from any central point to which they were mutually attached and in this respect differ from the sporangia of *Asterotheca*, which are united to each other at the base and thus form a synangium.

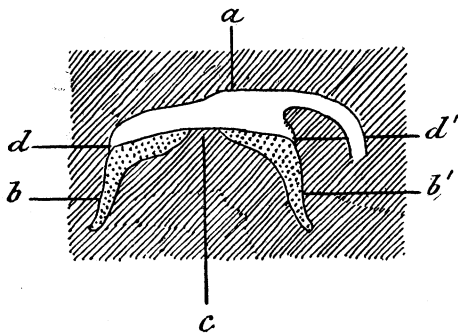


FIG. 8.

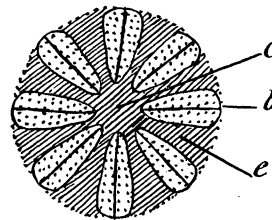


FIG. 9.

Professor ZEILLER thought that perhaps the sporangia on the specimens of *Crossotheca* examined by him were in some cases united to each other in small groups.† This does not appear to be the case in any of the specimens I have

* ZEILLER, 'Éléments de Paléobotanique,' p. 62, 1900; SELLARDS, 'Amer. Journ. of Science,' vol. 14, p. 196, 1902.

† ZEILLER, 'Ann. d. Sciences Nat.,' 6e Sér., Bot., vol. 16, p. 181, 1883.

examined, where their state of preservation allowed their structure to be seen, and it seems probable that the suggested union of the sporangia by ZEILLER arises from the imperfect preservation of his specimens.

The limb of a fertile pinnule, with remains of the nervation, is seen on Plate 28, fig. 59. The veinlets seem to radiate from the point of entrance of the vein from the pedicel and it therefore seems evident from the arrangement of the sporangia that the part of the sporangium embraced by the limb was attached to a veinlet, this attachment extending to the extremity of the vein. The free portion of the sporangium extending beyond the limb was bent downwards and gave the appearance of a marginal fringe. In a figure given by ZEILLER, of *Crossotheca Crepini*, one of the fertile pinnules is flattened out and shows that the sporangia extend inwards towards the centre of the sorus.* The microsporangia in the sorus of *Crossotheca* are thus arranged according to the type described by BOWER as a "radiate uniseriate sorus."†

The sporangia of *Dactylotheca*‡ show some characters which may well be compared with those of *Crossotheca*. In *Dactylotheca* the sporangia are oblong pointed, free, and attached by their longer axis to the ultimate veinlets. They also dehisce by a longitudinal cleft. On the narrower pinnules which have a single row of sporangia on each side of the midrib we have only to imagine the sporangia increased in length till they extend past the margin of the pinnule and their apices bent downwards, where, if the pinnule were stalked, we would now have a *Crossotheca*, for it is not necessary that in *Crossotheca* the microsporangia be arranged in a circle. It is not, of course, known whether the sporangia of *Dactylotheca* are unilocular or bilocular, but still one can easily see how such a genus, which occurs in the Culm, could give rise to a form like *Crossotheca*.

I am aware that *Dactylotheca* is classed with the "ferns" at present, but I have little doubt its supposed sporangia are the microsporangia of a Pteridosperm.

The most remarkable character in *Crossotheca* is the bilocular microsporangia. From the fact that the microsporangia are borne on modified pinnules of the ordinary fern type, so long as stamens are held to be foliar in nature, any comparison with them is inadmissible. Among recent plants it is difficult to find a parallel case and though in the *Marattiaceæ* the sporangia may become abnormally bilocular through septation,§ I do not think that in *Crossotheca* this is their mode of origin. In fact, the sporangia forming the synangium of the *Marattiaceæ* arise in all cases, according to BOWER, from a process of septation, and though one cannot trace the course of development of the microsporangia of *Crossotheca*, they arise as individual organs, and at no period are the members of a sorus connected with each other as far as I have been able to observe.

* 'Flore foss. Bassin houil. d. Valen.,' Plate 13, fig. 3. Third fertile pinnule from base on left side.

† BOWER, "Studies in the Morphology of Spore-Producing Members. III.—Marattiaceæ," 'Phil. Trans.,' B, vol. 189, 1897, p. 57.

‡ ZEILLER, 'Ann. d. Sciences Nat.,' 6e Sér., vol. 16, p. 184, Plate 9, figs. 12–15, 1883.

§ BOWER, *loc. cit.*, 'Studies in Morphology. III.—Marattiaceæ,' p. 40.

Though it is impossible to trace the origin of the bilocular microsporangia of *Crossotheca* by the ordinary means of research open to the student of recent botany, still I think it most probable that it has arisen through the coalescence of two sporangia and, in support of this view, the occurrence in Devonian and Lower Carboniferous rocks of a series of fructifications showing intermediate conditions may be here shortly referred to.

In *Palæopteris* from the Upper Devonian, the sporangia are quite free, placed, as a rule, on pinnules entirely deprived of the limb (fig. 12, *b*). In *Telangium* from the Calciferous Sandstone Series, the sporangia are united at their base around the apex of a common pedicel, but free for the greater part of their course (fig. 10). *Telangium* has been shown by Miss BENSON to be unilocular.*



FIG. 10.—*Telangium affine*, L. & H. sp.

Syngangium showing microsporangia. $\times 4$. West Calder, Midlothian. *Horizon*.—Oil Shale Group, Calciferous Sandstone Series. Collected by the late C. W. PEACH, F.L.S. (No. K/648.)

The next link in the chain occurs in *Diplothecca*, KIDSTON, from the Carboniferous Limestone Series, where the sporangia all unite at the base in a disc-like structure, from which the sporangia go off in pairs, each pair being at first united to each other for a short distance, but in the greater portion of their length they are free. Fig. 11, A, B, C, shows three specimens of *Diplothecca stellata*, KIDSTON, natural size. D and E are two of the same specimens enlarged two times. At *a* the central disc is seen, at *b* the basal united part of the geminate sporangia, and at *c* the free portion. I have no doubt that these fossils are the microsporangia of one of the *Cycadofilices*.†

We have here only to continue the union of the sporangia, accompanied by a reduction in thickness of the coalesced walls, when a bilocular sporangium would be formed, very similar to that found in *Crossotheca*.‡

* BENSON, 'Ann. of Bot.,' vol. 18, p. 161, Plate 11, 1904.

† *Diplothecca stellata*, KIDSTON, 'Mem. of the Geol. Survey of the United Kingdom,' "Summary of Progress for 1902," p. 131, 1903. There is a probability that *Diplothecca stellata* is the microsporangia of *Sphenopteris elegans*, BRONGT., as they occur associated with this plant. In text-fig. 11, A, the two stellate syngangia probably belong to the stem which lies between them, but no connection can be traced. On B, *c*, a small characteristic fragment of the rachis of *Sphenopteris elegans* occurs, and on C, *d*, part of a pinna of the same plant is seen. No actual connection has, however, been found between *Diplothecca stellata* and *Sphenopteris elegans*, so their relationship to each other remains uncertain. STUR'S "Fruchtstand eines Farnes" ('Culm Flora,' Heft 1, Plate 1, fig. 2) apparently belongs to *Diplothecca*.

‡ It may be mentioned that in *Stangeria* some of the sporangia remain for a time united in pairs (LANG, "The Microsporangia of *Stangeria paradoxica*" ('Ann. of Bot.,' vol. 11, p. 425, 1897).

These forms occur in regular geological sequence, though of course several of them run concurrently after they once appear. I do not, of course, maintain that the

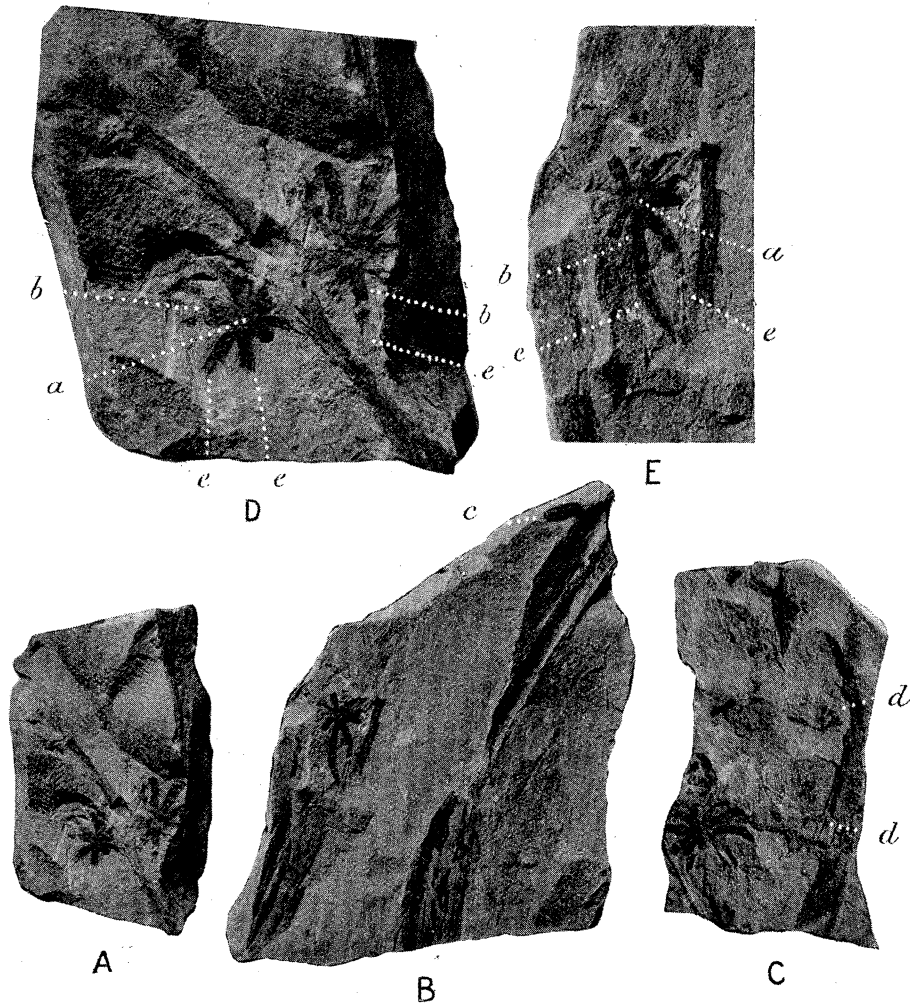


FIG. 11.—*Diplothecca stellata*, KIDSTON.

A, B, C, three specimens, natural size; D and E (A and B) enlarged two times to show more clearly the union of the microsporangia in pairs. Macrihanisch Water, near Wimbleton Pit, Campbeltown, Kintyre, Argyllshire. Collected by Mr. A. MACCONOCHIE. Specimens in the collection of the Geological Survey of Scotland. (Nos. M/3172E, M/3173E, M/3174E.)

bilocular sporangia of *Crossothecca* have been derived from this series, but still this series shows a possible explanation as to how bilocular sporangia amongst the Pteridospermeæ may have arisen.

The Relationship of the Pteridosperms to other Groups.

The genus *Crossothecca* contains eight species, the sterile foliage of all of which is known with the exception of *Crossothecca Hughesiana*, but the foliage of the various species is of a very diverse character; in some cases it is sphenopteroid, in others pecopteroid.

The following table contains the species at present included in *Crossotheca*, and mentions the type of sterile foliage possessed by each :—

Name.	Type of foliage.
1. <i>Crossotheca sagittata</i> , LESQX. sp.*	Pecopteroid—allied in foliage to <i>Pecopteris Miltoni</i> , ARTIS sp.
2. <i>Crossotheca ophioglossoides</i> , LESQX. sp. †	Pecopteroid.
3. <i>Crossotheca Crepini</i> , ZEILLER †	Sphenopteroid, with rounded lobes to pinnules.
4. <i>Crossotheca Boulayi</i> , ZEILLER §	Sphenopteroid, with rounded lobes to pinnules.
5. <i>Crossotheca Schatzlarensis</i> , STUR sp. ...	Sphenopteroid, pinnules with Rhodæan type of foliage.
6. <i>Crossotheca trisecta</i> , SELLARDS ¶	Pecopteroid.
7. <i>Crossotheca Höninghausi</i> , BRONGT. sp. ...	Sphenopteroid, cuneate or rounded lobes to pinnules.
8. <i>Crossotheca Hughesiana</i> , KIDSTON ** ...	Foliage unknown.

Having shown that the supposed sporangia of one species of the genus are, in reality, the microsporangia of one of the Pteridosperms, I think we are justified in provisionally concluding that all the remaining species also belong to the

* *Staphylopteris sagittatus*, LESQX., 'Geol. Survey Illin.,' vol. 4, p. 407, Plate 14, figs. 4–6, 1870. *Sorocladus sagittatus*, LESQX., 'Coal Flora,' vol. 1, p. 329, 1880; 'Atlas,' Plate 48, figs. 10, 10*b*, 1879; vol. 3, p. 760, Plate 100, figs. 4, 5, 1884. *Crossotheca sagittata*, SELLARDS, 'Amer. Journ. of Science,' vol. 14, p. 196, Plate 7, figs. 1–3*c*, 8, 1902. *Pecopteris abbreviata* (?), LESQX. (*non* BRONGT.), 'Coal Flora,' vol. 1, p. 248, Plate 46, figs. 4–6*a*, 1880.

† *Sorocladus ophioglossoides*, LESQX., 'Coal Flora,' vol. 1, p. 329, 1880; 'Atlas,' Plate 48, fig. 11, 1879. *Sphenopteris* (*Crossotheca*) *ophioglossoides*, WHITE, 'Foss. Flora of Lower Coal Measures of Missouri,' p. 60, Plate 20, figs. 3, 4, 1899.

‡ *Crossotheca Crepini*, ZEILLER, 'Ann. d. Sciences Nat.,' 6e Sér., Bot., vol. 16, p. 181, Plate 9, figs. 1–9, Aug., 1883; ZEILLER, 'Flore foss. Bassin houil. d. Valen.,' p. 112, 1888; 'Atlas,' Plate 13, figs. 1–3, 1886. *Sorothecca Crepini*, STUR, 'Zur Morph. u. System d. Culm- u. Carbonfarne,' p. 175, fig. 39, Dec., 1883. *Sorothecca Crepini*, STUR, 'Carbon-Flora,' Abth. 1, "Die Farne," p. 275, Plate 33, figs. 1, 2; Plate 35, figs. 3, 4, 1885.

§ *Sphenopteris* (*Crossotheca*) *Boulayi*, ZEILLER, 'Flore foss. Bassin houil. d. Valen.,' p. 115, 1888; 'Atlas,' Plate 4, fig. 4, 1886.

|| *Calymmothecca Schatzlarensis*, STUR, 'Carbon-Flora,' Abth. 1, "Die Farne," p. 265, Plate 38, figs. 1, 2, 1885. *Crossothecca Schatzlarensis*, KIDSTON, 'Ann. and Mag. Nat. Hist.,' ser. 6, vol. 2, p. 27, Plate 1, figs. 1–8, 1888; KIDSTON, 'Roy. Phys. Soc. Edin. Proc.,' vol. 9, p. 516, Plate 21, figs. 1–8, 1888. *Sphenopteris* (*Crossothecca*) *Schatzlarensis*, ZEILLER, "Étude sur la flore fossile du bassin houil. d'Héraclée (Asie Mineur)," 'Mém. Soc. Géol. d. France,' Paléont., Mém. No. 21, p. 13, Plate 2, fig. 7, 1899.

¶ *Crossothecca trisecta*, SELLARDS, 'Amer. Journ. of Science,' vol. 14, p. 198, Plate 7, figs. 4, 4*c*, 9, 1902.

** ZEILLER thinks it probable that the *Pecopteris exigua*, RENAULT ('Cours d. botan. foss.,' vol. 3, p. 115, Plate 19, figs. 13–18), and the *Pecopteris pinnatifida*, GUTBIER sp. (*Neuropteris pinnatifida*, 'Vers. d. Zwick, Schwarzkohle,' p. 61, Plate 8, figs. 1–3, 1835; *ibid.*, 'Versteinerungen d. Rothl. in Sachsen,' p. 13, Plate 5, figs. 1–4, 1848), belong to *Crossothecca* (ZEILLER, 'Bassin houil. et perm. de Brieve,' fasc. 2, "Flore foss.," p. 22, Plate 6, figs. 1, 2, 1892). That *Pecopteris pinnatifida*, GUTBIER sp., belongs to *Crossothecca* there can, I think, be little doubt, from the figures given by POTONIE on his Plate 18, figs. 9, 10 (POTONIE, "Ueber das Rothliegende des Thüringer Waldes," 'Abhandl. d. König. Preuss. Geol. Landesanstalt,' Neue Folge, Heft 9, p. 89, Plate 4, fig. 8 (?); Plate 10, fig. 1; Plate 11, fig. 2; Plate 18, figs. 9, 10, 1893).

Pteridospermea, even though we do not possess a complete knowledge of the structure of their microsporangia.

Whether we can regard the genus *Crossothea*, as at present defined, a "good" genus, is a question that only future discoveries can show. So long as *Crossothea* was regarded as a genus composed of ferns with exannulate sporangia, one had reason to believe that it formed a true genus; now that it is known that its sporangia are the microsporangia of Pteridosperms, the whole aspect of the case is altered, for, instead of knowing the complete fructification, only the male members of the species (with the exception of *Crossothea Höninghausi*) are known. I am inclined to think that a much greater similarity of structure will be found in the microsporangia than in the seed, and that if the structure of the seeds of the different species of *Crossothea* was known, there would be found important structural differences among them. Analogy would lead us to infer this, but at present such views can only be treated as suggestions, the correctness or falseness of which remain to be seen.

There is, however, one point about which there can be no doubt, and it is one to which attention has been frequently called, and which the variation in type of the sterile foliage found in *Crossothea* strongly accentuates—that it is impossible from the sterile condition of "ferns" or "fern-like" plants of the Carboniferous formation to have any idea of what their fructification may be, and to place in genera, founded on their fructification, species only known in the sterile condition, must lead, as it has in the past, to endless confusion and increase of a synonymy already overburdened.

So many of our most common and largest genera of Carboniferous "*ferns*" having crossed the boundary line which separates the vascular cryptogams from the gymnosperms, the question of the relationship of these plants to each other demands reconsideration.

Professor ZEILLER, in a most interesting article, "Une Nouvelle Classe de Gymnospermes: Les Pteridospermées,"* points out that even if we admit the existence of true ferns in Carboniferous times, the great preponderance of Pteridosperms makes it difficult to believe that the latter were derived from the true ferns, nor is it necessary to believe that the true ferns were derived from the Pteridosperms—but may they not have a common origin? †

While admitting that the evidence for a conclusive answer to these questions may not be complete, it is, I believe, sufficient to go a considerable distance in answering them.

There does not seem to be any satisfactory evidence of the existence of "ferns" or "fern-like" plants further back in time than the Old Red Sandstone or Devonian period, ‡ and the few which have shown their fructification from these rocks have only

* 'Revue Générale des Sciences pures et appliquées,' 16e année, No. 16, p. 718, Aug. 30, 1905.

† ZEILLER, *loc. cit.*, p. 726.

‡ I think it more than probable that the plants described by POTONIE as Silurian in "Die Silur- und Culm-Flora des Harzes und des Magdeburgischen" ('Abhandl. d. König. Preuss. Geol. Landesanstalt,' Neue Folge, Heft 36, 1901) belong to a higher horizon.

done so in the form of impressions. They are all more or less of the same type and consist of fusiform or slightly clavate sporangia. Such sporangia have been observed on *Archæopteris hibernica*, FORBES sp.,* and a similar type of fructification is described by DAWSON from the Devonian of Canada in connection with *Archæopteris Gaspiensis* and *Archæopteris Jacksoni*.† The fructification of *Palæopteris hibernica*, var. *minor*, has been described by CRÉPIN from the Upper Devonian of Belgium,‡ and Dr. SCHMALHAUSEN describes the sporangia of *Archæopteris archetypus* from the Devonian of Russia,§ LESQUEREUX the fruit of *Archæopteris minor* from the Pre-Carboniferous Rocks of Pennsylvania,|| and to NATHORST we are indebted for a knowledge of the fructification of *Archæopteris fimbriata*, NATH., and *Archæopteris Roemeriana*, GÖPP. sp., from the Upper Devonian of Bear Island, and *Archæopteris fissilis* from the same horizon in Ellesmere-Land.¶

In the whole of these fructifications there is only one type of sporangium—a fusiform or slightly club-shaped structure. No trace of any annulus has been observed on them. They are apparently borne, in normal condition, on the veins of the pinnules which are entirely deprived of the limb, though, in some rare cases, pinnules of the ordinary sterile form bear a few sporangia attached to their margin (fig. 12c).

These sporangia, as far as they afford data for their comparison, are very similar in general form to some of the so-called “exannulate sporangia” of the Carboniferous Rocks, and may be well compared with the sporangia of *Dactylotheca*, ZEILLER,** or

It should also be noted that the plants referred to the Middle Devonian by the late Sir WILLIAM DAWSON from St. John, New Brunswick (‘Geol. Survey of Canada,’ “Fossil Plants of Devonian and Upper Silurian Formations of Canada,” 1871), are in reality of Upper Carboniferous age. This opinion was arrived at independently by Mr. DAVID WHITE, of the United States Geological Survey and myself from the examination of specimens (see D. WHITE, ‘Science,’ New Series, vol. 16 (No. 397), 232, 1902).

* SCHIMPER, ‘Traité d. Paléont. Végét.’ vol. 1, p. 475, Plate 36, 1869; KIDSTON, ‘Ann. and Mag. Nat. Hist.’ June, 1888, p. 412.

† DAWSON, ‘Geol. Survey of Canada,’ “Fossil Plants of the Erian (Devonian) and Upper Silurian Formations of Canada,” Part II, Montreal, 1882.

‡ CRÉPIN, “Description de quelques plantes fossiles de l’étage des Psammites du Condroz (Dévonien Supérieur),” ‘Bull. Acad. Roy. de Belgique,’ 2me Sér., vol. 38, No. 8, Plate 3, 1874.

§ SCHMALHAUSEN, “Devonische Pflanzen aus dem Donetz-Becken,” ‘Mém. du Comité Géolog.’ vol. 8, No. 3, p. 22, Plate 1, fig. 9; Plate 2, figs. 15–22, 1894.

|| LESQUEREUX, ‘Coal Flora,’ vol. 1, p. 302, Plate 49, fig. 5; Plate 50, figs. 1–4, 1879.

¶ NATHORST, “Zur fossilen Flora der Polarländer.” Erster Theil. Dritte Lief.: “Zur Oberdevonischen Flora der Bären-Insel,” ‘Kongl. Svenska Vetenskaps-Akad. Handl.’ vol. 36, No. 3, 1902, *Archæopteris fimbriata*, p. 15, Plate 2, figs. 18, 21; Plate 3, figs. 1–6; Plate 4, fig. 2; *Archæopteris Roemeriana*, GÖPP sp., p. 19, Plate 4, figs. 3–13; Plate 5, figs. 1–4; Plate 6, figs. 1–4; Plate 7, figs. 1–3a; NATHORST, ‘Report of Second Arctic Expedition in the “Fram,” 1898–1902, No. 1, “Die Oberdevonische Flora des Ellesmere-Landes, 1904, *Archæopteris fissilis*,” p. 17, Plate 2, figs. 6–9; Plate 3; Plate 7, figs. 1–4.

** ZEILLER, *Dactylotheca dentata*, ‘Ann. d. Sciences Nat.’ 6e Sér., Bot., vol. 16, p. 184, Plate 9, figs. 12–15, 1883; ZEILLER, ‘Flore foss. Bassin houil. d. Valen.’ p. 196, Plate 26, figs. 2, 2A–2E, 1886; *Dactylotheca plumosa*, KIDSTON, ‘Roy. Soc. Edin. Trans.’ vol. 38, p. 205, Plate 2, figs. 5, 5b, 9, 9a–9c, 14, 1896.

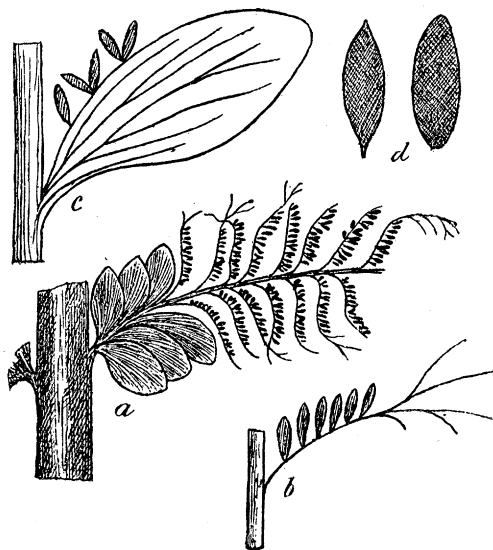


FIG. 12.—*Archæopteris hibernica*, FORBES sp.

a, Pinna showing sterile pinnules at the base and fertile pinnules above (reduced); *b*, Fertile pinnule, showing sporangia; *c*, pinnule of ordinary sterile form, bearing a few marginal sporangia; *d*, sporangia (? microsporangia) enlarged. From the Upper Old Red Sandstone of Kiltorcan, Kilkenny. Specimens in the collection of the Geological Survey of Ireland, Dublin.*

even with those of *Crossothea*,† and if we further compare the pinnules of *Archæopteris hibernica* which bear a few marginal sporangia with those of *Crossothea*, is there not given here a glimpse of the ancestry of *Crossothea*?

If, then, the whole of the data afforded by the fructification of the so-called “ferns” of Upper Devonian age be taken into consideration, it appears to me that it can only lead to the conclusion that among these plants, as far as at present known, there is no satisfactory support for the view that there existed among the Devonian plants a single *true* fern, and even if future investigations should show that such did exist in Devonian times, it is most unlikely that they will be found in preponderating proportion. On the other hand, the glimpses we obtain of the fructification of the Devonian “ferns”—with perhaps one exception, entirely restricted to the genus *Archæopteris* at present—point also from the structure of their sporangia that they, too, may belong to the group of the *Cycadofilices*.

Continuing our investigations into the Carboniferous Formation for the evidence of the existence of the true ferns at that period, let the plants of the Lower Carboniferous or Culm be first examined, and here there is the help of specimens which show their internal structure.

* KIDSTON, ‘Geol. Soc. Glasgow Trans.’ vol. 9, 1891, p. 30, Plate 3, fig. 31.

† ZEILLER, *Crossothea Crepini*, ‘Ann. de Sciences Nat.’ Bot., *loc. cit.*, Plate 9, figs. 6–9; ZEILLER, ‘Flore foss. Bassin houil. d. Valen.’ Plate 13, figs. 1D, 2, 3, 3A, 1886.

Of such stems I am not aware of any from British Lower Carboniferous Rocks which could be referred to true ferns;* of those showing *Cycadofilicinian* structure there is *Heterangium*,† and at least three other stems of whose existence I am aware belonging to the Cycadofilices, though they are at present undescribed.

Of "fern" fructifications few are known, and these include *Telangium affine*, L. & H. sp., and *Telangium bifidum*, L. & H. sp.,‡ from the Calciferous Sandstone Series, and *Dactylothecca aspera*, BRÖNGT. sp., and *Diplothecca stellata*, KIDSTON, from the Carboniferous Limestone Series.

Turning to the Culm of the Continent, UNGER described some specimens from Thuringia,§ which were subsequently examined and re-described by GRAF ZU SOLMS-LAUBACH, when many new structural characters of great interest were pointed out.|| Among the stems re-described by SOLMS-LAUBACH, *Calamopityx Saturni*, UNGER, is clearly referable to the Cycadofilices, there are others from the same deposit which perhaps also fall to be classed here, but associated with these fossils there does not appear to be any evidence for the existence of plants which could be referred to true ferns.

GRAF ZU SOLMS-LAUBACH has also described the internal structure of a number of plants from the Culm of Falkenberg, Silesia.¶ Among the plants occurring at Falkenberg are a few of special interest in our present line of thought. Of these is *Protopityx Buchiana*, GÖPP—a plant which, though standing somewhat alone, shows some relationship to the *Cycadofilices*.** *Zygopteris Roemeri*, SOLMS, and *Zygopteris tubicaulis*, GÖPP, occur in the same bed, and cause one to infer the presence of the *Botryopterideæ*. The globular annulate sporangia which are found along with these fossils probably point to some allied group, for the annulus is formed of a band of

* Petioles occur possessing true filicinian structure, but the petioles of the Pteridosperms also show true filicinian characters, as in *Lyginodendron Oldhamium*.

† WILLIAMSON, *Heterangium Grievii*, 'Phil. Trans.,' 1873, p. 377; "On the Organisation of the Fossil Plants of the Coal-Measures, Part IV, *Dictyoxylon*, *Lyginodendron*, and *Heterangium*" (Plate 28, figs. 30, 31, 34, 46; Plate 29, figs. 32, 33, 35; Plate 30, figs. 36-44; Plate 31, figs. 45, 47, and 49). WILLIAMSON and SCOTT, "Further Observations, etc.," 'Phil. Trans.,' B, vol. 186 (1895), Part III, *Lyginodendron* and *Heterangium*, Plates 26, 27.

‡ KIDSTON, 'Roy. Soc. Edin. Trans.,' vol. 33, *Calymmothecca bifida*, p. 140, Plate 8, figs. 1-6a; Plate 9, figs. 16, 17. *C. affinis*, p. 145, Plate 9, figs. 18-22, 1887. M. BENSON, 'Ann. of Bot.,' vol. 18, p. 161, 1904.

§ UNGER, in RICHTER and UNGER, "Beitr. zur Paläontologie des Thüringer Waldes," 'Denks. d. Math.-Natur. Classe d. Kaiserlich. Akad.,' vol. 11, p. 53, Plates 1-13, Vienna, 1856.

|| SOLMS-LAUBACH, "Ueber die seinerzeit von UNGER beschriebenen strukturbietenden Pflanzenreste des Unterculm von Saalfeld in Thüringen," 'Abhandl. d. Königl. Preuss. Geol. Landesanstalt,' Neue Folge, Heft 23, Berlin, 1896, pp. 1-100, Plates 1-5.

¶ SOLMS-LAUBACH, "Ueber die in den Kalksteinen des Kulm von Glätzisch-Falkenberg in Schlesien enthaltenen strukturbietenden Pflanzenreste, Part I," 'Bot. Zeit.,' Jahrg. L, Plate 2, 1892; Part II, *ibid.*, Jahrg. LI, Heft 12, p. 197, Plates 6, 7, 1893; Part III, *ibid.*, Jahrg. LV, Heft 12, p. 219, Plate 7, 1897.

** SOLMS-LAUBACH, *loc. cit.*, Part II.

several rows of cells. It is interesting to notice that the Pettycur material (Calceiferous Sandstone Series) also contains a *Zygopteris* (*Z. duplex*, WILL. sp.),* associated with annulate sporangia of a type identical to those described by SOLMS-LAUBACH. The *Botryopterideæ* are a very ancient type, and although at present one must regard them as ferns, they form a group very different from any existing, and perhaps hold but little closer relationship to existing ferns than do the *Cycadofilices* or *Pteridosperms*.

The Culm has also yielded the impressions of the fructification of several "Fern-like" plants, some of which were placed in *Calymmotheca* by STUR.† His "Fruchtstand eines Farnes"‡ would, from the union in pairs of what in the Scotch examples are evidently sporangia, probably find a place in *Diplothecca*.

NATHORST figures from the Lower Carboniferous Rocks of Spitzbergen what he believes to be the fertile condition of *Sphenopteris flexilis*, HEER.§ These have a somewhat similar structure to those of *Telangium* and, like them, are most probably the microsporangia of one of the *Pteridosperms*.

What, then, is the evidence for the occurrence of true ferns in the Devonian and Lower Carboniferous Rocks? The majority of the species upon which a definite opinion can be stated, belong to the *Cycadofilices* or *Pteridosperms*. Although so definite an opinion cannot be expressed upon others, such forms as *Archæopteris* belong almost certainly to the *Pteridosperms*, their known fructification being, most probably, the microsporangia of the respective species.

In the Lower Carboniferous *globular* sporangia with a compound *annulus* do occur along with petioles (*Zygopteris*) which apparently belong to the *Botryopterideæ*, but the *Cycadofilices* far outnumber these. If the *Botryopterideæ* be classed with true ferns, then the Lower Carboniferous or Culm is the earliest period at which they are at present known to occur. Even classing the *Botryopterideæ* with true ferns, they form a group altogether different from any fern at present existing, and are as extinct as the *Cycadofilices* themselves.

Passing now to the Upper Carboniferous Rocks or Coal Measures, the Lanarkian Series|| of Lancashire and Yorkshire, and especially the "Halifax Hard Bed" of that series, have yielded many "fern" remains showing their internal structure, but as these are so well known through the writings of BINNEY, WILLIAMSON, SCOTT, and others, they shall only be referred to very briefly.

* *Rachiopteris duplex*, WILL., "Memoir VI, Ferns," 'Phil. Trans.,' vol. 164, 1874.

† STUR, 'Culm-Flora,' Heft 2, Plate 8, figs. 5, 6, 7 (*C. stangeri*—the cupule only), 1877.

‡ STUR, *loc. cit.*, Heft 1, Plate 1, fig. 2.

§ NATHORST, "Zur fossilen Flora der Polarländer." Erster Theil. Erste Lief.: "Zur Paläozoischen Flora der Arktischen Zone," 'Kongl. Svenska Vetenskaps-Akad. Handl.,' vol. 26, No. 4, p. 21, Plate 3, fig. 7, 1894.

|| "Lower Coal Measures of some Districts," see KIDSTON, 'Quart. Journ. Geol. Soc.,' vol. 61, p. 308-321, 1905.

Amongst the remains found are those of the *Cycadofilices*, *Pteridospermeæ*,* *Botryopterideæ*, numerous petioles of uncertain allocation, annulate and exannulate sporangia. The annulate sporangia have, in the great majority of cases, *if not in all*, an annulus composed of more than one row of cells, and possibly belong to a group of "ferns" allied to the *Botryopterideæ*, for they are generally globular or oval and not club-shaped as in that group. It is an open question if an upright or oblique annulus with a single row of cells has yet been discovered in these beds. Of the exannulate sporangia, *Telangium* is evidently the microsporangium of a Pteridosperm. Other globular exannulate sporangia also occur, and recently such a type of sporangium has been shown by Dr. SCOTT to terminate the naked branchlets of *Stauropteris Oldhamia*, BINNEY. ††

In addition to the sporangia found in the "Coal balls," one occasionally finds impressions of "ferns" showing the sporangia on the pinnules beautifully preserved. Of such is the genus *Renaultia*§ where the small sporangia are globular or oval, and exannulate, in form very similar to those of *Stauropteris*, but placed on the veinlets of the limb of the pinnule.

Another type, *Urnatopteris*,|| has fusiform sporangia, borne upon pinnæ entirely deprived of foliage pinnules. In *Sphyropteris*,¶ the broad based dumpy sporangia sit upon a peculiar hammer-like expansion at the ends of the pinnæ and pinnules. The

* To the Pteridosperms belong the well-known *Lyginodendron Oldhamium* of WILLIAMSON (*Crossothea Höninghausi*, BRONGT.). The *Medullosa anglica*, SCOTT, is also most probably to be referred to this group (SCOTT, "On the Structure and Affinities of Fossil Plants from the Palæozoic Rocks. III.—On *Medullosa anglica*, a new Representative of the Cycadofilices," 'Phil. Trans.,' B, vol. 191 (1899), pp. 81–126, Plates 5–13).

† SCOTT, "The Sporangia of *Stauropteris Oldhamia*," BINNEY, 'New Phytologist,' vol. 4, p. 114 (figs.), 1905.

‡ See also FELIX, "Untersuchungen über den inneren Bau westfälischer Carbon-Pflanzen," 'Abhandl. d. König. Geolog. Landesanstalt,' vol. 7, Heft 3, pp. 1–73, Plates 1–6, 1886. SEWARD, "Notes on the BINNEY Collection of Coal-Measure Plants, Part II, *Megaloxylon*, gen. nov.," 'Cambridge Phil. Soc. Proc.,' vol. 10, Part 3, p. 158, Plates 5–7, and text-figs. 1–4. PENHALLOW, "*Myelopteris Topekensis*, n. sp., a New Carboniferous Plant," 'Bot. Gazette,' vol. 23, p. 15, Plates 2, 3. As dealing generally with this subject, consult also RENAULT, 'Recherches sur la Structure et les Affinités Botaniques des Végétaux Silicifiés recueillis aux environs d'Autun et de St. Étienne,' Autun, 1878, pp. 1–216, Plates 1–30. RENAULT, "Bassin houil. et permien d'Autun et d'Épinac," 'Flore foss.,' Deux. part, pp. 1–578, Plates 28–89, 1893–1896, and other writings by this Author. BERTRAND, "Les Poroxyllons végétaux foss. de l'époque houillère," 'Soc. Belge de Microscopie Mém.,' vol. 13, pp. 1–49, woodcuts 1–39, 1889.

§ *Renaultia*, ZEILLER, 'Ann. de Sciences Nat.,' 6e Sér., Bot., vol. 16, p. 185, Plate 9, figs. 16, 17, 1883. KIDSTON, *Sphenopteris (Renaultia) microcarpa*, 'Ann. and Mag. Nat. Hist.,' ser. 5, vol. 10, p. 9, Plate 1, figs. 7–14, 1882.

|| KIDSTON, 'Ann. and Mag. Nat. Hist.,' *loc. cit.*, p. 7, Plate 1, figs. 1–6 (*Eusphenopteris tenella*). *Urnatopteris*, KIDSTON, 'Quart. Journ. Geol. Soc.,' vol. 40, p. 594, 1884.

¶ *Sphyropteris*, STUR, 'Morph. u. Syst. d. Culm -u. Carbonfarne,' p. 23, figs. 6, 7, 1883; STUR, 'Carbon-Flora,' I, "Die Farne," p. 16, 1885. *Sphyropteris obliqua*, KIDSTON, 'Roy. Soc. Edin. Trans.,' vol. 35, p. 402, Plate 1, figs. 3, 3a, 3b, 1889.

first, *Renaultia*, dehisces by a longitudinal cleft, the two latter by a terminal pore. These have generally been classed with the *Marattiaceæ*, but in the light of recent discoveries are much more probably the microsporangia of the Pteridosperms. If these were really Marattiaceous ferns one would expect to find in the "Coal-ball" material some stems having a structure showing affinity with that group of ferns, as all these genera occur in the *Lanarkian Series*. Such, however, is not the case, and the *Myelopteris* petioles, which from their structure were at one time believed to be Marattiaceous, are now known to belong to the *Medullaceæ*, a group of *Pteridosperms*. The structure of the petiole of *Stauropteris*, which bears small globular exannulate sporangia, also shows no Marattiaceous characters. It would appear, then, that there is very little ground for referring such genera as *Renaultia*, *Urnatopteris*, and *Sphyropteris* to the *Marattiaceæ*, it seems more likely that they are founded on the microsporangia of the *Pteridospermeæ*.

That the *Pteridospermeæ* were all important in the Lanarkian Series* gains additional force from the occurrence of two new species of *Lagenostoma*† on this horizon, and the description of *Aneimites* (*Wardia*) *fertilis*, WHITE, with its attached small winged seeds, from the Lower Pottsville of West Virginia, though this latter seems to come from a lower horizon than the Lanarkian Series.‡

In the *Westphalian Series*§ which overlie the Lanarkian Series there is a great increase in the number of "ferns," and here a number of "ferns" with annulate sporangia occur. Amongst these are *Oligocarpia* GÖPP,|| *Hymenophyllites*, GÖPP,¶ *Kidstonia*, ZEILLER,** *Senftenbergia* CORDA,†† where (with perhaps the exception of *Hymenophyllites*), the annulus is compound and differs from that of any existing leptosporangiate ferns, still they show characters which may well be compared with the fructification of some existing genera. It would therefore appear that we have now arrived at a period, when, as far as our present knowledge enables us to judge, true ferns did form part of the Flora of the Westphalian Series along with *Cycadofilices*, *Pteridospermeæ*, and *Botryopterideæ*.

Among the genera with exannulate sporangia occurring here is *Asterotheca*

* *Neuropteris heterophylla*, one of the most common species in the Lanarkian and Westphalian Series, bore Rhabdocarpus-like seeds (KIDSTON, 'Phil. Trans.,' B, vol. 197, pp. 1-5, Plate 1, 1904).

† ARBER, 'Roy. Soc. Proc.,' B, vol. 76, 1905, p. 245, Plates 1, 2.

‡ WHITE, 'Smithsonian Miscellaneous Collections,' Quarterly Issue, vol. 47, Part III, p. 322, Plates 47, 48, 1904.

§ The middle coal measures of many British coal-fields.

|| *Oligocarpia*, GÖPP, 'Die Gatt. d. fossilen Pflanzen,' Lief. 1, 2, p. 3, Plate 4, figs. 1, 2, 1841. ZEILLER, 'Ann. des Sciences Nat.,' 6e Sér., Bot., vol. 16, p. 190, Plate 10, figs. 6-15, 1883.

¶ *Hymenophyllites*, GÖPP, 'Syst. Fil. Foss.,' p. 251. ZEILLER, 'Ann. d. Sciences Nat.,' loc. cit., p. 195, Plate 10, figs. 22-32, 1883.

** *Kidstonia*, ZEILLER, 'Bull. Soc. Bot. d. France,' vol. 44, p. 207, text-figs. 4-6, 1897. ZEILLER, 'Mém. Soc. Géol. d. France,' "Paléont. Mém.," No. 21, p. 21, Plate 2, figs. 5, 6, 6A, 6B, text-figs. 6-8, 1899.

†† *Senftenbergia*, CORDA, 'Beitr. z. Flora d. Vorwelt,' p. 91, Plate 57, figs. 1-6, 1845. ZEILLER, 'Ann. d. Sciences Nat.,' loc. cit., p. 188, Plate 10, figs. 1-5, 1883.

(*Pecopteris*), of which one species, *Pecopteris Miltoni*, ARTIS sp., is frequent in the Westphalian of England. Not only the structure of the sporangia of *Asterotheca*,* but also the structure of the *Psaronius* stems which are believed to have borne these *Asterothecous* fronds point to *Asterotheca* having been a Marattiaceous fern, and the evidence for this opinion is so strong that there is little ground for doubting its accuracy.

It is not so necessary to continue this line of investigation into the *Radstockian Series*† and *Upper Coal Measures* of the Continent, but it may be stated that in these rocks, the *Cycadofilices*, the *Pteridospermeæ*,‡ the *Botryopterideæ* and the Marattiaceous species of *Asterotheca* and some allied genera, all occur. In these rocks, the *Asterotheca* attain their maximum development. The *Cycadofilices* and *Pteridosperms*, however, outnumber the true ferns or such plants as we at present believe to belong to that class, which even at this time hold a subordinate place in the flora of Carboniferous and Permo-carboniferous periods.

Summarising the results of the foregoing observations, the following generalisations seem warranted :—

I. That the earliest definite occurrence of “fern-like” plants is in the Upper Devonian, where they are represented by *Sphenopteris*§ and *Archæopteris*, DAWSON, unless the specimen described by PENHALLOW as *Kalymma grandis*,|| UNGER, from the Middle Devonian, Moreland, Kentucky, be the petiole of a *Calamopitys* as some suppose. The structure of the sporangia of *Archæopteris* seems to point almost conclusively to their belonging to the group of *Cycadofilices*.

II. That beyond all doubt, in the Lower Carboniferous (Culm), the *Cycadofilices* and *Pteridosperms* were present and the former at least are strongly represented. That the presence of the *Botryopterideæ* is also indicated by the occurrence of *Zygopteris* petioles. Exannulate and annulate sporangia,¶ whose annulus is composed of more than one row of cells, also occur.

* *Asterotheca*, PRESL., in “Corda,” ‘Beitr. z. Flora d. Vorwelt,’ p. 89, 1845; *Asterocarpus*, GÖPP (*non* NECKER, ECKLOW, et ZEYHER), ‘Syst. fil. foss.,’ p. 188, Plate 6, figs. 1, 2, 1836 (see also GRAND’EURY, ‘Flore Carbon du Départ. de la Loire,’ 1877).

† KIDSTON, ‘Quart. Journ. Geol. Soc.,’ vol. 61, p. 320, 1905.

‡ One of the most interesting examples of this group—the *Pecopteris (Dicksoniites) Pluckenetii*, SCHL. sp.—with winged seeds attached to the but little modified pinnules, has been described, from the St. Étienne basin, by Mons. F. CY. GRAND’EURY, “Sur les graines trouvées attachées au *Pecopteris Pluckenetii*, SCHL.,” ‘Comptes rendus,’ vol. 140, p. 920, 1905.

§ *Sphenopteris Hookeri*, BAILEY, occurs at Kiltorcan along with *Archæopteris hibernica*, FORBES sp. It has very much the characters of *Sphenopteris elegans*, BRONGT., but is larger in all its parts. Explanations to accompany Sheets 147 and 157 of the maps of the Geological Survey of Ireland, illustrating parts of the counties of Kilkenny, Carlow, and Wexford. Dublin, 1861, p. 15, fig. 2.

|| PENHALLOW, in DAWSON and PENHALLOW, “Notes on Specimens of Fossil Wood from the Erian (Devonian) of New York and Kentucky,” ‘Canad. Record of Science,’ vol. 4, p. 244, Plate 1, 1891.

¶ The British examples are from the Calciferous Sandstone Series. These globular annulate sporangia are very similar to those described by SOLMS-LAUBACH, *loc. cit.*

If the occurrence of these annulate sporangia be regarded as proof of the occurrence of true ferns in the Lower Carboniferous, they probably belong to a group distinct from any at present existing.

III. That in the Upper Carboniferous the *Cycadofilices* and *Pteridospermeæ* are strongly represented. The *Botryopterideæ* are also well represented, but not so strongly as the other two groups, and plants with annulate sporangia, whose annulus however appears to be generally, *if not always*, formed of more than one row of cells, are more frequent. The structure of some of these sporangia may point to affinities with the *Osmundaceæ*, *Schizaceæ* or *Lygodium*. The sporangia of the genus *Hymenophyllites** have walls only one cell thick, but the structure of the annulus does not seem to be stated. This genus probably belongs to the true ferns, along with such genera as *Oligocarpia*, *Senftenbergia* and *Kidstonia*. In the Upper Carboniferous also occur the important genus *Asterotheca* (*Pecopteris*) and some allied genera which, especially in the *Radstockian* Series and Upper Coal Measures of the Continent, play an important part both in the number of the species and their frequency of occurrence. These appear to belong to the *Marattiaceæ*.

The *Cycadofilices* are undoubtedly the oldest group of "fern-like" plants of which we have fossil evidence. These are succeeded by plants with compound annulate sporangia and these again by others of a Marattiaceous type. It seems therefore to be highly improbable that the *Cycadofilices* could have descended from plants to which the name of "fern," as understood in recent botany, can be applied. What the progenitors of the *Cycadofilices* were, for the present remains unknown.

As to the ancestry of the *Cycadofilices*, I believe that they and the *Marattiaceæ* have descended from a common stock and this seems borne out by the fact that the microsporangia of some of the *Cycadofilices*—those with a single loculus—have considerable resemblance to the sporangia of the *Marattiaceæ*, for to the *Cycadofilices* I would refer such genera as *Telangium*, *Dactylothea*, *Urnatopteris*, *Sphyropteris* and most probably *Renaultia*, believing that what have been regarded simply as "sporangia," are in reality *microsporangia*.

There is another most distinct character of *Archæopteris* which persists to the present time amongst the *Marattiaceæ*, and that is the stipular appendages at the base of the petiole (fig. 13).

Such a structure has been observed on *Archæopteris hibernica*, FORBES sp., *Archæopteris fimbriata*, NATHORST, and *Archæopteris Roemeriana*, GÖPP sp. †

* *Hymenophyllites*, ZEILLER, 'Ann. d. Sciences Nat.,' 6e Sér., Bot., vol. 16, p. 195, Plate 10, figs. 22–32, 1883. RENAULT, 'Flore foss. Bassin houil. et perm. d'Autun et d'Épinac,' Deux. part, p. 19, woodcuts 16, 17, Plate 30, fig. 11, 1896.

† *Archæopteris hibernica*, KIDSTON, 'Ann. and Mag. Nat. Hist.,' June, 1888, p. 415. NATHORST, "Zur Oberdevonischen Flora der Bären-Insel," 'Kongl. Svenska Vetenskaps-Akad. Handl.,' vol. 36, No. 3, 1902. *Archæopteris fimbriata*, NATH., p. 17, Plate 3, figs. 5, 6; Plate 4, fig. 2; *Archæopteris Roemeriana*, GÖPP sp., p. 19, Plate 4, figs. 3, 4; Plate 5, fig. 1.

FIG. 13.—*Archæopteris hibernica*, FORBES sp.

Base of petiole, showing stipular appendages (much reduced). From the Upper Old Red Sandstone of Kiltorcan, Kilkenny. Specimen in the collection of the Geological Survey of Ireland, Dublin.

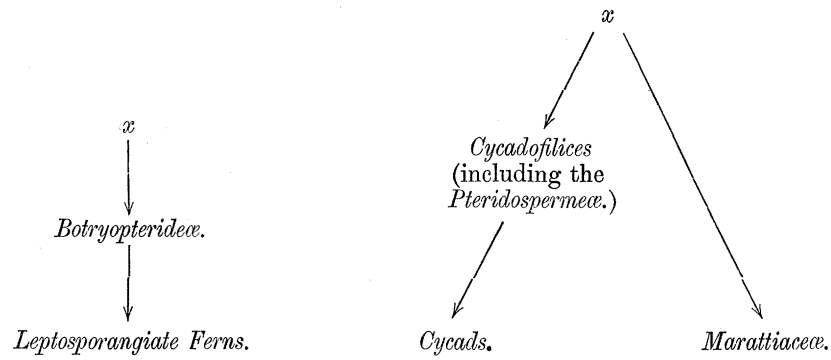
There is no satisfactory evidence in support of the view that the true ferns have been derived from the *Cycadofilices*, although these appear to have considerably antedated them in time.

The descent of the Leptosporangiate ferns from the *Botryopterideæ* seems to me much more probable than from any other palæozoic group, as far as known to us at present. In such existing genera as *Lygodium*, *Gleichenia*, and *Trichomanes*, which have protostelic cylinders, there is a great resemblance in general type of structure to the stems of the *Botryopterideæ*, though they differ in many details. In fact, these existing genera have a most archaic *facies*, not only in the structure of their stems, but also in some cases in their dichotomously divided fronds, and amongst palæozoic "ferns" dichotomy of the main rachis and pinnæ was of very frequent occurrence. Not only in these points do some of these genera agree with the *Botryopterideæ*, but there is still occasionally seen on the sporangia of *Lygodium* and *Schizæa* an annulus formed, in part at least, of more than one row of cells, though the annulus here occupies a different position on the sporangium from the corresponding structure in the *Botryopterideæ*.

Future discoveries may give good ground for altering some of these views, but from what is at present known of these ancient types of vegetation, these conclusions seem quite justified.

Whether the *Cycadofilices* (including the *Pteridospermeæ*, which may eventually engulf the remaining *Cycadofilices*) and the *Botryopterideæ* have descended from a common ancestor cannot at present be determined, as on this point the veil of obscurity is still unlifted.

The following scheme shows what I believe to be the most probable line of descent of the existing ferns and cycads :—



Before concluding, I wish to express my indebtedness to Mr. H. W. HUGHES, F.G.S., for giving me the opportunity of describing the fertile specimens of *Crossotheca Höninghausi*, BRONGT. sp., and *Crossotheca Hughesiana*, n. sp., and to Dr. JOHN HORN, F.R.S., for permission to figure the specimens of *Diplothea stellata*, KIDSTON, contained in the collection of the Geological Survey of Scotland.

EXPLANATION OF PLATES 25-28.

Crossotheca Höninghausi, BRONGT. sp.

PLATE 25.

- Fig. 1.—Portion of sterile pinna. $\times 2$.
 Fig. 2.— „ „ $\times 2$.
 Fig. 3.— „ „ $\times 2$.
 Fig. 4.—Pinna showing sterile and fertile pinnules. $\times 2$.
 Fig. 5.—Other half of the same nodule. $\times 2$.
 Fig. 6.—Portion of a pinna with a sterile pinnule *b* and fertile pinnules. $\times 2$.
 Fig. 7.—Other half of the same nodule.
 Fig. 8.—Portion of same specimen. $\times 4$.
 Fig. 9.—Specimen showing sterile and fertile pinnules. $\times 2$.
 Fig. 10.—Other half of the same nodule. $\times 2$.
 Fig. 11.—Termination of a fertile pinna. $\times 2$.
 Fig. 12.—Portion of a fertile pinna. $\times 2$.
 Fig. 13.—Microspore. $\times 500$.
 Fig. 14.— „ $\times 500$.
 Fig. 15.— „ $\times 500$.
 Fig. 16.—Two microspores. $\times 500$.

PLATE 26.

- Fig. 17.—Portion of a fertile pinna. $\times 2$.
 Fig. 18.—Fertile pinna, natural size.
 Fig. 19.—Portion of same specimen. $\times 4$.
 Fig. 20.—Fertile pinna, natural size.
 Fig. 21.—The same specimen. $\times 2$.
 Fig. 22.—Portion of the same specimen. $\times 4$.
 Fig. 23.—Fertile pinna preserved in carbonate of lime. $\times 2$.
 Fig. 24.—Sorus *k* on fig. 23. $\times 6$.
 Fig. 25.—Microsporangia showing the two loculi. $\times 10$.
 Fig. 26.— „ „ $\times 10$.
 Fig. 27.— „ „ $\times 10$.
 Fig. 28.—Microspore. $\times 500$.
 Fig. 29.— „ $\times 500$.
 Fig. 30.—Sterile pinna with ultimate pinnæ circinately coiled. $\times 2$.
 Fig. 31.—Portion of a fertile pinna. $\times 2$.
 Fig. 32.—Specimen with sterile and fertile pinnules. $\times 2$.

Crossothecca Hughesiana, KIDSTON n. sp.

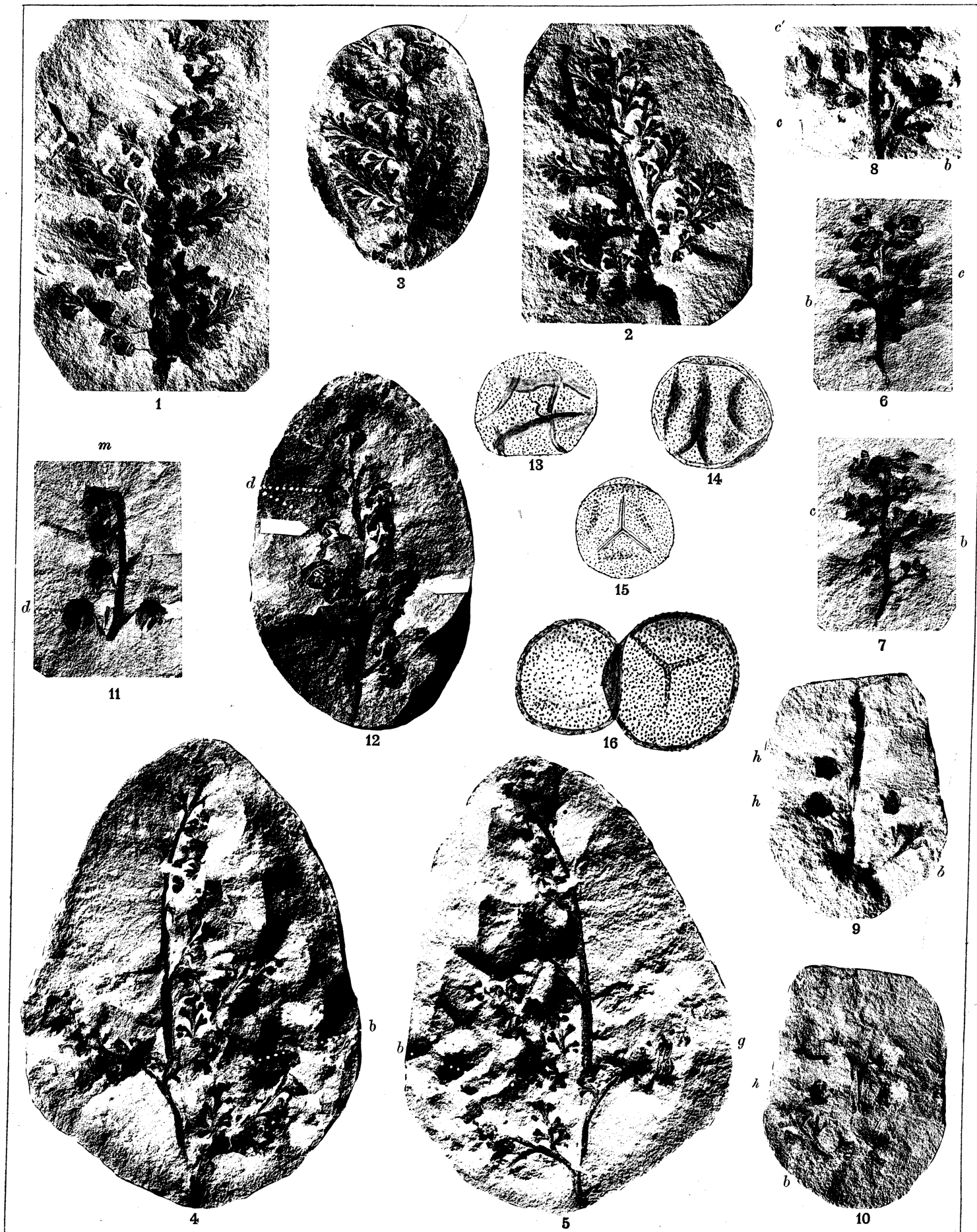
PLATE 27.

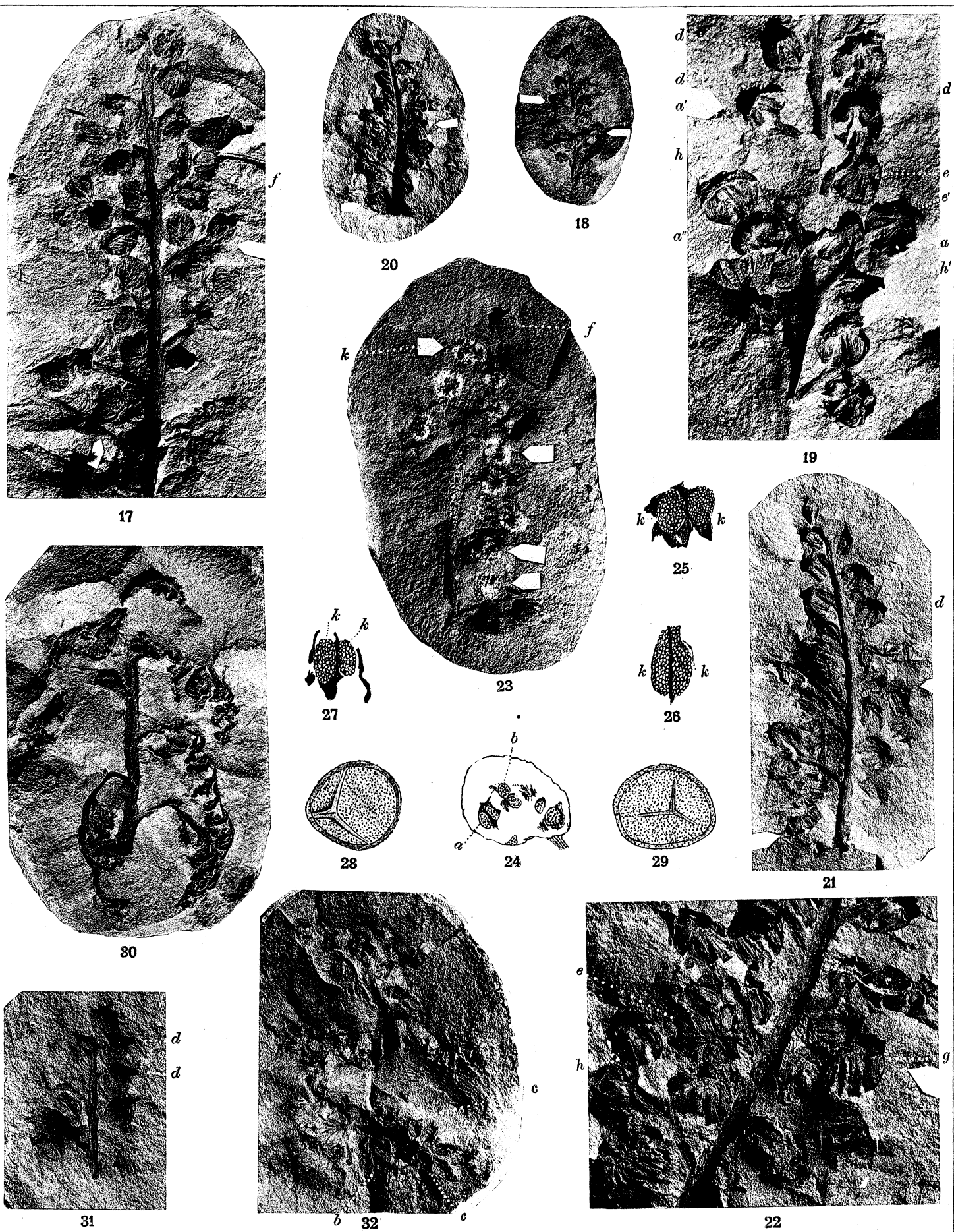
- Fig. 33.—Apical portion of a fertile pinna, natural size.
 Fig. 34.—Portion of same specimen. $\times 2$.
 Fig. 35.—Other half of nodule shown at fig. 33. Natural size.
 Fig. 36.—Portion of fig. 35. $\times 2$.
 Fig. 37.—Portion of a fertile pinna. $\times 2$.
 Fig. 38.—Microsporangium showing the two loculi. $\times 10$.
 Fig. 39.—Microspore. $\times 500$.
 Fig. 40.—Basal portion of a fertile pinna. Natural size.
 Fig. 41.—Portion of same specimen. $\times 2$.
 Fig. 42.—Apical portion of a fertile pinna. Natural size.
 Fig. 43.—Microspore. $\times 500$.
 Fig. 60.—Single sorus. $\times 2$.

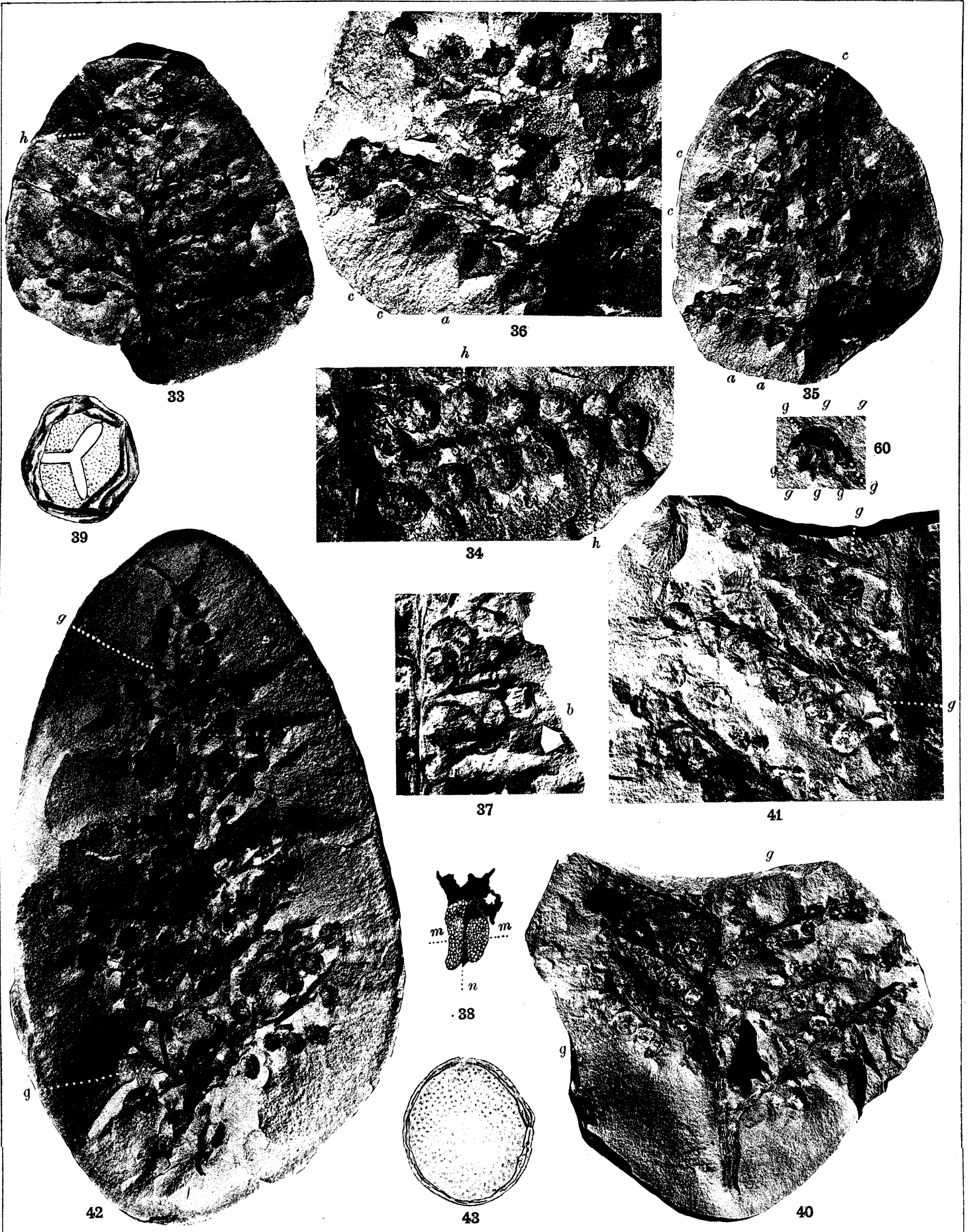
PLATE 28.

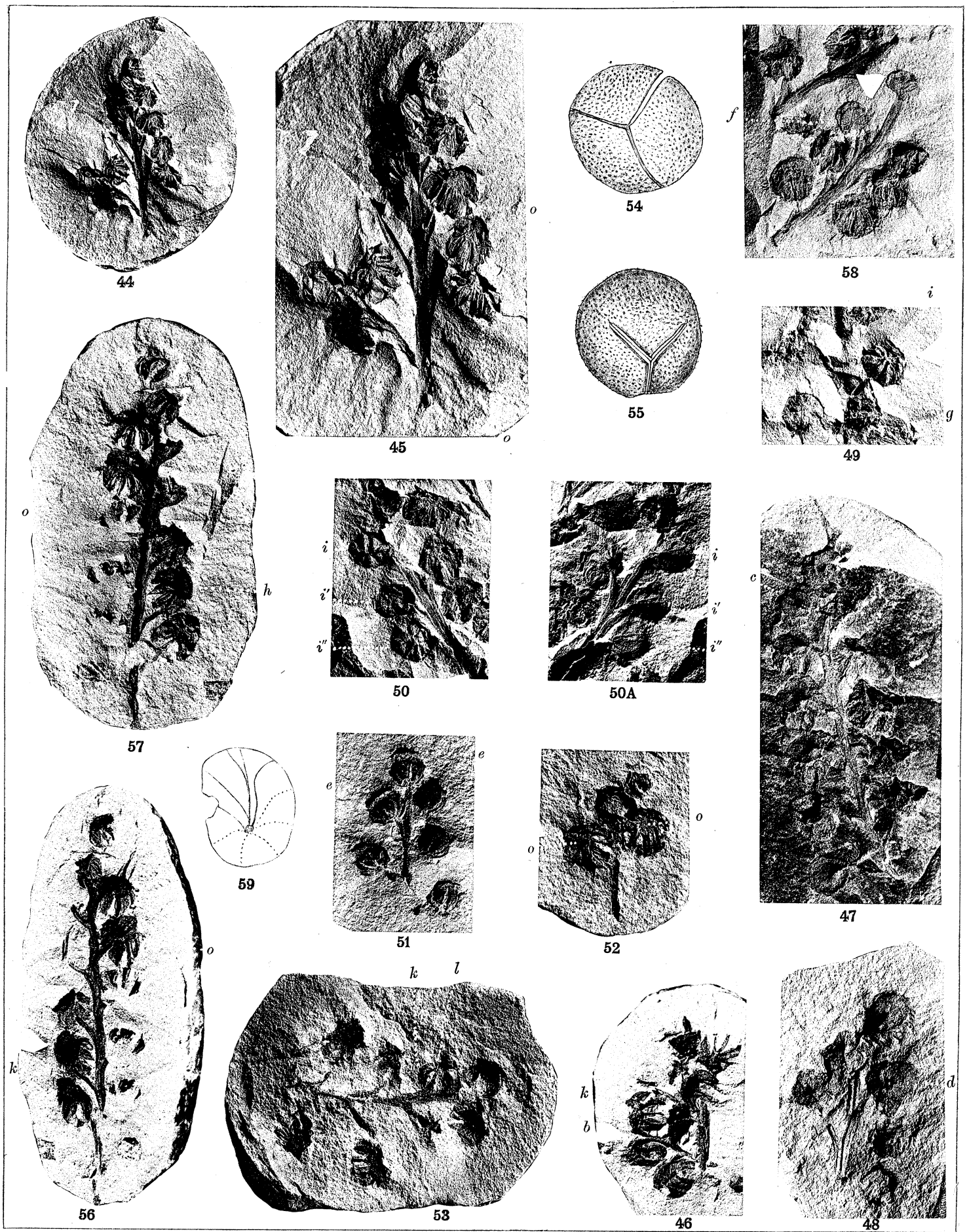
- Fig. 44.—Terminal portion of a fertile pinna. Natural size.
 Fig. 45.—Same specimen. $\times 2$.
 Fig. 46.—Portion of a fertile pinna. $\times 2$.
 Fig. 47.— " " $\times 2$.
 Fig. 48.— " " $\times 2$.
 Fig. 49.— " " $\times 2$.
 Fig. 50.— " " $\times 2$.
 Fig. 50A.—Corresponding portion of same specimen from other half of nodule. $\times 2$.
 Fig. 51.—Portion of a fertile pinna. $\times 2$.
 Fig. 52.— " " $\times 2$.
 Fig. 53.— " " $\times 2$.
 Fig. 54.—Microspore. $\times 500$.
 Fig. 55.— " $\times 500$.
 Fig. 56.—Portion of a fertile pinna. $\times 2$.
 Fig. 57.—Other half of the same nodule. $\times 2$.
 Fig. 58.—Portion of a fertile pinna. $\times 2$.
 Fig. 59.—Nervation of a fertile pinnule. $\times 6$.

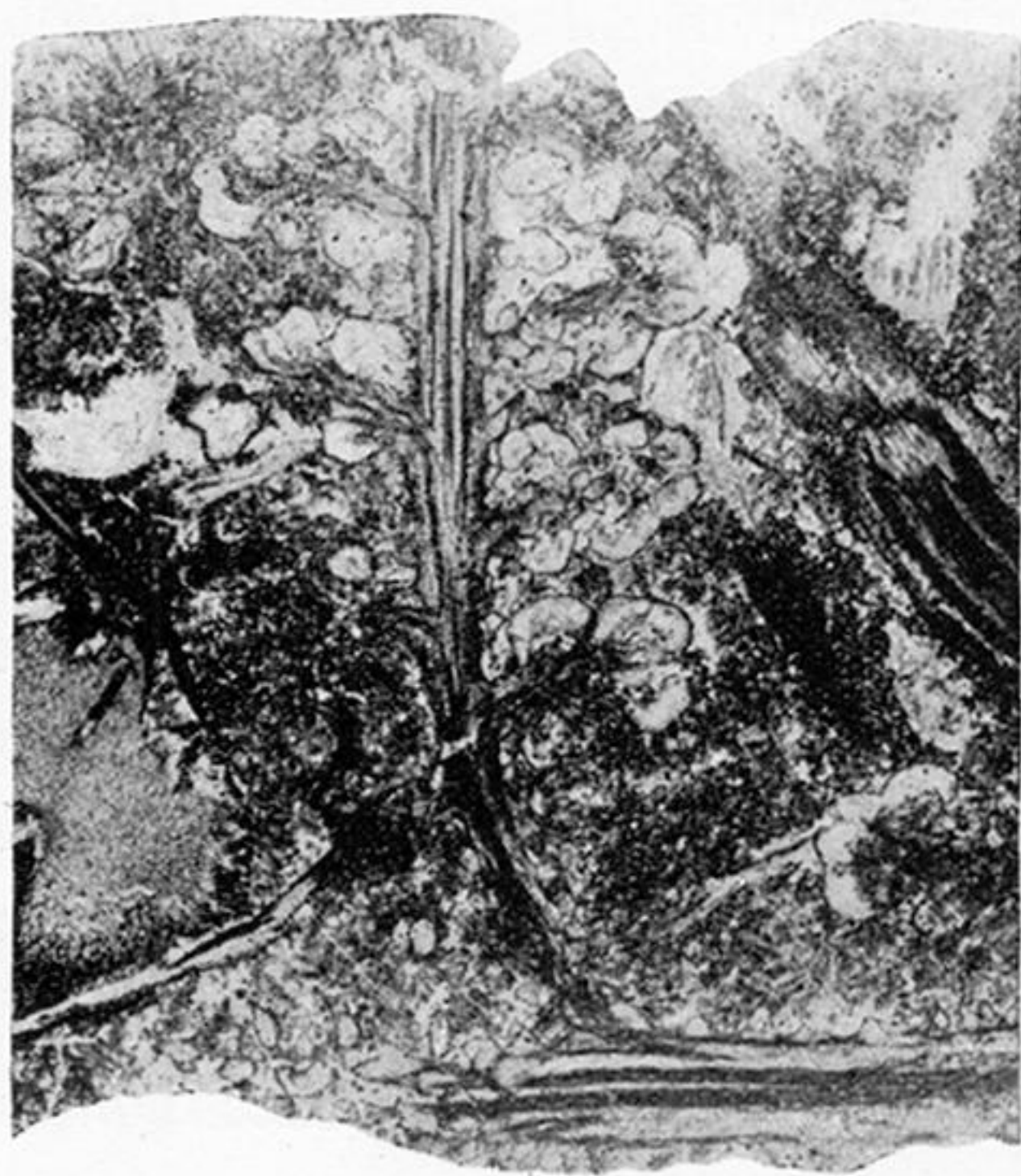
All the specimens are from the "10-feet Ironstone Measures" which form the roof of the "Thick Coal," Coseley, near Dudley (Westphalian Series), and were communicated by Mr. H. W. HUGHES, F.G.S., except fig. 11, which was received from Mr. J. T. STOBBS, F.G.S., Stoke-upon-Trent, to whom my thanks are also due.



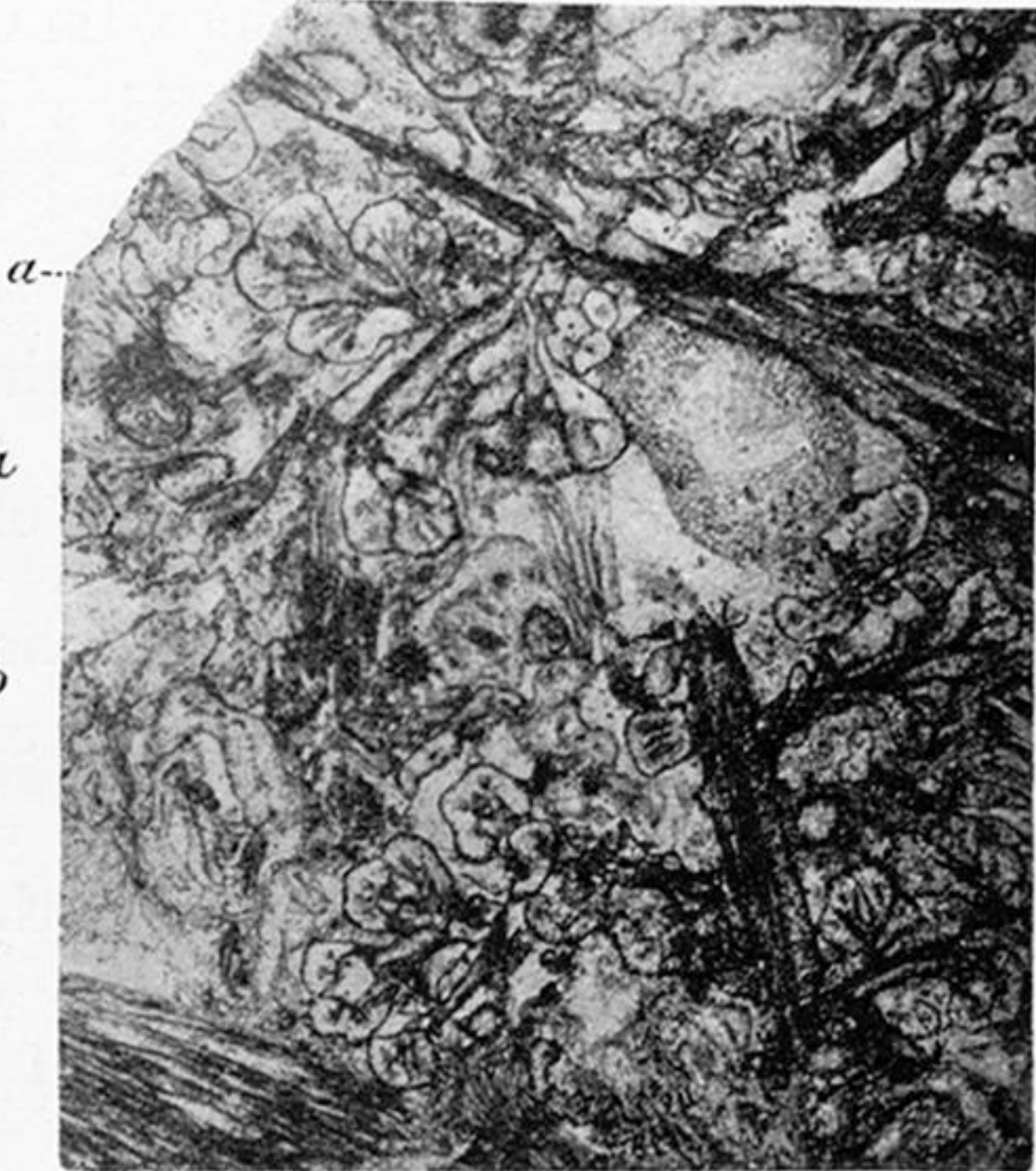








A



B

FIG. 1.—*Crossotheca Höninghausi*, BRONGT. sp. (*Lyginodendron Oldhamium*, WILLIAMSON).

A. Form of sterile pinnules, with convex segments. Halifax. *Horizon*.—Halifax Hard Bed, Lanarkian Series. $\times 6$. (K/632.) B. Form of sterile pinnules, with flattened segments. Dulesgate. *Horizon*.—Halifax Hard Bed, Lanarkian Series. $\times 6$. (K/664c.)

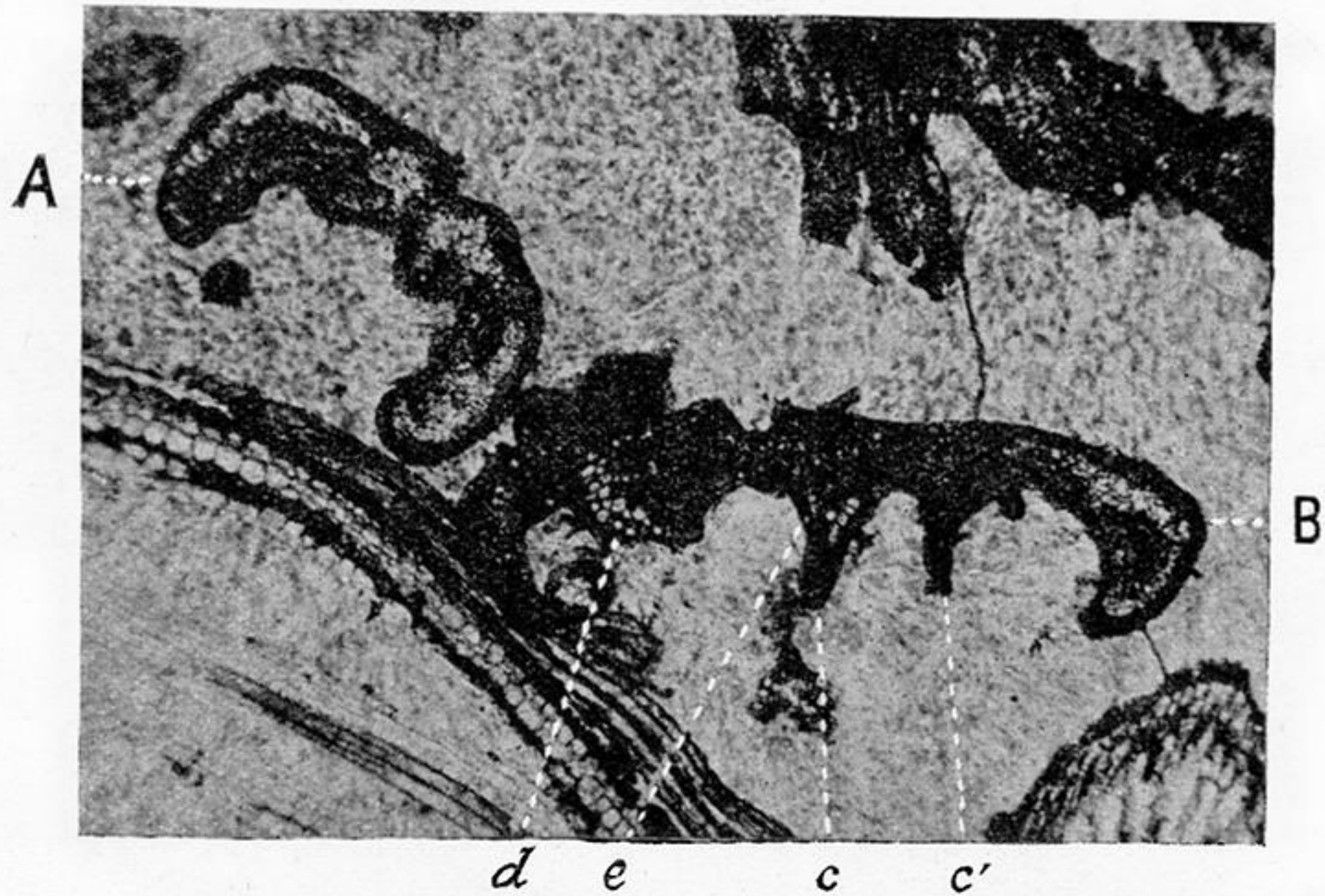


FIG. 2.—*Crossotheca Höninghausi*, BRONGT. sp. (*Lyginodendron Oldhamium*, WILL.).

Transverse section of foliage, showing convex form of pinnule at A, and spines springing from the surface of fragment of another pinnule, B, at *c*, *c'*; at *d* is seen the midrib of the pinnule, and at *e* one of the lateral veinlets. Dulesgate. *Horizon*.—Halifax Hard Bed. × 22. (K/664A.)



FIG. 3.—*Crossotheca Höninghausi*, BRONGT. sp.

Form of sterile pinnules with convex segments. From pit sinking, Tullygarth Pit, near Clackmannan.

Horizon.—Lanarkian Series. Natural size. (K/938.)



FIG. 4.—*Crossotheca Höninghausi*, BRONGT. sp.

Form of sterile pinnules with flattened segments, showing the spines attached to the foliage, *a*, and the spiny rachis, *b*. $\times 4$. DOULTON'S marl quarry, Netherton, South Staffordshire. *Horizon*.—Between Fireclay Coal and Bottom Coal, Westphalian Series. Collected by Mr. H. W. HUGHES, F.G.S. (K/940.)

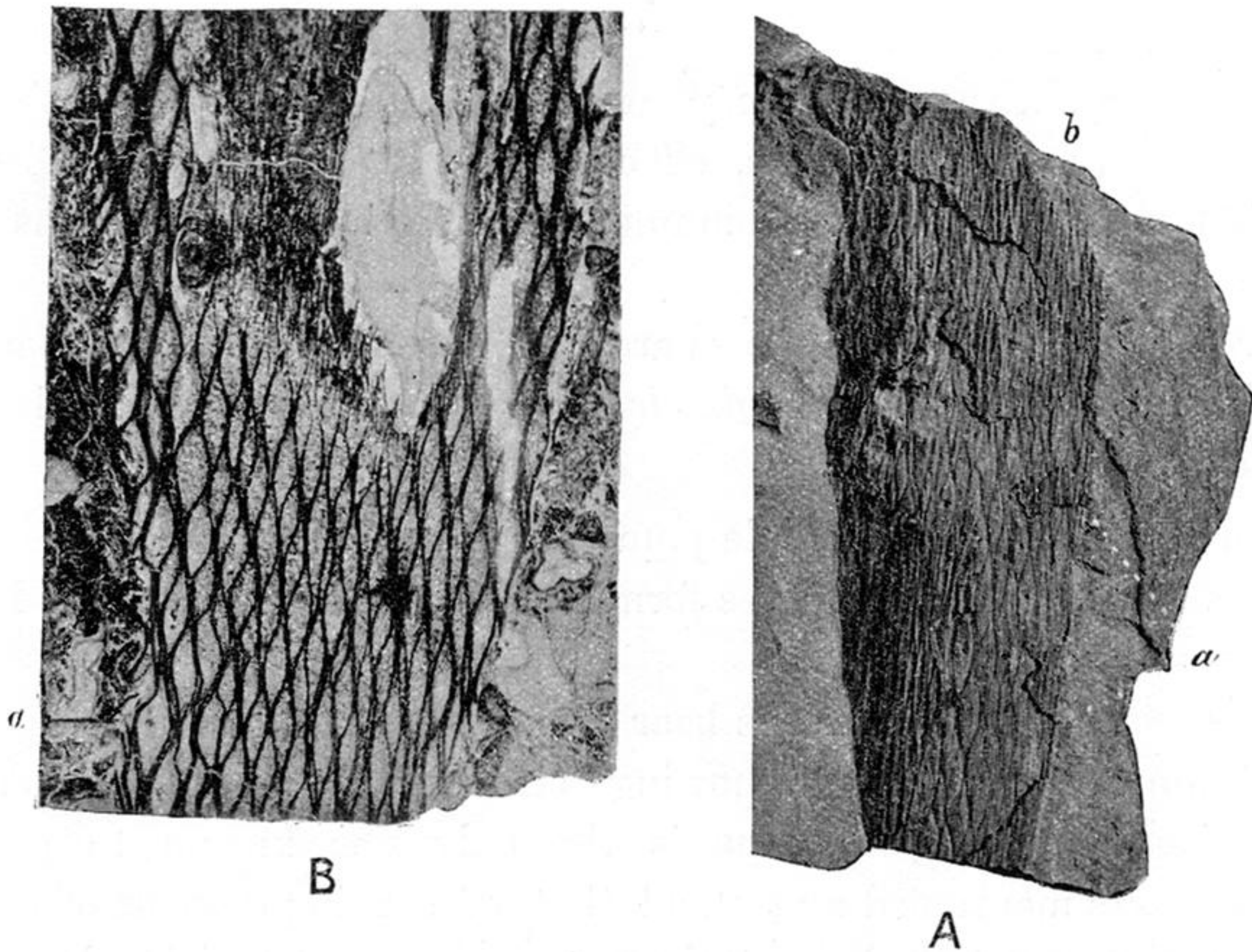


FIG. 5.—*Crossotheca Höninghausi*, BRONGT. sp. (*Lyginodendron Oldhamium*, WILL.).

- A. Impression of outer surface of stem, showing at *a* and other portions of the fossil the rhomboidal areas formed by the sclerenchymatous bands, in the centres of some of which the scars of the spines are seen. Compressed and carbonised portions of the sclerenchymatous outer cortex are seen adhering to the impression, as at *b*. Whitehall Colliery, Rosewell, Midlothian. *Horizon*.—Lanarkian Series. Natural size. (K/3218.)
- B. Tangential section through the outer cortex of stem, showing the net-like structure of the sclerenchymatous bands. At *a* the punctiform remains of two spines are seen. Dulesgate. *Horizon*.—Halifax Hard Bed. Lanarkian Series. $\times 2$. (K/592G.)

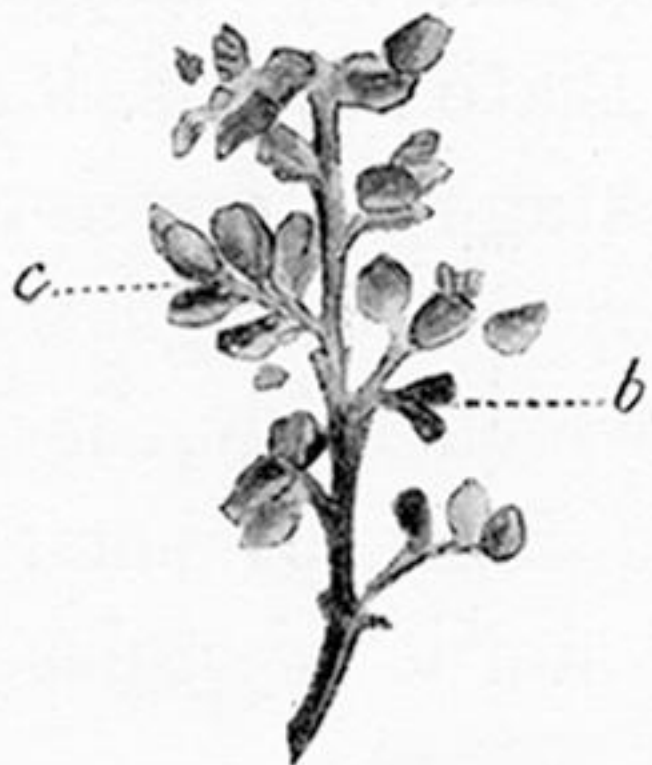


FIG. 6.—*Crossotheca Höninghausi*, BRONGT. sp.

Specimen given on Plate 25, fig. 7, drawn without surrounding matrix to show upper surface and form of the fertile pinules. $\times 2$.

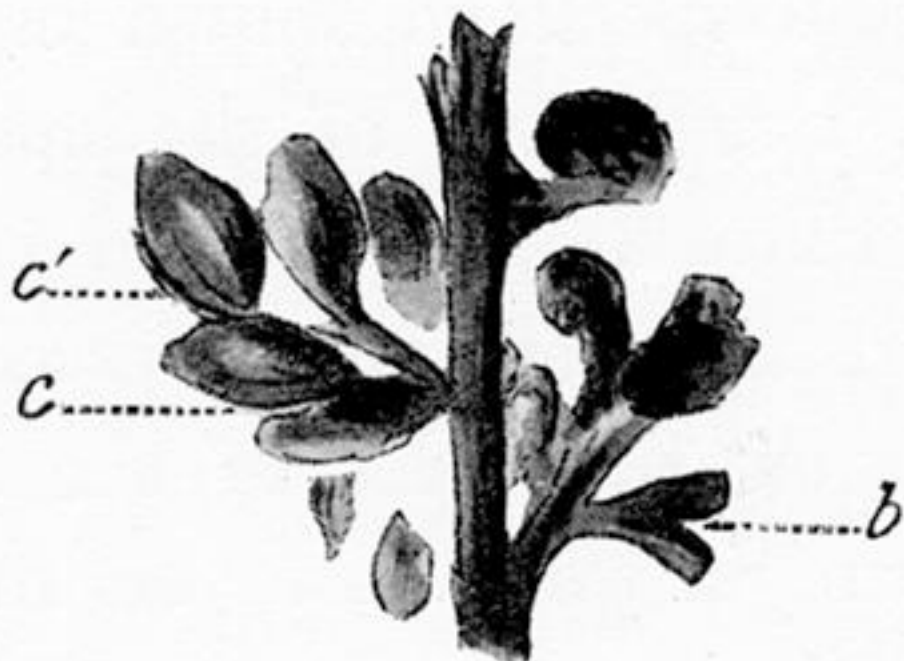


FIG. 7.—*Crossotheca Höninghausi*, BRONGT. sp.

Portion of specimen shown on Plate 25, fig. 7, and at text-fig. 6, enlarged 4 times.



FIG. 10.—*Telangium affine*, L. & H. sp.

Synangium showing microsporangia. $\times 4$. West Calder, Midlothian. *Horizon*.—Oil Shale Group, Calciferous Sandstone Series. Collected by the late C. W. PEACH, F.L.S. (No. K/648.)

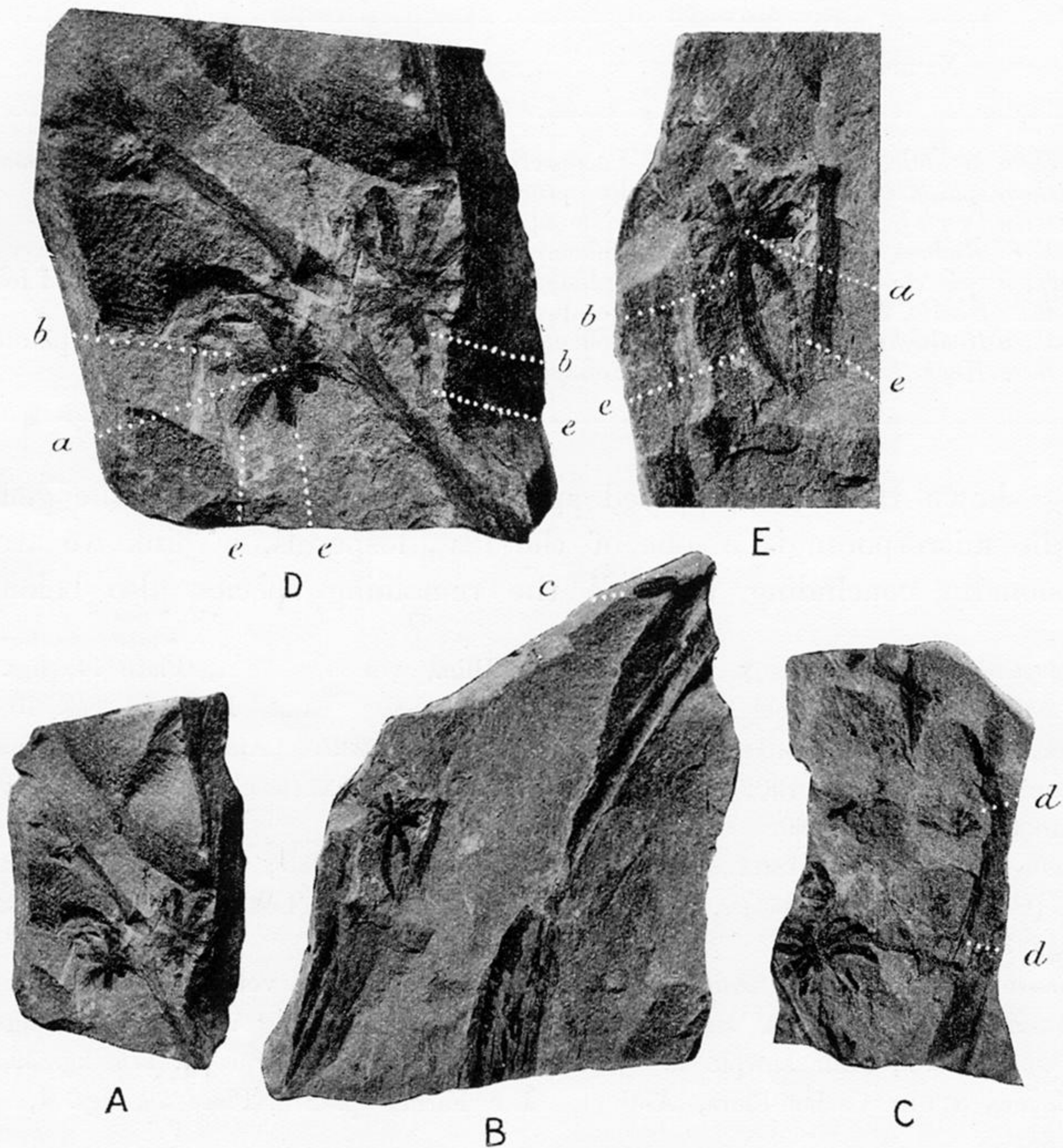


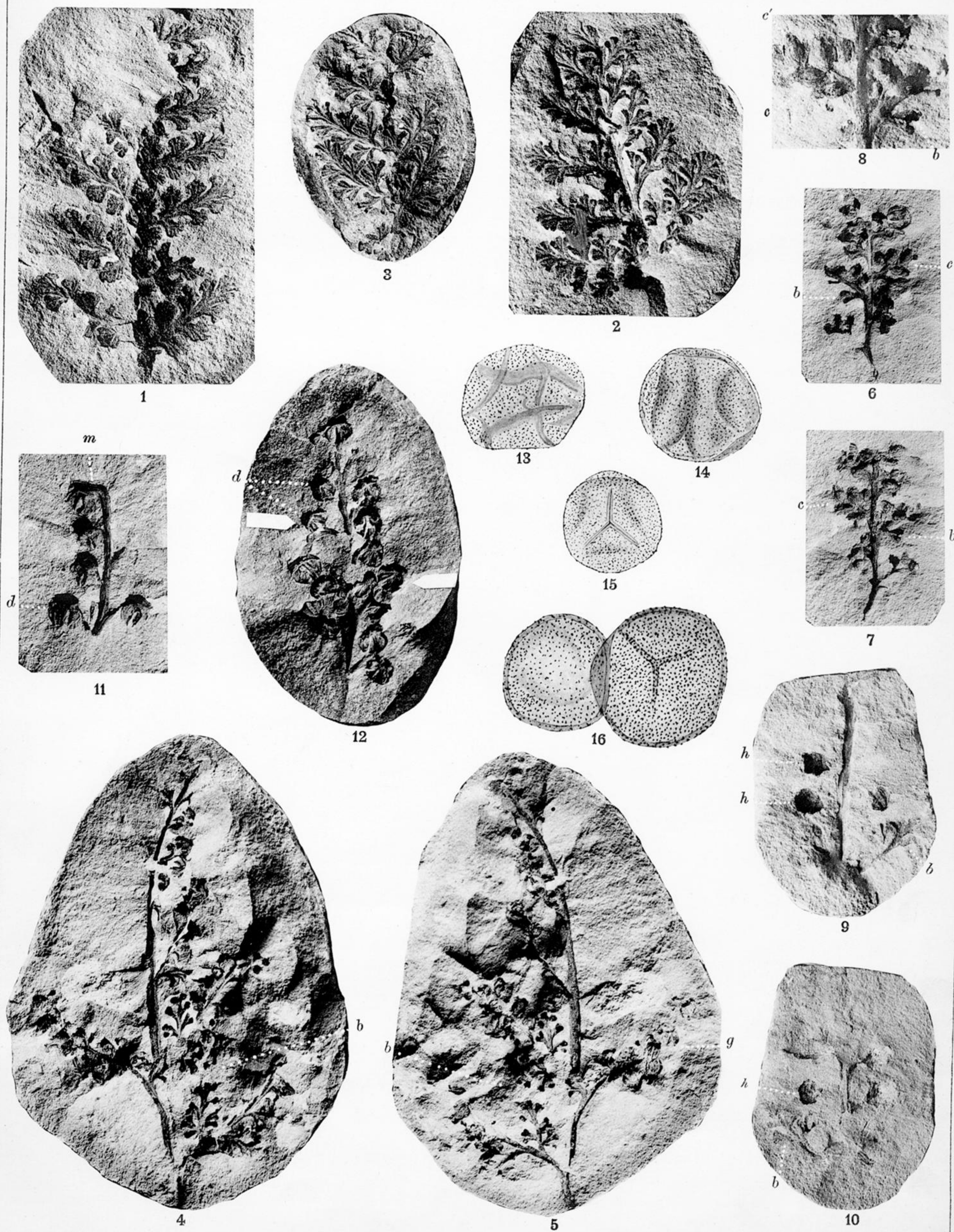
FIG. 11.—*Diplothecca stellata*, KIDSTON.

A, B, C, three specimens, natural size; D and E (A and B) enlarged two times to show more clearly the union of the microsporangia in pairs. Macrihanisch Water, near Wimbleton Pit, Campbeltown, Kintyre, Argyllshire. Collected by Mr. A. MACCONOCHIE. Specimens in the collection of the Geological Survey of Scotland. (Nos. M/3172E, M/3173E, M/3174E.)



FIG. 13.—*Archæopteris hibernica*, FORBES sp.

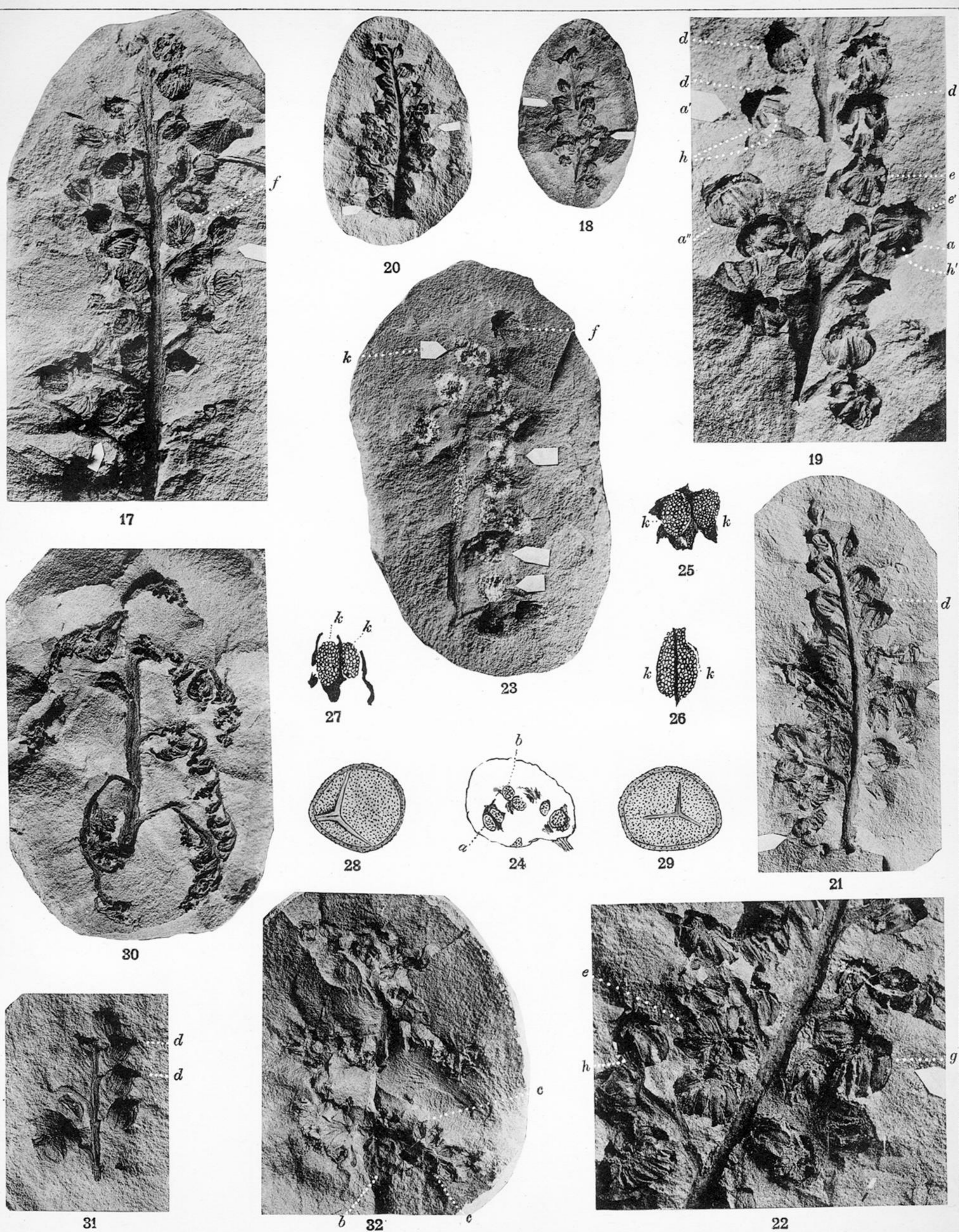
Base of petiole, showing stipular appendages (much reduced). From the Upper Old Red Sandstone of Kiltorcan, Kilkenny. Specimen in the collection of the Geological Survey of Ireland, Dublin.



Crossotheca (Lyginodendron) Höninghausi, Brongt. sp.

PLATE 25.

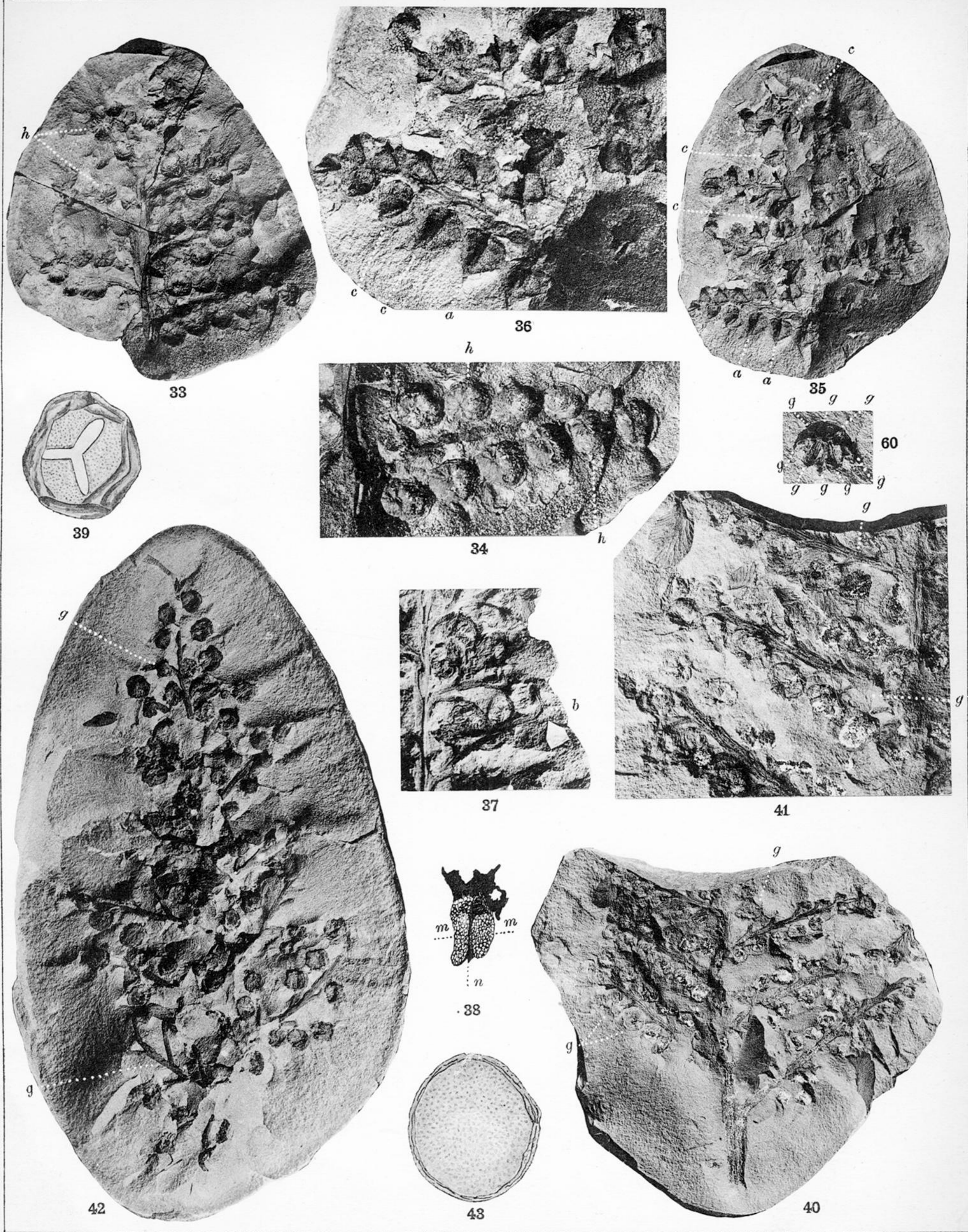
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 Fig. 2.— " " $\times 2$.
 Fig. 3.— " " $\times 2$.
 Fig. 4.—Pinna showing sterile and fertile pinnules. $\times 2$.
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 Fig. 8.—Portion of same specimen. $\times 4$.
 Fig. 9.—Specimen showing sterile and fertile pinnules. $\times 2$.
 Fig. 10.—Other half of the same nodule. $\times 2$.
 Fig. 11.—Termination of a fertile pinna. $\times 2$.
 Fig. 12.—Portion of a fertile pinna. $\times 2$.
 Fig. 13.—Microspore. $\times 500$.
 Fig. 14.— " $\times 500$.
 Fig. 15.— " $\times 500$.
 Fig. 16.—Two microspores. $\times 500$.



Crossothea (Lyginodendron) Höninghausi, Brongt. sp.

PLATE 26.

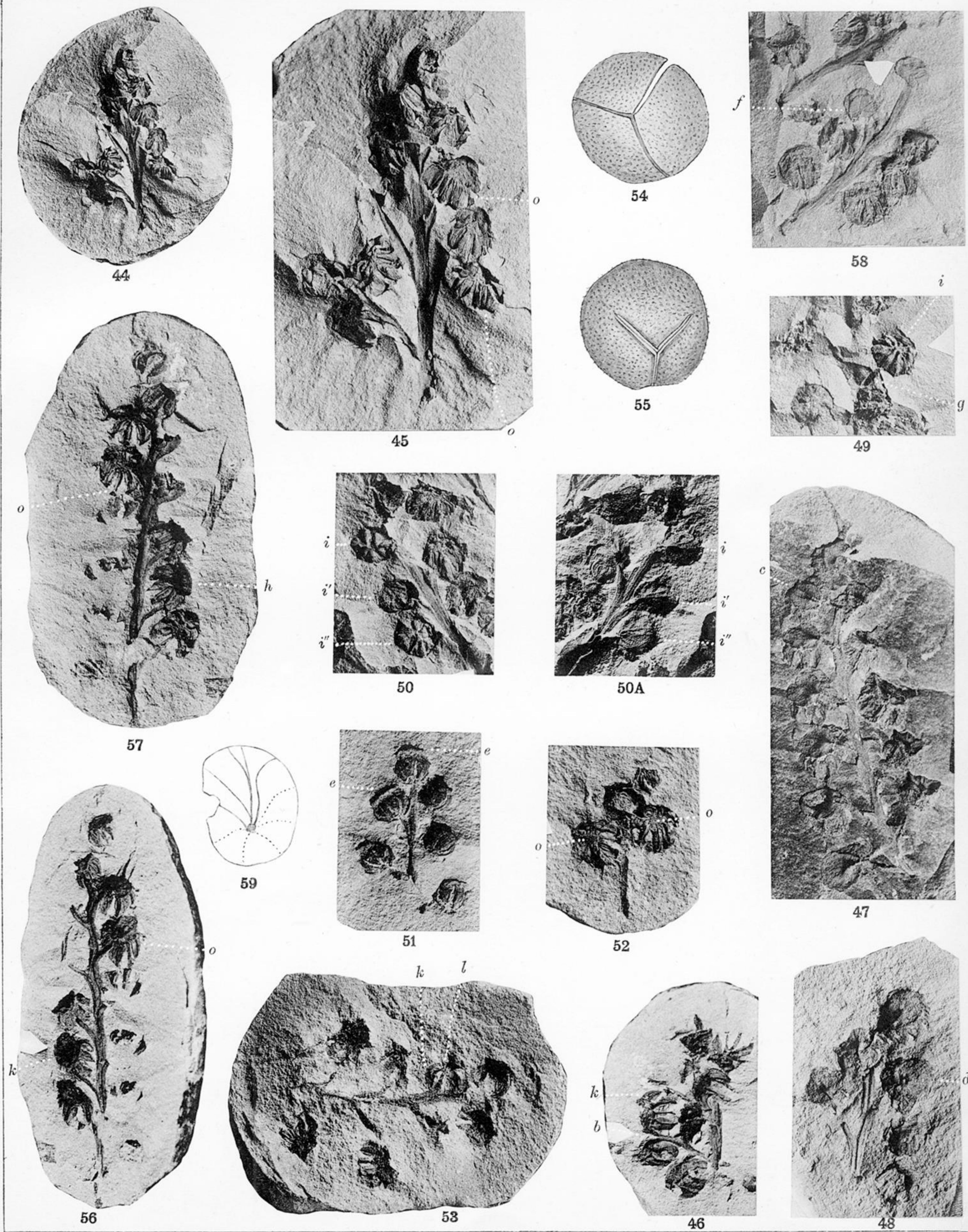
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 Fig. 27.— " " " $\times 10$.
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 Fig. 30.—Sterile pinna with ultimate pinnæ circinately coiled. $\times 2$.
 Fig. 31.—Portion of a fertile pinna. $\times 2$.
 Fig. 32.—Specimen with sterile and fertile pinnules. $\times 2$.



Crossotheca Hughesiana, Kidston n. sp.

PLATE 27.

- Fig. 33.—Apical portion of a fertile pinna, natural size.
 Fig. 34.—Portion of same specimen. $\times 2$.
 Fig. 35.—Other half of nodule shown at fig. 33. Natural size.
 Fig. 36.—Portion of fig. 35. $\times 2$.
 Fig. 37.—Portion of a fertile pinna. $\times 2$.
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 Fig. 43.—Microspore. $\times 500$.
 Fig. 60.—Single sorus. $\times 2$.



Crossotheca Hughesiana, Kidston n. sp.

PLATE 28.

- Fig. 44.—Terminal portion of a fertile pinna. Natural size.
 Fig. 45.—Same specimen. $\times 2$.
 Fig. 46.—Portion of a fertile pinna. $\times 2$.
 Fig. 47.— " " $\times 2$.
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 Fig. 50.— " " $\times 2$.
 Fig. 50A.—Corresponding portion of same specimen from other half of nodule. $\times 2$.
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 Fig. 57.—Other half of the same nodule. $\times 2$.
 Fig. 58.—Portion of a fertile pinna. $\times 2$.
 Fig. 59.—Nervation of a fertile pinnule. $\times 6$.