

Contributions to the Knowledge of Lower Carboniferous Plants. I. On the Genus Rhacopteris, Schimper. II. On the Morphology of Sphenopteris Teiliana, Kidston, and Its Bearing on the Position of the Fructification on the Frond of Some Lower Carboniferous Plants

John Walton

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[201]

IV. Contributions to the Knowledge of Lower Carboniferous Plants.

I.—On the Genus Rhacopteris, SCHIMPER.

II.—On the Morphology of Sphenopteris Teiliana, KIDSTON, and its Bearing on the Position of the Fructification on the Frond of some Lower Carboniferous Plants.

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(Communicated by Prof. F. E. WEISS, F.R.S.)

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(PLATES 16, 17.)

CONTENTS.

				PAGE
I.	. The Form-genus <i>Rhacopteris</i> , Schimper.			
	(a) Introductory			. 201
	(b) The Nature of the Stem of <i>Rhacopteris</i>			. 203
	(c) The Fructification of <i>Rhacopteris</i>			. 205
	(d) Rhacopteris circularis sp. nov.; R. petiolata Göpp. sp.; R. sp.; Sphenopteris (Rhad	copt	eris)
	<i>Weissii</i> , sp. nov			. 208
II.	. The Morphology of Sphenopteris Teiliana, KIDSTON.			*
	(a) The Morphology of Sphenopteris Teiliana, KIDSTON.			. 212
	(b) The Position of the Fructification on the Frond of some Lower Carboniferous	Pl	ants	s 216

I.—THE FORM-GENUS Rhacopteris, SCHIMPER.

(a) Introductory.

The genus *Rhacopteris* was instituted by SCHIMPER* in 1869 for a type of fern-like frond of Carboniferous Age.[†] It included one species *Rhacopteris elegans*, ETTINGS-HAUSEN sp. In 1879[‡] the conception of the genus was extended and the following species were included: *Rhacopteris inæquilatera* and *R. petiolata*, GÖPPERT spp.,

* Schimper, W. Ph. (1869), р. 481-482.

It has been pointed out by KIDSTON ((1923), Part 3, p. 203) that the suggestion that the frond was bipinnate arose from a misinterpretation of the specimen on which this diagnosis is based.

‡ Idem (1879), in Zittel, p. 112–113.

VOL. CCXV.-B 424.

2 D

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202

JOHN WALTON ON CONTRIBUTIONS TO THE

R. paniculifera and R. transitionis, STUR spp., R. speciosa, ETT., and Rhacopteris sp. GOMES. The Upper Carboniferous representatives differ in some respects from those of the Lower Carboniferous, and OBERSTE-BRINK* suggests a subdivision of the genus into Eurhacopteris and Anisopteris; Eurhacopteris, including the Upper Carboniferous forms, R. elegans, ETT. sp., R. asplenites, GUTBIER sp., R. dubia, LINDLEY and HUTTON sp., R. Busseana, STUR, and R. Moyseyi, ARBER; Anisopteris, including all the Lower Carboniferous forms. OBERSTE-BRINK regards this as a more natural grouping of the constituents of *Rhacopteris*, SCHIMPER, considering, moreover, that it receives support from the fact that this division of the genus corresponds to a stratigraphical separation of no small order. OBERSTE-BRINK states that no Rhacopterids have been recorded from strata lying between the Middle Productive (Westphalian Series, Upper Carboniferous) Measures and the Culm (Lower Carboniferous). Since it is doubtful whether the division of the genus he suggests is a natural one, and not one with a stratigraphical bias, it seems on the whole inadvisable to adopt this nomenclature. The term *Rhacopteris* is of such widespread use among authors for these Lower Carboniferous fronds that it would merely increase the synonymy without any obvious advantage from the point of view of the systematist. We are concerned only with the Lower Carboniferous species in this communication.

The fern-like fronds of *Rhacopteris* are characteristically pinnate,[†] linear, and contracted towards the base. The pinnules are opposite or alternate, often asymmetric, contracted at the base, entire or divided into lobes, each of which has one or more veins. The texture of the lamina in many of the species was probably coriaceous. No midrib is present in the pinnule, but in some species by a series of unilateral dichotomies a one-sided arrangement results, from which it appears that a main vein passing along the lower margin of the pinnule gives rise to a series of more or less equal veins, which traverse the lamina to the upper margin, dichotomising one or more times on the way. No anastomoses have been observed between the veins.

One fructification has been described. *Rhacopteris paniculifera*, STUR,[‡] of which only one specimen is known, consists of a frond, the lower part with foliage pinnules pinnately arranged on it, the upper part bearing terminally an apparently dichotomously branched frond, the ultimate branches of which bear sporangia. KIDSTON'S definition§

[†] KIDSTON, R. (1923), p. 203, para. 2, with reference to the supposed bipinnate structure of *Rhacopteris* elegans, ETT. sp. *Ibid.*, Plate LIII, figs. 1 and 1A. In *Rhacopteris transitionis*, STUR, the dissection of the lamina is such that the frond can be considered bipinnate.

‡ STUR, D. (1875), pp. 72-75, Plate VIII, fig. 3.

§ KIDSTON, R. (1923), p. 203. "Frond, linear, narrowing toward the base and contracted into a point at the apex. Rachis straight or rarely slightly flexuous. Pinnules alternate, close, overlapping or touching, sometimes more or less distant, flabelliform, semi-flabelliform, or rhomboidal, entire, crenate, lobed or divided into narrow linear segments, placed at right angles or slightly obliquely to the axis. Fructification (in the only known case) consists of a terminal dichotomous panicle which bears exannulate sporangia."

^{*} Oberste-Brink, K. (1914), p. 95.

of the genus, given in the memoir on Carboniferous plants, may be taken as a brief summary of the knowledge of the genus. It will be noticed that there is no reference to the nature of the stem which bore these fronds, to the method of vernation, or to the habit of the plants which bore them. It is remarkable how little is known about this genus of plants so characteristic of the Lower Carboniferous Rocks. Under these circumstances the discovery by Mr. P. J. W. KILPATRICK, of King's College, Cambridge, of a portion of a stem with two fronds in organic connection with it is of considerable interest. The specimen is in the collection of Lower Carboniferous plants (2015*a*) in the Sedgwick Museum, Cambridge.

While engaged in an investigation of the Lower Carboniferous Flora of the Upper Black Limestone at Gwaenysgor, Flintshire, I found the fructification of a *Rhacopteris* which differs in some respects from the only other *Rhacopteris* fructification known. At the same locality several species of sterile *Rhacopteris* fronds were found. In addition to *R. petiolata*, Göpp., which has already been figured and described from that locality by KIDSTON,* two types were found which exhibit distinctive characters and cannot be assigned to any hitherto described species. At a lower horizon in the same neighbourhood another type of frond was found, which is probably referable to *Rhacopteris*.

A definite conclusion cannot be drawn for the present to what phylum of plants *Rhacopteris* belongs. The evidence suggests a relationship with the ferns. The fertile frond is not unlike the fertile lobe of *Botrychium*. The sterile fronds are very similar to the sterile part of the frond of *Botrychium lunaria*,[†] but these features of resemblance appear in other families of ferns as well. There is also the possibility that *Rhacopteris* may prove to be a Pteridosperm, but from our present knowledge of the group and in consideration of some additional facts to be demonstrated below, it would seem that the evidence is perhaps in favour of a Fern rather than a Pteridosperm connection.

(b) On the Nature of the Stem of Rhacopteris.

Rhacopteris inæquilatera, Göppert, sp.‡

The specimen which is figured natural size on Plate 16, fig. 1, was found by Mr. KILPATRICK in a large block of grey, sandy mudstone from the upper part of the strata exposed in Hailes Quarry, Kingsknowe, Midlothian, belonging to the Wardie Shales, Oil-Shale Group, Calciferous Sandstone Series. The fossil is seen to consist of two fronds and a portion of a shoot. In the actual specimen, about one centimetre more of the tops of the two fronds is represented than is shown in the figure. The fronds converge towards the base, and one is seen to be in organic connection with the shoot; the other is also attached close beside the first, but the actual connection is not shown in the specimen,

^{*} KIDSTON, R. (1923), Part 3, p. 215; Plate LIII, figs. 3 and 3A.

[†] STUR, D. (1875), p. 72, places R. paniculifera in the Ophioglossacea.

[‡] An adequate synonymy is given by KIDSTON (1923), Part 3, p. 208.

204

JOHN WALTON ON CONTRIBUTIONS TO THE

as it exists at present, for the base of the second frond is covered by matrix. The removal of this matrix would have involved the risk of damaging the upper part of the shoot, and was, therefore, not attempted.

Each frond has a simple rachis, 1.7 mm. wide near the top, gradually expanding to $2 \cdot 5$ mm. at the base, where it is attached to the stem. The pinnules, the lowest of which is inserted about 3 cm. from the point of attachment of the rachis or petiole, are at first arranged in opposite pairs, but farther up the frond they alternate in position. Each pinnule is inserted on the rachis about 11 mm. from the point of insertion of the pinnule above or below it on the same side of the frond. This distance seems to be almost constant on the parts of the frond visible in the specimen. The lower pinnules are narrow and cuneate and slit distally into several segments. Farther up the frond from the base the pinnules are of larger size and overlap. Each pinnule is set at an angle to the principal plane of the frond, so that, although they overlap, the upper margin of the lower pinnule is separated by a considerable thickness of matrix from the lower margin of the pinnule next above it. This set of the pinnules has resulted in most of their extremities being broken off and removed in the counterpart of the speci-The larger pinnules higher up on the fronds, when completely represented, are men. seen to be semi-flabelliform or cuneate, and asymmetric. The footstalk or base of each pinnule is set obliquely to the rachis. The upper margins of the pinnules when completely represented are irregularly lobed or crenulate. The venation is indistinct, but the veins are seen to be closely set and to dichotomise at least twice after leaving the base of the pinnule.

The shoot of the specimen is represented by a film of carbonaceous matter with an irregular, broken surface. It is about 3 cm. long and about $1\cdot 3$ cm. wide. The margin of the black film representing the shoot, seen most distinctly along the upper side (Plate 16, fig. 1), has short irregular projections. The constriction of the shoot seen just below the insertion of the frond is not an original feature, but is due to a portion having been removed in the counterpart. There are parts of three, or possibly more, elongated structures attached to the upper end of the shoot and one just below the right-hand frond on the upper side. These larger projections which are attached to the apex of the shoot have a smoother surface and consist of a thinner coaly layer The shoot has an abrupt termination about 3 cm. below the bases of than the rest. the fronds. There are a few small linear structures attached to the shoot at the lowest point represented in the figure. There are several fragments of similar structures lying about in different parts of the slab.

Discussion.

In placing the photograph in the position and with the orientation shown in the plate, it is assumed that the fronds were orientated vertically in their growth posture. The larger projections at the apex of the branch are probably the bases of the petioles of other fronds. It will be noticed that the largest of them is attached to the lower side of the shoot as represented in the figure and is bent toward the upper side. This

indicates quite definitely that the shoot was of radial construction, and also suggests that it was inclined to the vertical, very approximately in the position shown in the figure. The small linear structures attached to the base of the shoot are possibly adventitious roots. The other projections seen along the upper side of the shoot may represent the remains of petioles of older fronds which had fallen off before fossilisation occurred. Of the fronds, judging from the dimensions of those of *Rhacopteris Lindsexformis* and *R. inæquilatera** with which this specimen is most closely allied, only about one-half of the original length is represented.

The two species R. Lindseæformis, BUNB. sp. and R. inæquilatera are closely related forms, and it is difficult to distinguish the one from the other in specimens in which the preservation is either not sufficiently good to allow of an estimation of the number of veins terminating in unit length of the margin of the pinnule or do not consist of the greater part of an entire frond.

KIDSTON says, "At one time I regarded them as forming a single species, but the discovery of more perfect specimens . . . has shown me that the two plants, though closely related, are clearly specifically distinct." He continues: "In R. Lindsexformis the pinnules are more obliquely placed on the rachis, the basal margin is convex or concavo-convex, the nervation is more distant, and the pinnule is more wedge-shaped. In R. inæquilatera the pinnules are longer in proportion to their width, the lower margin is concave and the pinnule is more horizontal and sometimes bent slightly downwards, with a fine crenulated upper margin; the veins are much more numerous and closer together."

Fortunately, a comparison can be made between corresponding parts of the frond of the specimen (Plate 16, fig. 1) and those of R. Lindseæformis and R. inæquilatera. The basal parts of both these species of fronds are figured by KIDSTON.[†] Some of the figures of fronds of R. inæquilatera are so similar to the Hailes Quarry specimen that an attribution of this specimen to R. inæquilatera GÖPPERT is amply justified.

(c) On the Fructification of Rhacopteris.

Rhacopteris fertilis sp. nov.

Frond bearing sporangia without any sterile pinnules. Rachis about 3 mm. broad at the base, forking about two-thirds of the way up into two equal arms. Each arm pinnately branched in the plane of the frond. The sporangia are borne on the branches of each arm or on their subdivisions. Sporangia exannulate, ovoid, striated, about 0.7 mm. wide and 1.5 mm. long.

The following description is based on the fossil figured in Plate 16, fig. 2, which was found in the quarry at Teilia Farm, Gwaenysgor, in Flintshire, in beds forming the basal part of the Upper Black Limestone, Mountain Limestone Series, Lower Carboniferous.[‡]

- * KIDSTON, R. (1923), Part 3, pp. 205 and 208, Plate XLIX, fig. 1, and Plate L, fig. 2.
- † KIDSTON, R. (1923), Part 3, p. 206, Plate XLIX, figs. 5 and 6, Plate L, fig. 4.
- ‡ Morton, G. H. (1891), p. 9.

TRANSACTIONS SOCIETY SCIENCES SCIENCES

206

JOHN WALTON ON CONTRIBUTIONS TO THE

The specimen consists of a bare rachis with a terminal branching system bearing sporangia. The rachis is 2.5 mm. broad, coarsely striated longitudinally, and slightly flexuous, terminating somewhat abruptly at the base, where some black carbonaceous material is preserved. The upper part of the frond is divided into two parts by a forking of the rachis 8.5 cm. above its base. The two parts are of equal size, are symmetrical as regards the axis, and are almost completely covered with the remains of large numbers of sporangia. They are freely branched; the bases of two of the lesser branches can be seen at the base of the right branch of the frond (Plate 16, fig. 2), and the extremity of another can be seen quite distinctly as a thin, curved, black band, 0.3 mm. wide, on the left-hand side of the left-hand division of the frond (Plate 16, fig. 3, near the bottom of the figure slightly to the left of the centre line). Small branches were present on the inner sides also of the two main branches, as is clearly shown by the distribution of the masses of sporangia (Plate 16, fig. 2). The three sporangia shown above the middle in fig. 3 must have been attached to a branch arising on the right-hand side of that division of the frond. The length from the tip of the main branch of each half of the frond to the main fork of the rachis is approximately 4 cm. The sporangia are borne in dense clusters, and are for the most part poorly preserved. One group of three has a definite outline, and allows one to make out the shape of the individual sporangia (Plate 16, fig. 4). As they appear in this group they are not quite symmetrical. Even after repeated attempts no spores were obtained by maceration of the coaly residue from the remains of the sporangia. The sporangia are ovoid, or approximately ovoid, about 0.7 mm. wide and 1.5 mm. long. They are distinctly striated (Plate 16, fig. 4).

Discussion.

The only fructification of *Rhacopteris* hitherto described is that figured by STUR in the Culm Flora. Without the evidence afforded by STUR's plant, the frond of which was partly fertile and partly sterile, it would have been impossible to assign the Gwaenysgor specimen to the genus Rhacopteris. STUR's specimen consists of an axis, the lower part of which is sterile (3.5 mm. wide) and bears pinnules, while the upper part, which is repeatedly branched, bears sporangia. OBERSTE-BRINK points out that the pinnules of R. paniculifera resemble those of R. inæquilatera, GÖPP., remarking, however, that they are more triangular in shape than those of that species. He does not mention in his account of the genus Rhacopteris Lindsexformis, BUNBURY sp.,* so was possibly unaware of this species; otherwise he would have no doubt recognised the still closer similarity between the pinnules of R. paniculifera and those of R. Lindseceformis, a similarity which KIDSTON considers affords sufficient ground for assigning R. paniculifera STUR to R. Lindsexformis, BUNB. The upper portion of the frond is divided into two by a bifurcation of the rachis, and each of the branches thus formed builds up by successive forkings an anadromic system of branches, unlike the

* BUNBURY, C. F. (1861), p. 151, fig. 26.

Gwaenysgor specimen, in which each main branch gives off branches on both sides, and is therefore pinnate, but such as is seen in the frond of *Dictyophyllum exile*, BRAUNS sp.* The sporangia are attached to these lesser branches or to their sub-divisions. The sporangia are exannulate, ovoid, and about 1 mm. wide.

It will be seen on comparing the Gwaenysgor specimen with the figure of R. paniculifera, STUR, that the ratios of the length of the frond above, to that below the main fork of the rachis (5:10 in the former and 6:10 in the latter specimen), indicate that in the Gwaenysgor specimen a larger proportion of the main rachis or sterile part of the frond is represented, assuming that the ratio of length of sterile to fertile part was the same in the complete frond in both plants originally. I am therefore disinclined to accept the absence of any trace of foliage pinnules in the Gwaenysgor specimen as an indication that it corresponds only to the upper part of STUR'S plant, above the region of attachment of the pinnules. Also, if sterile pinnules had been present—pinnules of the same substantial build as those of R. paniculifera—there would have been some indication of a disturbance in the outline of the rachis at the points of attachment of the pinnules, even if the latter had been removed before fossilisation had taken place. The definite basal part of the rachis as represented in the fossil suggests that it became detached by abscission, rather than by actual break or maceration, and may be compared with the base of the sterile frond of R. circularis figured in Plate 16, fig. 5. The appearance of completeness of the frond of R. fertilis and its association in the same beds with Rhacopteris fronds which are shorter than those of R. Lindsexformis, the supposed foliage of R. paniculifera, lend support to the idea that the Gwaenysgor specimen is a complete fertile frond, differing from R. paniculifera in possessing no sterile foliage pinnules on the lower part of the rachis.

STUR refers to the possibility of the sporangium-like bodies representing fertile pinnules,[†] enveloping the sporangia, which are not themselves visible. The structures of the bodies as shown in the Gwaenysgor specimen (Plate 16, figs. 3 and 4) is, I think, definitely contrary to this, and suggests not only that these bodies must be taken to be sporangia, but that they were also probably exannulate. One cannot help being impressed by the close similarity which the *Rhacopteris* pinnules bear to the pinnules of *Botrychium lunaria*. The position of the fertile region of the frond has been regarded as an objection[‡] to assigning, as STUR does, *Rhacopteris* to the *Ophioglossaceæ*. He remarks on the variation in the position of the fertile region in the genus Osmunda,§ and points out that the spike in *Helminthostachys*, and frequently in *Botrychium*, is clearly situated at the base of the sterile lamina, and thus by analogy with the Osmundaceæ the position of the fertile region in *Rhacopteris paniculifera* at the apex of the frond can be reconciled with the condition in the *Ophioglossaceæ*.

* SEWARD, A. C. (1910), pp. 380–383, fig. 281.
† STUR, D. (1875), p. 73, l. 43.

- ‡ ZEILLER, R. (1900), pp. 55 and 104.
- § STUR, D. (1875), p. 74, l. 22.

 $\mathbf{208}$

JOHN WALTON ON CONTRIBUTIONS TO THE

A "dichotomy" of the frond is present in both fertile specimens of *Rhacopteris*, and is a remarkable character in view of the fact that the sterile fronds are, so far as we know, always unforked. It is possible that this arrangement was derived by an arrest of the apex of the frond and by the vigorous growth of two lateral pinnæ, an explanation which, as will be shown later, is thoroughly justified when applied to certain other Lower Carboniferous fronds.

(d) Rhacopteris circularis, sp. nov. (Plate 16, figs. 5, 6, 7, 8; Plate 17, figs. 13, 14.) Frond pinnate, linear-lanceolate, rachis fairly stout, with fine longitudinal striations and with a short expanded region at the base. Pinnules distant near the base of the frond but overlapping farther up, alternate or opposite, set obliquely to the rachis, but not overlapping it. Margin of pinnules entire, more rarely crenulate or lobed. Pinnules circular to semi-flabelliform, contracted at the base to form a short footstalk. The veins radiate from the footstalk and dichotomise two or three times in the lamina before attaining the margin. There is a tendency to asymmetry in the higher pinnules on the frond. Vernation circinate.

No complete frond of this species has been found, but one specimen showing the base (Plate 16, fig. 5) and another the apex (Plate 17, fig. 14), with several others, give sufficient data for a fairly accurate reconstruction of the frond. The longest fragment is $14 \cdot 5$ cm. long. The rachis is straight or slightly flexuous, and in the specimen figured on Plate 16, fig. 8, has fine longitudinal striations. It varies from about $1 \cdot 5$ to $2 \cdot 5$ mm. in width. The base of the petiole has a short expansion (Plate 16, fig. 5). The young fronds were circinately rolled up in the bud, as is shown by one example (Plate 17, fig. 14), the lower pinnules overlapping the bases of the pinnules above. The pinnules vary in shape from small strap-shaped structures, 2 mm. long (Plate 16, figs. 4 and 6), situated at the base of the frond, to sub-circular structures as much as 12 mm. in diameter (Plate 16, fig. 7), set higher up. The pinnule is attached to the stem by a short footstalk, which is set obliquely to the rachis. The pinnules, except those at the apical end of the frond, are almost symmetrical. The vascular supply to the pinnule as it leaves the footstalk and enters the lamina divides nearly equally (Plate 17, fig. 14).

Of all the described species it is most closely allied to R. *inæquilatera* GÖPP. and R. Lindseæformis, BUNBURY.* There are, however, differences by which it may be distinguished from either of these two species. In contrast to both, the pinnules of R. circularis are more circular in outline, and never show the same degree of asymmetry. It differs, too, in the fact that the pinnules do not overlap the rachis, nor do they overlap one another to any great extent. There is not the same pronounced unilateral branching of the vein-system as is found in R. inæquilatera and R. Lindseæformis, most of the veins radiating from the base of the pinnule; but this tendency is seen in some

* R. inæquilatera, FEISTMANTEL (non GÖPPERT), 'Mem. Geol. Surv. New South Wales,' 1890, Pal. No. 3, Plate IV. fig. 1, should possibly be assigned to R. circularis.

of the upper pinnules of the frond (Plate 16, fig. 7), where at the same time the pinnules lose their symmetrical shape and resemble those of R. inequilatera more closely. The veins are distant, as in R. Lindseæformis. Judging from the specimens as a whole, the length of the fronds may have been as little as 17 cm., and they were probably smaller on the average than those of R. Lindseæformis figured by KIDSTON, some of which are at least 28.5 cm. long.* About ten incomplete specimens of this species were found at Gwaenysgor. I have examined the specimen labelled R. Lindseæformis from Gwaenysgor in the KIDSTON collection (No. 3308), and find that it is referable to R. circularis, which is one of the commonest of the plants in the Teilia Beds at Gwaenysgor.

Rhacopteris petiolata, GÖPPERT, sp.

- (1852) Sphenopteris petiolata, GÖPPERT, "Foss. Flor. d. Uebergangsgebirges."
 'Verhandl. d. Kais. Leop.-Carol. Akad. d. Naturforsch.,' vol. 22, p. 143, Plate XLIV, fig. 3.
- (1873) Sphenopteris petiolata, FEISTMANTEL, 'Zeitschr. d. Deut. Geol. Gesell.', 25, Taf. XV, figs. 12, 12a, 11, 11a.
- (1889) Rhacopteris flabellata, TATE sp. KIDSTON, 'Trans. Roy. Soc. Edin.,' vol. 35, Part 2, No. 11, Plate II, figs. 4-6, ? fig. 7.
- (1914) Rhacopteris (Anisopteris) petiolata, OBERSTE-BRINK, 'Jahrb. d. k. Preuss. Geol. Landesanstalt,' 1914, vol. 35, Teil 1, Heft 1, Plate VII, fig. 1.
- (1923) Rhacopteris petiolata, KIDSTON, 'Mem. Geol. Surv. of Gt. Britain, Palæont.,' vol. 2, Part 3, Plate LIII, figs. 2, 3, 4.

Several specimens have been found at Gwaenysgor[†] of fronds which I assign to this species. They all possess deeply divided pinnules. The divisions of the pinnules are linear, uninerved, with acute apices, and are free for the greater part of their length (Plate 16, fig. 11). The terminal part of the frond appears to consist of a bunch of the linear pointed segments.[‡] I have found several specimens of this plant, but none of them show any new feature of interest. The type of the species figured by Göppert§ is the basal part of a frond, and I am inclined to believe that the frond of *R. dichotoma*, KIDSTON, || must have had a similar base. It will be noticed that the shape of some of the pinnules of the latter plant resemble the highest pinnule on the left side of Göppert's specimen.

I accept the synonymy given by KIDSTON, ¶ with the exception of one specimen which I assign with some hesitation to *R. cf. petiolata*, GÖPPERT.

- * KIDSTON, R. (1923), Part 3, Plate XLIX, fig. 1.
- † KIDSTON, R. (1889), Plate II, figs. 5 and 6.
- ‡ Ibid., Plate II, fig. 6.
- § GÖPPERT (1852), Plate XLIV, fig. 3.
- | KIDSTON, R. (1923), Part 3, p. 215, Plate LII, figs. 1 and 2.
- ¶ Ibid., Part 3, p. 211.

VOL. CCXV.-B.

BIOLOGICAL

THE ROYAL

PHILOSOPHICAL TRANSACTIONS 209

JOHN WALTON ON CONTRIBUTIONS TO THE

Rhacopteris cf. petiolata, GÖPPERT, sp., Plate 16, figs. 10, 12; text-fig. 1.

? (1875) Rhacopteris flabellata, KIDSTON, ex parte, 'Trans. Roy. Soc. Edin.,' vol. 35, Part 2, No. 11, Plate II, fig. 7, non figs. 4–6.

? (1923) Rhacopteris petiolata, KIDSTON, ex parte, 'Mem. Geol. Surv. Gt. Britain, Palæont.,' vol. 2, Part 3, Plate LIII, fig. 5.



TEXT-FIG. 1.—*Rhacopteris, cf. petiolata*, GÖPPERT, sp. Outline sketch of two fragments of a frond. $\times \frac{2}{3}$ natural size.

Frond pinnate, lanceolate, apex acute, rachis slightly flexuous with expanded base. Pinnules twice as long as broad, sometimes touching or overlapping, usually alternate; semiflabelliform in shape, footstalk of pinnule very short, and oblique to the rachis. Pinnules dissected, segments six to eight in number, with a terminal notch. The main vascular supply to the pinnule on leaving the footstalk passes along the posterior margin of the pinnule, and gives off a series of veins which pass out to the segments on the anterior side.

The specimen from Gwaenysgor, of which an outline drawing is given in text-fig. 1, was found in two separate parts, but there is little reason to doubt that the two fragments belonged to the same frond. The nature of the matrix did not allow of a satisfactory photograph being taken. Owing to the presence of a weathered-out joint in the limestone, about a centimetre of the middle part of the frond is missing. The frond was at least 23 cm. long. Another specimen (Plate 16, fig. 10) was found which consisted of the middle part of what was possibly a still longer frond (22 cm. without apex or base preserved). The rachis (text-fig. 1) is slightly flexuous. The pinnules are attached along the whole length of the frond. The vertical distance between adjacent pinnules on the same side of the rachis is about a centimetre. At the base the members of the series on the one side are opposite those on the other side, but farther up the frond they alternate in position. The short basal part of the rachis is slightly expanded (4 mm.). Where the lowest pinnules are attached the rachis has a breadth of 3 mm., while at the apex of the frond it is only 1 mm. in width. The pinnules are asymmetrical; those at the base have a strong backward curvature. The lower margin is entire, while the upper margin is dissected into numerous segments. Most of the segments have a small notch at the tip, indicating a subdivision of the pinnule, which becomes more pronounced in the pinnules in the middle of the frond (on the right-hand

side of text-fig. 1 and in Plate 16, fig. 10). The pinnules are dissected to about half

BIOLOGICA

THE ROYA

PHILOSOPHICAL TRANSACTIONS

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their width. The base of each pinnule is contracted, so that each appears to have a short footstalk.

Discussion.

These two specimens are closely allied to R. petiolata, GÖPPERT,* sp. and R. robusta, KIDSTON,† but exhibit characters which possibly serve to distinguish them from either of these species. Among the specimens assigned by KIDSTON to R. petiolata, and figured by him, is one which is of rather different habit to the others. The pinnule segments, borne in pairs, are webbed to a greater degree, and have blunter apices than is usual in R. petiolata GÖPP. sp. This particular specimen described by KIDSTON was found at Gwaenysgor and agrees in these details of form with the two specimens figured here. R. petiolata, as most generally recognised, has pinnules which are dissected almost to the base, each segment terminating in an acute apex. The apex of frond in R. petiolata does not taper off to such a fine point as in the Gwaenysgor plant (textfig. 1), but terminates somewhat abruptly, and the segments of the pinnules of the apex are as long as those of the pinnules about the middle of the frond. In the latter

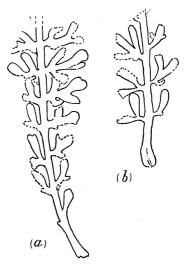
the pinnules at the apex are much smaller and have small segments (text-fig. 1). *R. robusta* KIDSTON has considerably larger pinnules than are found on the Gwaenysgor fronds. Figures 11 and 12, Plate 16, show the difference between the pinnules of the typical form of *R. petiolata* and the other type of frond from Gwaenysgor.

Rhacopteris sp.

A fragmentary specimen of a *Rhacopteris* was found at Gwaenysgor, which could not be placed satisfactorily in any of the described species; it is figured in Plate 16, fig. 9. The pinnules are all lying to one side of the rachis, and are distinctly crenulate. The specimen belongs to the *Lindseæformis—inæquilatera* group of Rhacopteris.

Sphenopteris (Rhacopteris) Weissii, sp. nov. (Plate 17, figs. 22 and 23; text-fig. 2, a, b.)

Frond pinnate, rachis stout, expanded at the base and marked with fine longitudinal striations. Basal pinnules simple or divided into two segments or lobes; upper



TEXT-FIG. 2.—Sphenopteris (Rhacopteris) Weissii, sp. nov. Outline sketches of the basal portions of two fronds. (b) is drawn from the specimen figured on Plate 17, fig. 22. $\times \frac{2}{3}$ natural size.

pinnules with two or more lobes. Footstalk of pinnule fairly stout. Lobes of pinnules broadly clavate, the basal lobe on the abaxial side of a pinnule sometimes bent out of

† KIDSTON, R. (1923), Part 3, p. 216, Plate LI, figs. 5, 6, and 7.

^{*} Göppert, H. R. (1852), Plate XLIV, fig. 3.

212

JOHN WALTON ON CONTRIBUTIONS TO THE

the plane of the frond and, therefore, imperfectly represented. These lobes are bent towards the same surface of the frond.

The specimens described under this name are from the Lower Brown Limestone, near Diserth in Flintshire. Several specimens were found, but none were in a very good state of preservation. The frond is simple and the rachis does not fork in any of the specimens found. The pinnules are deeply dissected (Plate 17, figs. 22, 23) into clavate lobes. The venation is not visible. The rachis is from 2 mm. to 3 mm. in width. The base of the petiole is swollen (text-fig. 2, b) and a median line is visible, which probably represents the vascular supply to the frond.

It is probable that this is one of the species of Sphenopteris mentioned by MORTON^{*} as occurring in the quarry between Pentre Bach and Pentre Cwm at Diserth. It is from the same locality and horizon. It bears a slight resemblance to Rhacopteris subcuneata KIDSTON,[†] but the pinnules are much broader than in that species. The form of the pinnules is not unlike that of the pinnules of Sphenopteridium dissectum, GÖPPERT, in some of its forms.[‡]

- II.—ON THE MORPHOLOGY OF SPHENOPTERIS TEILIANA, KIDSTON, AND ITS BEARING ON THE POSITION OF THE FRUCTIFICATION ON THE FROND OF SOME LOWER CARBONIFEROUS PLANTS.
 - (a) On the Morphology of Sphenopteris Teiliana, KIDSTON.
 - (1889) Sphenopteris Teiliana, KIDSTON, 'Trans. Roy. Soc. Edin.', vol. 35, p. 424, Plate II, fig. 3.
 - (1923) Sphenopteris Teiliana, KIDSTON, 'Mem. Geol. Surv. Gt. Brit., Palæont.,'
 vol. 2, Part 1, p. 96, Plate II, fig. 5, Plate XIX, figs. 6, 6A.

Among the plants from Gwaenysgor which were described by KIDSTON in 1889§ is a fern-like frond, to which the name *Sphenopteris Teiliana* was given. This plant has not been recorded from any other locality. The discovery of additional and more perfect specimens has made a revised description necessary. In the course of collecting at Gwaenysgor I found several specimens of this interesting species, including a virtually complete frond and other specimens exhibiting undescribed features.

The characters of a vegetative frond are well shown by the specimen figured in Plate 17, fig. 15, which is a photograph of the most complete frond of this species hitherto described. The rachis is moderately stout and its surface is covered with fine longitudinal striations, which from their occurrence right up to the edge of the rachis must represent some prosenchymatous tissue at or near the surface, probably cortical sclerenchyma. There

^{*} MORTON, G. H. (1870), p. 82.

[†] KIDSTON, R. (1894), p. 261, Plate V, fig. 2, Plate VI, fig 1. Idem, 1923, Part 3, p. 217, Plate LIV, figs. 3, 4.

[‡] FEISTMANTEL, O. (1873), Taf. XVI, figs. 26 and 27.

[§] KIDSTON, R. (1889), p. 424.

are no indications of transverse ridges of the Sphenopteridium type. The rachis varies from 2 to 3 mm. in width, except at the base, where there is a short expanded part about twice the width of the rachis immediately above it. The rachis is divided about 4.5 cm. above the base into two equal arms, which diverge at an angle of about 45° , but by an inwardly directed curvature (Plate 17, fig. 16) lie at a much smaller angle to one another, and in some instances are so curved that the tops of the arms almost touch (Plate 17, fig. 16). The two divisions into which the frond is thus divided are linear lanceolate.

The apex of one of the two divisions of another specimen is figured (Plate 17, fig. 20). The frond may for purposes of description be termed bipinnate. Pinnæ are attached both above and below the fork of the frond. A pinna is situated just at the base of each arm, and the next pinna above it on the arm is on the same side of the rachis (cf. Telangium bifidum, L. and H., Plate 17, fig. 24). As a rule the pinnæ on the main rachis are in opposite pairs. The pinnæ on the arms of the frond are, for the most part, attached alternately. They are usually deltoid, but some, particularly those on the rachis below the fork and on the inner side of the arms at their bases, may be divided into two equal parts by a dichotomy near the base of the pinna. The larger pinnæ may have as many as four pinnules on each side. The pinnules may be simple or divided into one or two segments, each of which is slightly cuneate. As the lowest pinnule is on the abaxial side of the pinna axis, the construction of the pinna is anadromic. Some pinnules (e.g., the lowest pair in Plate 17, fig. 17) are asymmetric, and altogether there is very considerable variation in the form of the pinnules found on corresponding parts of different fronds (cf. figs. 15 and 16, Plate 17). The course of the veins cannot be seen in the pinnule. The surface is evenly striated (Plate 17, fig. 21).

In more than half of the specimens a rachis-like structure is present in the angle of the fork of the main rachis. The otherwise almost complete frond (Plate 17, fig. 15) shows no trace of any structure in this position. It appears to be absent in the other large specimen (Plate 17, fig. 16). In a third specimen (Plate 17, fig. 17) an elongated structure can be seen attached to the top of the main rachis in the angle of the fork. This structure is $1 \cdot 3$ cm. long, $0 \cdot 15$ cm. wide, and terminates abruptly like one of the pinnule segments. A fourth specimen (Plate 17, fig. 18) has a definite branching axis in the same position in the angle of the fork, and, like the rachis, it is striated longitudinally. The two arms of the frond are set slightly farther apart than in the first three specimens. In actual thickness the rachis in the angle of the fork is comparable with one of the arms of the frond, and must have been a rigid structure. It is destitute of pinnules, and in the description that follows will be referred to as the naked rachis. It forks at a wide angle about 1.9 cm. above its point of attachment to the main rachis; it is, however, possible that branching may have occurred nearer its base at right angles to the plane of the bedding of the fossil. The pinnules seen in connection with the right-hand arm of this specimen are similar to those which are placed in the corresponding position on the third specimen (Plate 17, fig. 17). Just below the left

214 JOHN WALTON ON CONTRIBUTIONS TO THE

hand arm is a detached pinnule of the asymmetrical type found in the third specimen on the rachis below the fork. These two specimens are thus clearly comparable.

A fifth specimen (Plate 17, fig. 19) collected by E. B. LUXMOORE, Esq., in the possession of the Sedgwick Museum, Cambridge, has a larger naked rachis between the arms of the frond. This specimen is, unfortunately, imperfect and does not show the actual forking of the rachis. There is, however, no reason to doubt, in view of the specimens already described, that the zigzag naked rachis seen between the two arms of the frond is, both in origin and in method of insertion, similar to those seen in the other specimens. The naked rachis in this specimen apparently underwent at least three successive forkings, probably not all in the same plane, as only some of the branches are represented. The formation of this branching was probably by the almost equal division into two of the rachis, as is suggested by the equal size of the angles at the top of the naked rachis, between it and the branch on the left and between it and its continuation to the right. At each of the bends seen in the naked rachis a branch was probably attached.

Discussion.

Sphenopteris Teiliana, as KIDSTON remarks, shows several points of resemblance to the genus Sphenopteridium, SCHIMPER*: for instance, the frond appears to be divided into two equal parts by a division of the rachis, which bears pinnæ or pinnules below as well as above the point of division; also the veins of the pinnules are probably parallel to the margins of the pinnules or their lobes. It differs, however, from Sphenopteridium in having a longitudinally striated rachis; and no indications of transverse ridging. KIDSTON, while remarking on its close similarity to Sphenopteridium, refrains from placing it in that genus, because he was not able to observe the venation in any of the specimens he had under observation. The new characters which I have observed in the species are sufficient to make me hesitate to place it with any of the already defined genera. As there is the possibility that the discovery of more specimens may lead to a determination of the nature of the fructification, I intentionally retain the name Sphenopteris, provisionally.

Until one has the actual proof of connection of fructifications with these naked rachises, one can but give the reasons for regarding them as the probably fertile branches of the frond. In the first place, the wide-angle forking is unlike the branching of any other part of the frond; and, in the second place, there is great similarity between these naked axes with their peculiar wide-angled forking and the fructification-bearing branches of *Telangium bifidum* and *affine*, L. and H. spp.,‡ *Alcicornopteris Zeilleri*, VAFFIER§; *Calathiops acicularis*, GÖPPERT, and *Calathiops Schlosseri*, GOTHAN.¶

- * KIDSTON, R. (1923), Part 1, 96.
- † Ротоні́е, R. (1923), p. 422.
- ‡ Kidston, R. (1924), Part 5, p. 451, text-fig. 43.
- § VAFFIER, A. (1901), pp. 124–126, Plate VI, fig. 5, Plate VII, fig. 1 (a, b, c, d, e, f).
- || GOTHAN, W., and SCHLOSSER, P. (1924), pp. 5-7, Plate III, figs. 1, 1A.
- ¶ Ibidem, p. 7, Plate II, fig. 3, Plate III, fig. 2A.

The presence in the same beds at Gwaenysgor of fructifications possibly to be referred to the genus *Calathiops* has, no doubt, some significance.*

The positional relations of the pinnæ and naked rachis on the frond of *Sphenopteris Teiliana* compare at first sight so closely with the relations between the pinnæ and buds on the fronds of the living and fossil† representatives of the genus *Gleichenia* that an examination of available herbarium material was made in order to see what characters they had in common.

In most species of *Gleichenia* the frond owes its form to what appear to be successive dichotomies of the rachis, but no evidence, structural or developmental, has been put forward that this is really so. At these "dichotomies" there is present in most instances a bud in the angle of the fork. This bud may develop no farther, but sometimes it represents a temporarily arrested part of the frond, which when fully developed gives the frond the appearance of having a normal pinnate structure. In *Gleichenia cryptocarpa*, Hĸ., the frond may develop directly without temporary arrest, and is obviously pinnate except in secondary divisions of some of the pinnæ.

Several suggestions have been made as to the manner in which these fronds are to be interpreted : one suggestion, depending on the tacit supposition that the buds are adventitious and that the divisions of the frond are dichotomies, \ddagger is, I think, negatived by the evidence of *G. cryptocarpa*, in which the frond is apparently pinnate and is very unlikely to have developed from a series of dichotomies. It seems highly improbable that the two arms of the frond represent the result of equal divisions of the frond apex; no evidence has been brought forward to demonstrate it, and they can probably no more be regarded as branches of dichotomies than can the pinnæ of a pinnate frond (*e.g. Ceratopteris*), in which the laterals are known to originate at a definite distance below the apex and are in no definite relation to the primary segmentation of the apical cell§.

The simplest explanation, and one which accounts for the variations in the different species, is got by referring the whole structure of the frond to normal pinnate development.|| The apparent dichotomy is due to arrest, abortion, or, in some cases, suppression of the apex of the frond, and to the precocious development of two pinnæ just below it.

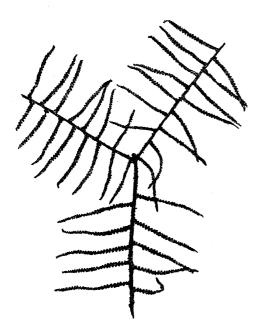
It was possible to find examples of secondary forkings¶ which are identical in the arrangements of the pinnules to *Sphenopteris Teiliana*, and an example of one of these is given in text-fig. 3. As in this fossil and in *Telangium bifidum*, L. and H. sp. (Plate 17, fig. 24), a pinna appears to be missing on the inside of the arm just above the fork. This

- * The description of these specimens is reserved for a later date.
- [†] HEER, O. (1864), p. 42, Plates IV-IX. SEWARD, A. C. (1926), pp. 76, 77, Plate 6, fig. 31.
- ‡ Boodle, L. A. (1901), pp. 704–5.
- § Bower (1923), p. 90, fig. 83.
- || GOEBEL, K. (1918), p. 1043.
- ¶ There are no pinnæ on the main rachis or petiole of *Gleichenia*.

$\mathbf{216}$

JOHN WALTON ON CONTRIBUTIONS TO THE

is due to suppression, for in other species all stages could be found between a normal pinna in this position, a reduced pinna, and the complete absence of one. In both Sphenopteris Teiliana, Telangium bifidum, and Gleichenia, the reduction or suppression



TEXT-FIG. 3.—Gleichenia circinnata, Sw. Part of a frond to illustrate the arrangement of the pinnæ in relation to the forking of the rachis. The small leaf-bud can be seen in the angle of the fork. $\times \frac{2}{3}$ natural size.

of this pinna is probably due to space considerations in the developing frond, and is not of any fundamental significance. In Pecopteris Pluckeneti, SCHLOTH. sp., an Upper Carbon*iferous* species, the structure of the frond is much like that of a Gleichenia of the section Acropterygium, Diels,* in which the bud in the main fork has developed and has formed more vegetative pinnæ.† As in *Gleichenia*, the further development of the apex of the frond of Sphenopteris Teiliana was arrested as the result of specialisation (here probably reproductive) and developments from below resulted in the production of the two arms. In other specimens the fertile part may have aborted or been suppressed, giving rise to the type of frond without any structure in the fork (Plate 17, fig. 15). I am, therefore, inclined to regard the frond of Sphenopteris Teiliana, in view of the nature of the available fundamentally evidence. pinnate asin structure.

(b) The Position of the Fructification on the Frond in some Lower Carboniferous Plants.

In many Lower Carboniferous fern-like fronds the distinction between sterile and fertile regions of the frond must have been well marked, but it is only in a few cases that we have any clue as to their relative positions on the frond. Indeed, in most cases where the difference in form of the sterile and fertile regions is great, as in *Rhacopteris*, *Telangium*, and *Calymmatotheca*, the only proof of specific or even generic identity lies in a demonstration of organic connection between the two parts. The extent of our knowledge of the external morphology of the genus *Rhacopteris* has been dealt with in the first part of this communication. In *Calymmatotheca*, STUR,[‡] beyond the close association of sterile and fertile fragments and the presence of hair-like emergencies on both,

* DIELS (1902), p. 353.

† Ротоніє́, Н. (1921), р. 74.

‡ STUR, D. (1877), pp. 151-161, Taf. VIII and IX.

there is nothing to prove their identity*; for example, in *C. Stangeri*, STUR,[†] the sterile and fertile parts which are assigned to this species have not been found in organic connection and there is no indication of the relation of these parts to one another on the frond.[‡] It is, of course, possible that the fronds were dimorphic, in which case the likelihood of ever proving that they belonged to the same plant is very remote.

The only account, so far as I am aware, in which any description is given of the relation between the sterile and fertile parts of *Telangium* (*Sphenopteris*) affine, L. and H. sp., is by PEACH,§ who remarks that the relation between *Staphylopteris* (*Telangium*) and *Sphenopteris affinis* is that of a parasite to its host. We thus get little in the way of precise information about the connection between them, but this strikingly suggests the marked difference in mode of branching and the relation between the fructification and frond of the closely allied species *Telangium bifidum*.

In Telangium bifidum, L. and H. sp., we have something more to warrant the placing of sterile and fertile parts in the same species. As long ago as 1887 KIDSTON described a specimen of a frond with the characteristic division of the rachis into two arms, and with numerous "synangia" grouped round the place where the rachis forks, "showing the position occupied by the fructification of this species, which is on the rachis below the dichotomy, as well as on the base of the two arms of the fork." A copy of the figure given in this early paper is reproduced in the Survey Memoir¶ and is stated to show the relation of the "cupules" to the pinnæ of the frond. As my investigation of Sphenopteris Teiliana had led me to view with suspicion the apparently dichotomous division of the frond, I examined this specimen, which is in the Collection of the Geological Survey, and by the courtesy of the Director was allowed to photograph the specimen and figure it in this paper (Plate 17, fig. 24). In KIDSTON'S figure in the text** the group of cupules on the left (see Plate 17, fig. 24, a) are shown attached to the pinna (b), which is inserted at the fork of the rachis, in its left-hand side. This connection, for such it appears to be in a drawing or photograph of the specimen, does not exist in reality, for the pinna lies in a higher plane, with a definite thickness of matrix separating it from the plane in which the cupules lie. The supposed connections between the other cupules and pinnæ are to my mind equally unconvincing.

* GOTHAN, W. (1923), p. 771, fig. 2, figures a specimen of *Diplothmema adiantoides* with Calymmatotheca or Diplothmema-like cupules attached to certain of the pinnæ; and (fig. 1) a specimen of *Sphenopteris Dicksonioides* with seeds in connection with part of the frond. In neither is the relation of the fertile part to the main plan of the frond clearly shown.

† STUR, D. (1877), p. 149.

‡ KIDSTON, R. (1924), Part 5, pp. 466–471. The writer has examined the two specimens here referred to by KIDSTON (footnote to p. 469); they both represent fragmentary rachises with fructifications attached and give no clue to the relationship in position of the sterile and fertile parts of the frond.

§ PEACH (1877), p. 135.

VOL. CCXV.-B.

^{||} KIDSTON, R. (1887), p. 142, Plate VIII, fig. 1.

[¶] Idem (1924, Part 5, p. 457) describes the fructifications as "cupules."

^{}** *Idem*, p. 457, text-fig. 44.

JOHN WALTON ON CONTRIBUTIONS TO THE

Isolated fructifications of *Telangium* consist of synangia or of seed-cupules attached to naked rachises, which exhibit "the characteristic dichotomisation of the fructifying branches of this species, and in fact of the genus *Calymmatotheca*."* The fact that none of the pinnæ *attached* to this particular frond show this type of branching is another argument against supposing them to be fertile divisions of the frond.

The thicker, forking rachis seen on the right (Plate 17, fig. 24, c), lying between the pinna at the base of the right-hand arm and the next one above it on the same side, is very like a typical *Telangium* fertile rachis. It is attached to some of the cupules and is, I think, the only fragment of fertile rachis visible on the specimen. This fertile rachis is not, however, seen in connection with the frond. It is clearly different from the pinnæ of the frond in its state of preservation, as it is in the form of a hollow cast, while they are in the form of flattened incrustations. All the usual places for the insertion of pinnæ are occupied in its immediate vicinity, so that it is not likely to be a modified pinna.

If the specimen is examined closely it will be seen that this fertile rachis slants down into the matrix to the left, in a direction that would carry it beneath the rachis of that arm of the frond which lies nearest to it, and also in the direction of the angle of the fork of the main rachis. Another important fact to notice is that there is an object in the angle of the fork, which appears in the photograph as a small black spot (Plate 17, fig. 24, d). This structure actually consists of two small cavities, at the bottom of which one can see carbonaceous matter. These cavities represent the cast of some organic body which was in connection with the frond in the angle between the two arms of the frond. This structure is not described by KIDSTON.

Taking all these facts into consideration, it seems highly probable that the fertile rachis, seen on the right of the specimen (Plate 17, fig. 24, c), was either itself attached to the top of the main rachis in the angle of the fork, in the position suggested by the presence of the small structure, or was a branch of some rachis attached in that position.

The attachments of the other groups of cupules are not shown, but the orientation of the several cupules is in most instances such that the cupule segments point towards the centre of a sphere on the surface of which the cupules lie. This centre of arrangement coincides very nearly with the small structure in the angle of the fork. There is, therefore, on the one hand, a clear suggestion of some relation between the ring of cupules and the forking of the rachis of the frond, and, on the other hand, it appears less likely that the cupules were related to the pinnæ attached to the sides of the main rachis or to the arms of the frond.

The similarity between the frond of *Telangium bifdum* and *Sphenopteris Teiliana* is most striking; one has merely to glance at figs. 17 and 24, Plate 17, to see that the arrangement of the pinnæ in relation to the forking rachis of the frond is identical. The definite fact of attachment of a *Telangium*-like rachis in the fork of the frond of *Sphenopteris Teiliana*, and the presence of fructifications in significant relation to the fork of the rachis in *Telangium bifdum*, give grounds for believing that in the former

* KIDSTON, R. (1887), p. 142.

218

BIOLOGICAL

THE ROYAL

PHILOSOPHICAL TRANSACTIONS KNOWLEDGE OF LOWER CARBONIFEROUS PLANTS.

the naked rachis was the fructification-bearing part of the frond, and that in the latter the fructification was connected to the frond in the angle of the fork.

That the equal forking in at least one other Lower Carboniferous frond type was not due to a dichotomy of the rachis is suggested by a specimen of *Diplothmema subgeniculatum* STUR,* in which there is a bud-like structure sitting in the angle of the fork of the frond. STUR† describes this structure as the fructification of *Diplothmema subgeniculatum*, but there is no clear evidence that such is the case. He compares this specimen with species of *Rhipidopteris*‡ and suggests that the bud-like structure in the fork of the fossil is comparable with the fertile frond of *Rhipidopteris*. OBERSTE-BRINK§ figures a specimen of *Sphenopteridium schimperi*, GÖPP. sp., which has a mark just in the angle of the main fork of the frond which may well represent the position of attachment of a bud or of a fructification rachis.

In many Carboniferous Pteridosperms the seeds were borne on but slightly modified pinnæ, which carried vegetative pinnules as well. In view of the structures described above, we have grounds for believing that in many Lower Carboniferous plants, some of which were Pteridosperms, the fructifications were borne on the terminal part of the frond, which had no vegetative pinnules; and that many of the fronds described by authors as being of dichotomous construction may represent the sterile part of a frond, the terminal part of which has either fallen off, aborted, or been suppressed.

SUMMARY.

1. A brief account is given of the extent of our knowledge of the morphology of the genus *Rhacopteris*.

2. A specimen of *Rhacopteris inæquilatera*, GÖPP. sp., consisting of a portion of a branch or stem with two fronds attached to it, is described and figured.

3. *Rhacopteris fertilis*, sp. nov., a fertile frond of *Rhacopteris*, without any sterile pinnules, is figured and described.

4. The following types of fronds are described and figured : *Rhacopteris circularis*, sp. nov.; *Rhacopteris petiolata*, Göpp. sp. Cf. *Rhacopteris petiolata*, Göpp. sp.; *Rhacopteris*, sp.; *Sphenopteris* (*Rhacopteris*) Weissii, sp. nov.

5. The presence of a rachis in the angle of the fork of the frond of *Sphenopteris Teiliana*, KIDSTON, is demonstrated in several specimens. This rachis is shown to have some of the characters of a fertile rachis of *Telangium*.

‡ *Rhipidopteris peltatum*, Sw. sp., has dichotomously forked sterile fronds and disc-shaped, entire fertile fronds, and is thus markedly dimorphic. The sterile and fertile parts being on separate fronds, the comparison with *Diplothmema* is not apt.

^{*} STUR, D. (1877), p. 135, Taf. XII, figs. 8, 9, 10.

[†] *Ibid*, p. 136.

[§] OBERSTE-BRINK (1914), Taf. 3, fig. 2.

^{||} KIDSTON, R. (1904), pp. 3-5; and KIDSTON, R., and JONGMANS, W. J. (1911), p. 25.

220 JOHN WALTON ON CONTRIBUTIONS TO THE

6. The presence of this rachis is interpreted as an indication of the fundamentally pinnate structure of the frond of *Sphenopteris Teiliana*. The apex is presumably fertile in some fronds, represented by rudimentary structure in others, and completely suppressed in yet others.

7. An examination of *Telangium bifidum* in the light of these new facts shows that very probably the fructification rachis was attached to the frond bearing the foliage pinnules in the angle of the main fork of the rachis; and that possibly in many Lower Carboniferous fronds, in which the main rachis apparently dichotomises, the frond is in reality pinnate in structure, this "dichotomy" being produced, as in *Sphenopteris Teiliana*, by the abscission of the fertile apex, or by its abortion or suppression.

My thanks are due to Mr. J. WILFRID JACKSON, of the Manchester Museum, and Mr. W. KING, of the Sedgwick Museum, Cambridge, for kindly facilitating the work of examining the specimens in their charge, and to the Royal Society for a grant to meet the expense of excavations which have yielded several of the specimens described in the above account.

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DESCRIPTION OF PLATES.

Plate 16.

All Figures are from untouched Photographs.

FIG. 1.—*Rhacopteris inæquilatera*, GÖPP. sp. Stem with two fronds in attachment. The specimen itself shows about one centimetre more of the top of the fronds. Natural size.

Locality :---Hailes Quarry, Kingsknowe, Midlothian.

Horizon :--- Upper Beds of the Wardie Shales exposed in the Quarry, Oil Shale Group, Calciferous Sandstone Series, Lower Carboniferous.

Sedgwick Museum, Cambridge. No. 2015a. (Mr. P. J. W. KILPATRICK, 1924.)

FIG. 2.—*Rhacopteris fertilis*, sp. nov. (fertile frond). Fertile panicle borne on a naked rachis. A small fragment of *Adiantites*, sp., with two pinnules is seen in contact with the base of the panicle. Natural size.

Locality :--- The quarry at Teilia Farm, Gwaenysgor, Flintshire.

Horizon :--- "Base of the Upper Black Limestone," Mountain Limestone Series, Lower Carboniferous.

The Manchester Museum. No. LL.48. (J. W., 1926.)

- Fig. 3.—Left-hand division of the panicle of the same specimen. Enlarged 2.7 diameters.
- FIG. 4.—Three sporangia from the same specimen, seen near the top of fig. 3. Enlarged 16 diameters.
- FIG. 5.—*Rhacopteris circularis*, sp. nov. Base of frond showing short expansion of the petiole and small entire pinnules. Natural size.

Same locality and horizon as for fig. 2. The Manchester Museum. No. LL.46. (J. W., 1925.)

- FIG. 6.—*Rhacopteris circularis*, sp. nov. Middle part of a frond with small basal pinnules. At the top of the figure the pinnules show asymmetry. Natural size. (See also Plate 17, fig. 13.)
 Same locality and horizon as for fig. 2.
 Manchester Museum. No. LL.40. (J. W., 1925.)
- FIG. 7.—*Rhacopteris circularis*, sp. nov. Middle part of a frond showing the characteristic circular outline of the pinnules. Natural size.
 Same locality and horizon as for fig. 2.
 Manchester Museum. No. LL.39. (J. W., 1925.)
- FIG. 8.—*Rhacopteris circularis*, sp. nov. Frond with irregularly lobed pinnules. Natural size. Same locality and horizon as for fig. 2. Manchester Museum. No. LL.41. (J. W., 1924.)
- FIG. 9.—*Rhacopteris*, sp. Portion of basal end of a frond. Both rows of pinnules are bent over to the same side of the frond so that their outlines are confused. Natural size.
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- FIG. 10.—Rhacopteris, cf. petiolata, GÖPP. sp. Upper part of a frond of which a length of 22 cm. is represented on the specimen. Neither apex nor base are preserved. Natural size.
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PHILOSOPHICAL TRANSACTIONS FIG. 11.—*Rhacopteris petiolata*, Görp. sp. Single, deeply dissected pinnule with pointed linear segments. Natural size.

Same locality and horizon as for fig. 2. Manchester Museum. No. LL.45. (J. W., 1925.)

FIG. 12.—*Rhacopteris*, cf. *petiolata*, GÖPP. sp. Single detached pinnule to show the characteristic bluntended segments. Natural size.

Manchester Museum. No. LL.44. (J. W., 1925.)

PLATE 17.

All figures are from untouched Photographs.

 FIG. 13.—*Rhacopteris circularis* sp. nov. Part of the frond shown in fig. 6 enlarged two-and-a-half diameters. Locality :—The quarry at Teilia Farm, Gwaenysgor, Flintshire.
 Horizon :—Base of the Upper Black Limestone, Mountain Limestone Series, Lower Carboniferous.

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FIG. 14.—*Rhacopteris circularis* sp. nov. Specimen of a young partially expanded frond with apex curved circinately. Natural size.

Same locality and horizon as for fig. 13.

The Manchester Museum. No. LL.42. (J. W., 1925.)

FIG. 15.—Sphenopteris Teiliana, KIDSTON. An almost complete frond (apparently sterile). A small part of the expanded base of the petiole is missing and the tips of the two arms of the frond are perhaps incomplete. Reduced ($\times 0.79$ diameter).

Same locality and horizon as for fig. 13.

The Manchester Museum. No. KK.995. (J. W., 1925). Counterpart of this specimen is in the Sedgwick Museum, Cambridge, No. 2016A.

FIG. 16.—Sphenopteris Teiliana, KIDSTON. Part of a larger specimen than that shown in fig. 15. The structure of the pinnæ is clearly shown on the left-hand side. Natural size.

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FIG. 17.—Sphenopteris Teiliana, KIDSTON. Specimen with a rachis-like structure in the angle of the fork. Natural size.

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FIG. 18.—Sphenopteris Teiliana, KIDSTON. Specimen with a well-developed rachis in the angle of the fork. This rachis itself forks at a wide angle about 1.5 cm. above the main fork of the frond. Natural size. Same locality and horizon as for fig. 13.

The Manchester Museum. No. LL.36. (J. W., 1925.)

FIG. 19.—Sphenopteris Teiliana, KIDSTON. Specimen with a rachis in the angle of the two arms of the frond. This rachis shows wide-angled forkings. There is no doubt that it was attached to the frond in the fork of the main rachis. Natural size.

Same locality and horizon as for fig. 13.

The Sedgwick Museum, Cambridge, No. 2007. (E. B. LUXMOORE, Esq.)

FIG. 20.—Sphenopteris Teiliana, KIDSTON. Apex of one of the arms of a frond showing the acute termination. Natural size.

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224 JOHN WALTON ON THE LOWER CARBONIFEROUS PLANTS.

FIG. 21.—Sphenopteris Teiliana, KIDSTON. The third pinna from the base on the right-hand side of the specimen shown in fig. 15. Enlarged (× 8 diameters). Same locality and horizon as for fig. 13.

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FIG. 22.—Sphenopteris (Rhacopteris) Weissii sp. nov. Lower part of frond showing the basal expansion of the petiole and portions of six pinnæ. Natural size.

Locality :--Small quarry on the West side of Moel Hiraddug, Ochry Voel, Diserth, Flintshire.

Horizon:-Near base of Lower Brown Limestone, Mountain Limestone Series, Lower Carboniferous.

The Manchester Museum. No. LL.49. (J. W., 1924.)

FIG. 23. Sphenopteris (Rhacopteris) Weissii sp. nov. Three incomplete pinnæ, probably from a fairly high position on the frond. Natural size.

Same locality and horizon as for fig. 22.

The Manchester Museum. No. LL.50. (J. W., 1924.)

FIG. 24. Telangium bifidum, LINDLEY and HUTTON sp. Frond with fructification in association with it in the vicinity of the main fork of the rachis (for description, see text, p. 217). Natural size.

Locality :--River Irthing, seven-eighths of a mile north of Lampert, Cumberland.

Horizon :---Calciferous Sandstone Series, Lower Carboniferous.

The Geological Survey and Museum, London. Kidston Collection No. 718. (Mr. JOHN JACKSON.)



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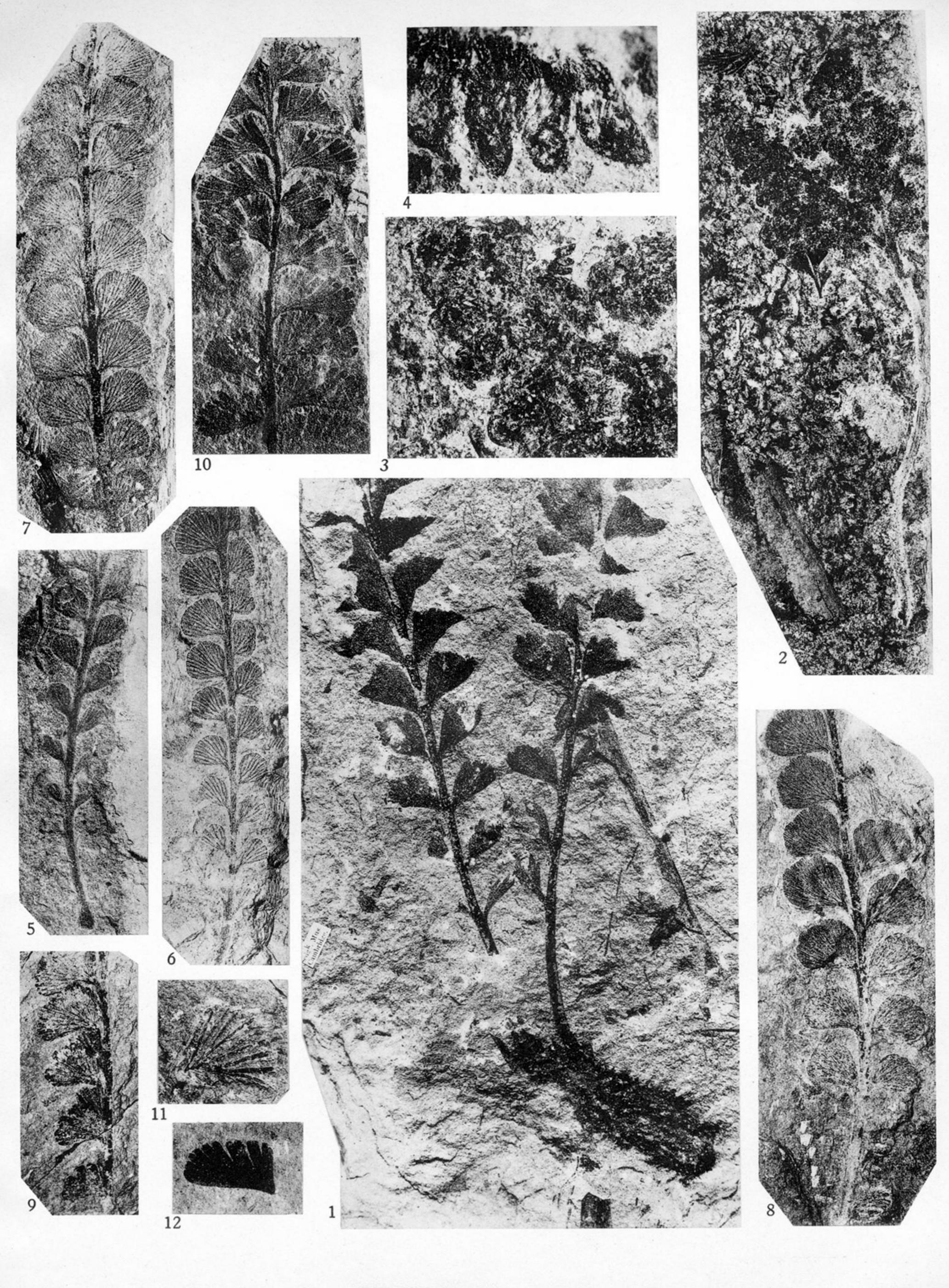
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RHACOPTERIS, SPHENOPTERIS, TELANGIUM.



RHACOPTERIS.

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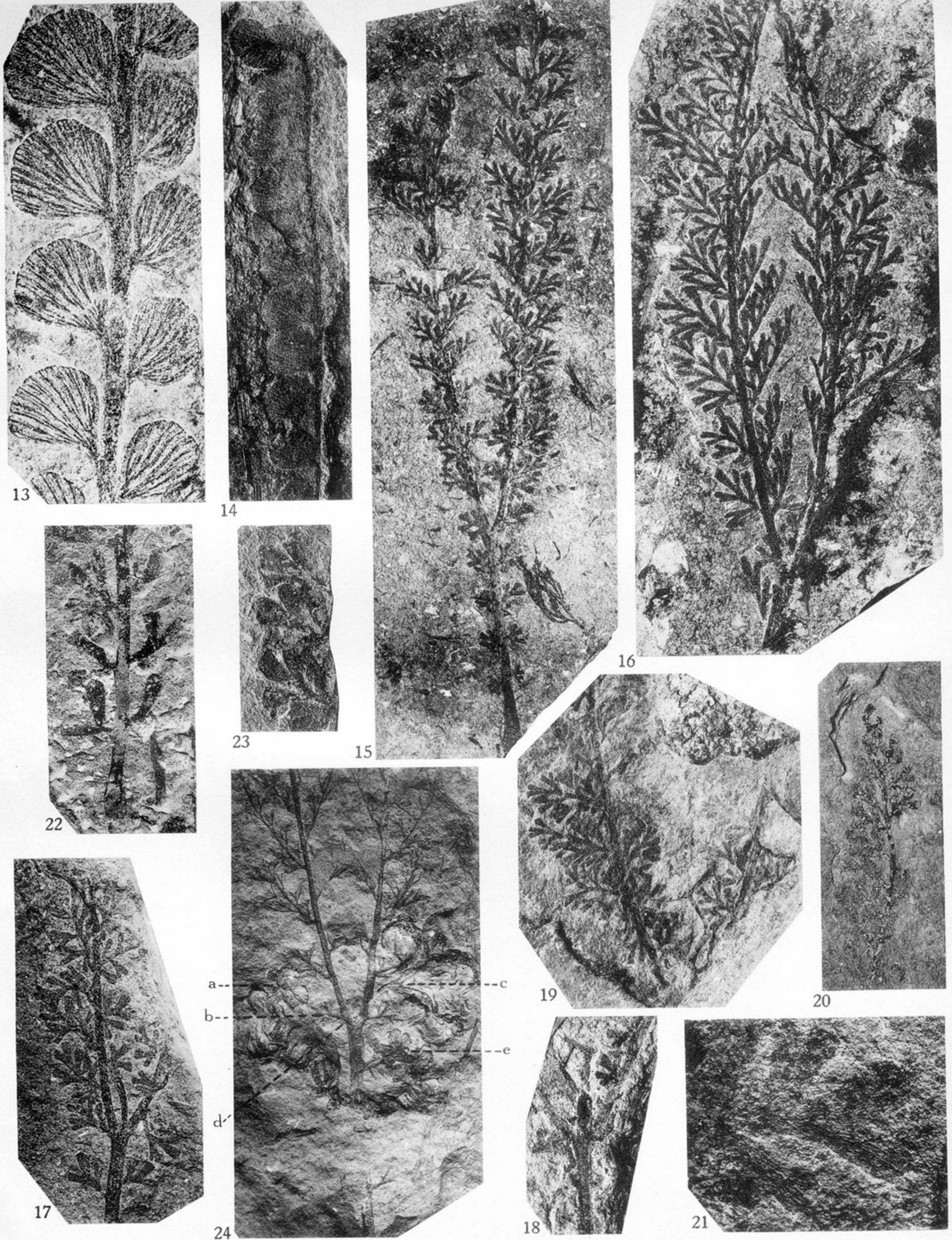
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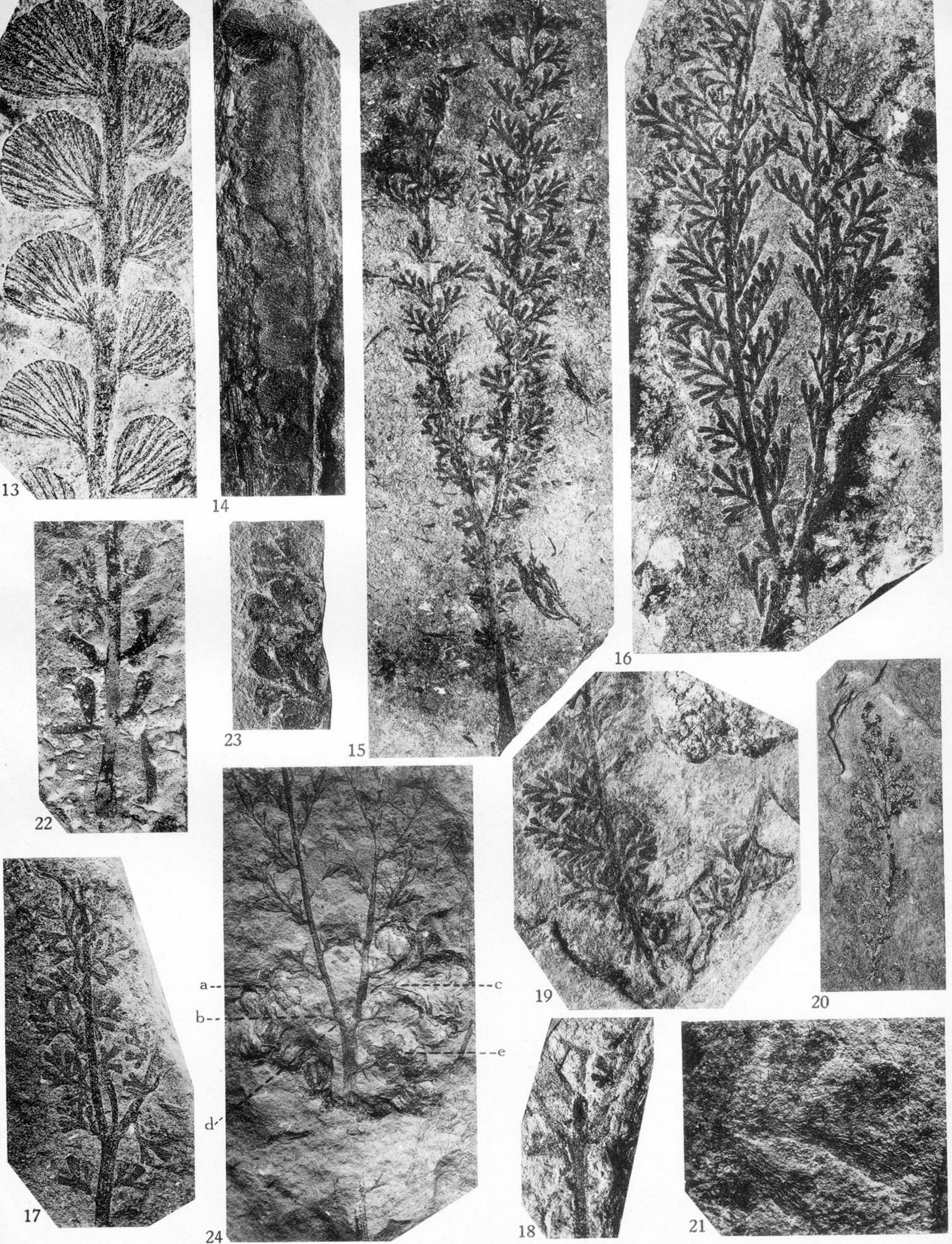
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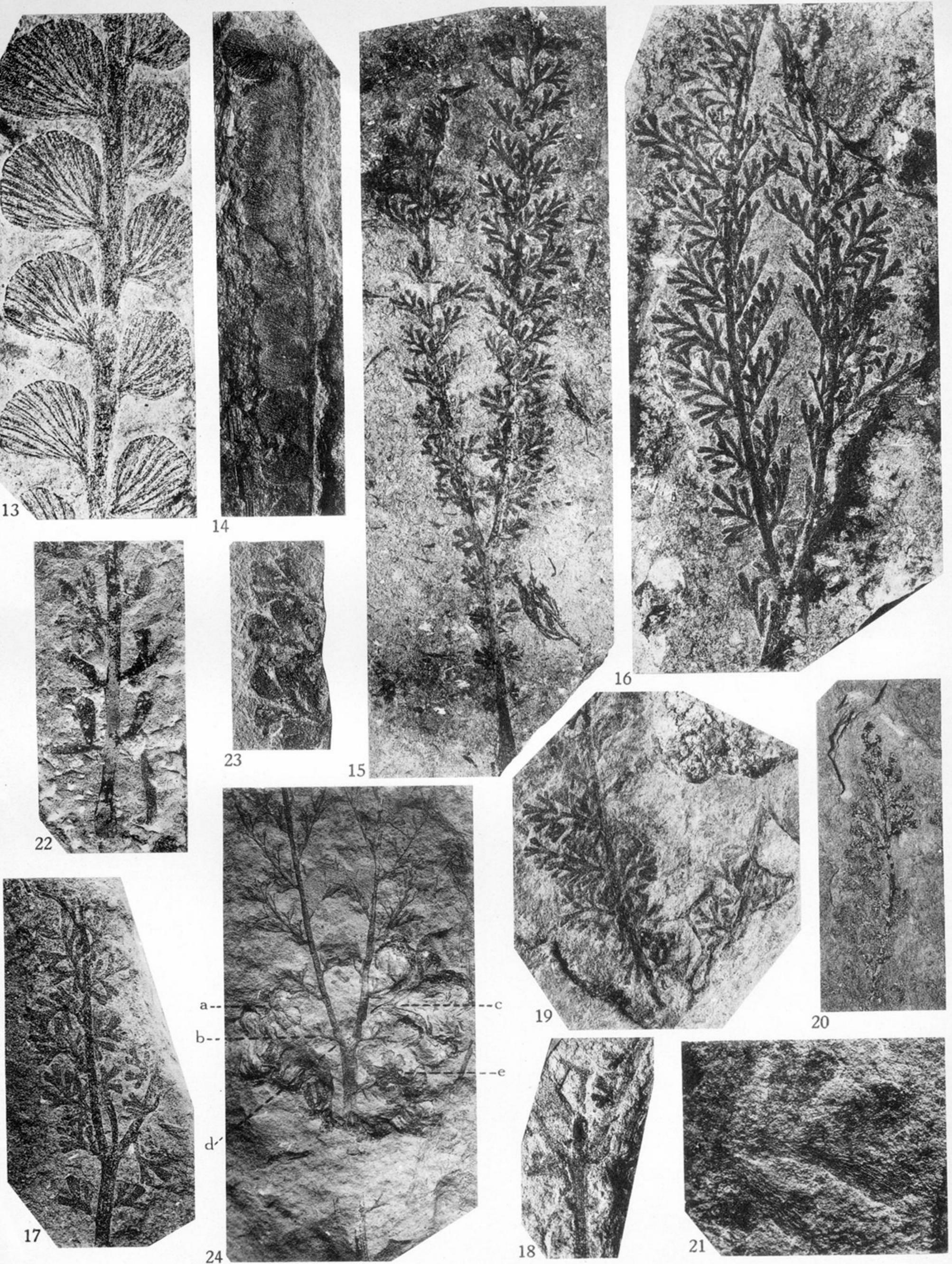
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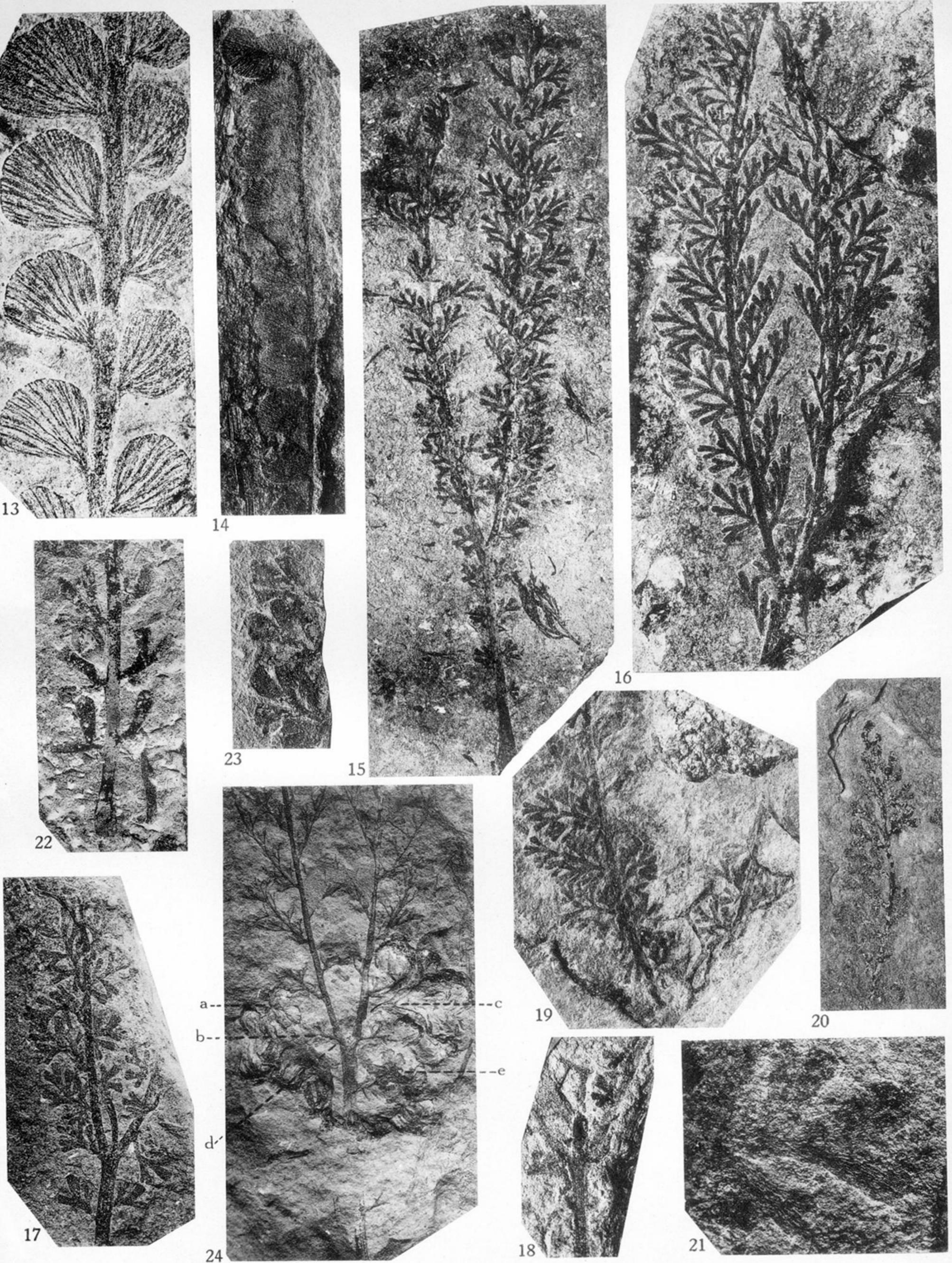
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