

TWO LITTLE KNOWN SPECIES OF *SPHENOPHYLLUM* FROM THE STEPHANIAN OF SPAIN AND FRANCE

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ABSTRACT

The impression species *Sphenophyllum incisum* Wagner is fully described for the first time, with due reference to intra-specific variation as shown by abundant material from a single locality in the Stephanian B of North-west Spain. The associated strobilus is also recorded. *Sphenophyllum nageli* Grand'Eury, a middle to late Cantabrian species, is redescribed from the type region in the Cévennes, southern France. Similar material is illustrated from Cantabrian and Stephanian A localities in North-west Spain. Brief comments are made on several other species of *Sphenophyllum* from the Stephanian of western Europe, and a range chart is provided.

INTRODUCTION

IT is well over twenty years ago since Doubinger and Vetter (1954) published a brief note on the various species of *Sphenophyllum* recorded from Stephanian strata. A monographic paper by Abbott (1958) filled in gaps with regard to the American species; a brief note by Obrhel (1967) brought the description of *Sphenophyllum nemejci* Obrhel from the Stephanian of Bohemia; and recent work on the Stephanian floras of Portugal and Spain has added several new species such as *Sphenophyllum guerreiroi* Teixeira, *Sphenophyllum incisum* Wagner, *Sphenophyllum galeanoi* Broutin, *Sphenophyllum casetasense* Knight, and *Sphenophyllum crenulatum* Knight. Even the well studied Stephanian of France yielded a new species, *Sphenophyllum miravallis* Vetter. The stratigraphic distribution of the various Stephanian species of *Sphenophyllum* has also become better known. Vogellehner (1967) introduced a new species, *Sphenophyllum intermedium*, for material resembling *S. emarginatum* in Stephanian A-B strata.

Most of these new species have been adequately figured and described (Teixeira, 1951; Vetter, 1968; Broutin, 1973; Knight, 1975), but *Sphenophyllum incisum* has only been diagnosed briefly on the basis of a single holotype (Wagner, 1964), and cannot yet be regarded as adequately known, despite further illustration of this species by Wagner (1965) and Stockmans and Willièrè (1965). This will be remedied in the present paper by providing a full description on the

basis of a large collection of specimens from a single locality.

Another little known species, *Sphenophyllum nageli* Grand'Eury, was actually described in 1890, but hardly mentioned afterwards. Doubinger and Vetter ignored it entirely in their synthesis of 1954, and the species did not reappear in the literature until 1970 when it was mentioned again from the original type area, the Cévennes, by Bouroz, Gras and Wagner. The material reported in that paper includes several well-preserved specimens which allow a redescription of *Sphenophyllum nageli* Grand'Eury, as provided in the present paper.

Although, it would undoubtedly be of interest to present a full synthesis of Stephanian species of *Sphenophyllum*, as known at present from West European localities, this must be regarded as outside the scope of the present paper. Only a few comments may be made on some of the more important species, stressing a few points of taxonomic interest and highlighting some of the more recently acquired information on stratigraphic ranges.

SYSTEMATIC DESCRIPTION

Sphenophyllum incisum Wagner

Pls. 1-4, figs. 1-12; Pl. 6, fig. 20

1964 *Sphenophyllum incisum* n. sp., Wagner: *C.R. 5è Congrès Carbonifère, Paris* 1963, II, p. 846, pl. III, fig. 24.

1964 *Sphenophyllum incisum* Wagner, Boureau: *Traité de Paléobotanique*, tome III. Sphenophyta, p. 66, fig. 41

(same as Wagner, 1965, pl. 51, figs. 104, 105).

- 1965 *Sphenophyllum incisum* Wagner: Wagner, *Mem. Inst. geol. Min. España*, LXVI (publ. March, 1966), pp. 52, 142, pl. 51, figs. 104, 105.
- 1965 *Sphenophyllum incisum* Wagner, Stockmans & Willière: *Mém. Inst. R. Sci. nat. Belgique*, 79 (publ. April, 1966), pl. XXXII, figs. 6-9.
- 1970 *Sphenophyllum incisum* Wagner: Wagner & Artieda, *La Cuenca Minera Ciénega-Matallana*, lám. XVII, fig. D (holotype. $\times 3$).
- 1971 *Sphenophyllum incisum* Wagner: Wagner, *Trab. Geol. Fac. Ci. Univ. Oviedo*, 4, p. 421.
- 1975 *Sphenophyllum incisum* Wagner: Alvarez-Ramis, *Estudios Geol.*, XXXI, p. 786, lám. II, fig. 3 (after Wagner, 1964, pl. III, fig. 24 — holotype), non fig. 2 (probably *Sphenophyllum angustifolium* Germar).

Description — Ribbed axes of variable width with closely spaced, overlapping verticils of six leaves showing straight sides and a deeply dissected distal border with elongate, pointed teeth, 4 or 6 in number. Length-breadth ratio of the leaves varying between 1.3 and 3 (generally about 2) and central cleft reaching most commonly a little over halfway down the leaf (compare Table 1 & Text-fig. 1). Leaf sizes between 4-11 mm length and 2-6 mm width (as measured on the distal border). Nervation corresponds closely to the segments of the deeply incised leaf.

Branches occur as one per node at intervals of several internodes. Leaf verticils very densely arranged at the end of branches where each verticil may overlap with several others. Lengthwise compression often gives a false appearance of simple leaves.

Fructification (associated, not in organic connection) consists of a strobilus with verticils of curved, rather spiky, apparently simple bracts carrying relatively large sporangia in the axils, probably in the proportion of one sporangium per bract. Sporangioophores not observed.

Remarks on Figured Material — The above description is based on some eighty samples collected from a single locality in 10 to 20 cm of rock at some distance above a thin coal, which is the first to occur above the basal breccia on the northern edge

TABLE 1 — MEASUREMENTS ON 59 LEAVES FROM DIFFERENT SPECIMENS OF *SPHENOPHYLLUM INCISUM* WAGNER AT LOC. 983 IN THE LA MAGDALENA COALFIELD (PROVINCE LEON, NW SPAIN)

	Length	Breadth	Central cleft	Length	Breadth	Central cleft
	11	5	6	7	4.5	5
	9	6	5	7	4	5
	9	5	6	7	4	5
	9	5	5.5	7	4	4
	9	5	5	7	4	4
	9	4	5	7	4	4
	9	4	5	7	4	4
	9	4	4	7	3.5	5
	9	4	4.5	7	3.5	5
	9	4	5.5	7	3.5	4
	9	3	5	7	3	5
	9	3	5	7	3	5
	8	5	5	7	3	4
	8	4	6	7	3	4
	8	4	5	6	4.5	4
	8	4	5	6	4	4
	8	4	4.5	6	4	3
	8	4	4	6	3	5
	8	4	6	6	3	4
	8	4	5	6	3	4
	8	4	5	6	3	4
	8	4	4	6	2.5	5
	8	3.5	5	6	2.5	3
	8	3.5	5	5.5	3.5	4
	8	3	5	5	4	3.5
	8	3	5	5	3	3
	8	3	4	5	3	3
	8	3	4	5	3	3
	7.5	3.5	5	4	2	2
	7.5	3.5	5			

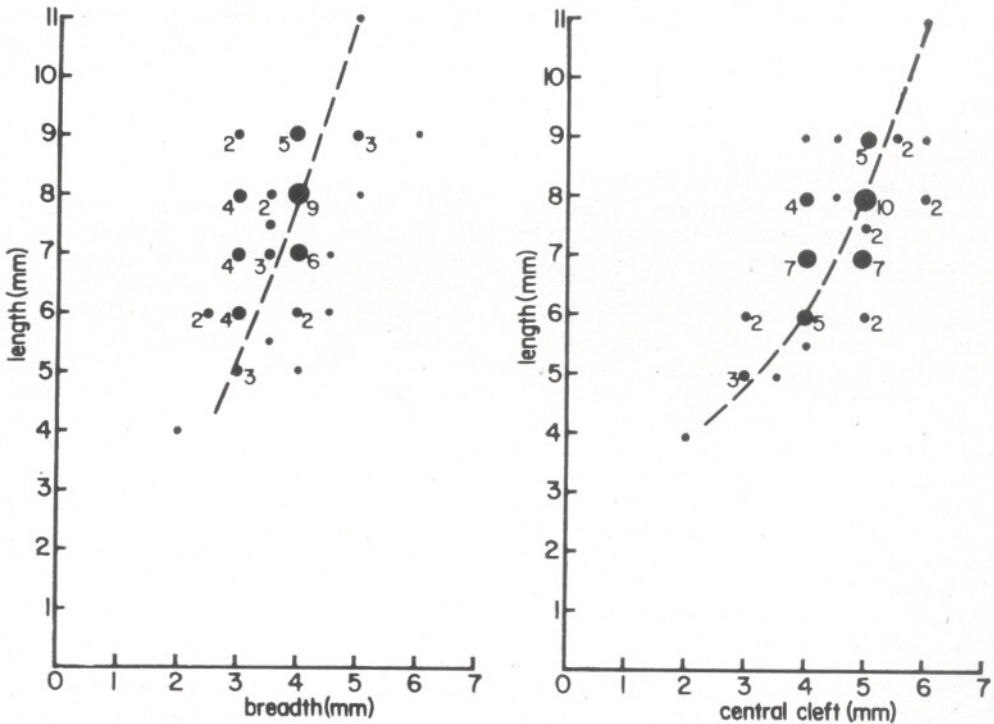
of the La Magdalena Coalfield in the province León, NW Spain. Material from this locality (Wagner loc. 983) was figured previously by Wagner (1965) and Stockmans and Willière (1965). Although other plant species are associated, *Sphenophyllum incisum* is the dominant sphenophyte in the bed which was sampled extensively over a number of years. Associated sphenophytes are *Annularia sphenophylloides* (Zenker) von Gutbier and *Asterophyllites equisetiformis* (von Schlottheim) Brongniart, a point worth remembering when assigning some associated strobili to *Sphenophyllum incisum* Wagner. Only one of these strobili shows a ribbed axis similar to those of *Sphenophyllum incisum* (not an infallible criterion anyway), the other strobilar axes being too thin for ribbing to occur. A comparison with published strobili of *Annularia sphenophylloides* (i.e. *Calamostachys calathifera* Weiss) and

Asterophyllites equisetiformis (i.e. *Calamostachys germanica* Weiss) show strongly divergent characters, particularly in view of the axillar position of the sporangia in the strobili associated with *Sphenophyllum incisum*. These appear to conform to the *Koinostachys* type of strobilus in the Sphenophyllales, a rather wide grouping of fructifications (Remy, 1955) which is based mainly on the axillar position of sporangiophores carrying either single or clustered sporangia (as a result of successive dichotomies of the sporangiophore) and on the absence of a shield in the peltate arrangement of sporangia. Both strobili and individual whorls with axillar, branching sporangiophores (as in *Sphenophyllum majus* Brong & *Sphenophyllum kidstoni* Hemingway) have been assigned to *Koinostachys* by Remy.

In the sterile foliage of *Sphenophyllum incisum* Wagner it is noticeable that the amount of variation is strictly limited. The large number of specimens collected from a single locality, and the reasonably

good preservation of these compressions and impressions have allowed the fairly accurate measurement of length, breadth and relative amount of incision at the central cleft of each leaf. Altogether, 59 leaves were measured for Table 1 (see also Text-fig. 1), each leaf being taken from a different specimen and using completeness of preservation as the sole criterion for the selection of specimens to be measured. The length-breadth ratio falls within reasonably narrow limits and the majority of specimens occupy a virtually straight line on the graph plotting length against breadth. The depth of the central cleft is only a little more variable (right hand graph of Text-fig. 1), in relation to the length of the leaf.

The apparently rather minor variation in length-breadth ratio and in the relative depth of incision at the central cleft is matched by the other characteristics such as the straight lateral sides, with only occasional flaring near the distal border (probably as a result of the deep incisions



TEXT-FIG. 1 — Graphs showing length of leaves of *Sphenophyllum incisum* plotted against breadth, and length against depth of incision at central cleft (actual number of specimens recorded with relative size of dot denoting position of larger or smaller number of specimens with certain ratios).

and at least partly attributable to preservation), and the invariable presence of deeply dissected leaves with long, pointed slips. There is none of the extreme polymorphism which characterizes some of the other species of *Sphenophyllum*, e.g. *Sphenophyllum cuneifolium* Sternberg, and more entire leaves are conspicuously absent in the assemblage.

An important characteristic of *Sphenophyllum incisum* seems to be the close spacing of leaf verticils, a feature which becomes even more pronounced near the tip of the ultimate branches.

Compression is either lengthwise or as spread-out verticils, with somewhat oblique compression being a not uncommon feature. Longitudinal compressions may not show the entire length of leaves and commonly produce the somewhat misleading aspect of simple leaves, whereas these are not, in fact, present. The narrowness of the leaves may have helped in producing this kind of preservational aspect. Only two successive dichotomies are present in the case of four teeth being present on the distal border. An additional dichotomy of inner slips of each pair in a foursome produced the six teeth that are very often present in the leaves of *Sphenophyllum incisum*. Also with regard to the presence of either four or six teeth and the concomitant rather narrow width of the distal border, the species shows relatively constant characteristics.

Comparison — *Sphenophyllum angustifolium* Germar, a characteristic element of Stephanian C floras and thus rather close in stratigraphic occurrence to *Sphenophyllum incisum* which has been found in Stephanian B, has narrower and longer leaves with a length-breadth ratio of about 5. Its leaves are also not quite as deeply cleft as in *Sphenophyllum incisum* (i.e. in relation to the length of the leaves). The rather massive strobili of *Sphenophyllum angustifolium* provide another distinctive feature of this species, those of *Sphenophyllum incisum* being more slender and, above all, more laxly built.

The deeply incised distal border of *Sphenophyllum incisum* occasionally appears to be flaring, thus showing a superficial resemblance to *Sphenophyllum kidstoni* Hemingway. However, the leaves of *Sphenophyllum kidstoni* have a stiffer appearance and also show either a larger number of leaves per verticil (i.e. more than 6) or a larger

number of teeth on the distal border. *Sphenophyllum kidstoni* is also characterized by groups of 4 sporangia per sporangiophore in the axils of apparently normal leaves, and does not possess strobili as such. This species is a middle Westphalian element, whereas *Sphenophyllum incisum* occurs in Stephanian B.

There may be a vague resemblance to the forma *saxifragaefolium* of the extremely polymorph *Sphenophyllum cuneifolium* (Sternberg) Zeiller, since this form also possesses a highly dissected leaf which may also have four sharp teeth on the distal border. However, *Sphenophyllum incisum* shows highly dissected leaves throughout, whereas *Sphenophyllum cuneifolium* shows a number of leaf shapes, the most common of which is an almost entire leaf with short, pointed teeth on a distal border without central cleft. The stratigraphic ranges of these two species are very different, since *Sphenophyllum cuneifolium* occurs in middle to upper Namurian and lower to middle Westphalian strata, and *Sphenophyllum incisum* in Stephanian B.

Remarks on Synonymy — *Sphenophyllum incisum* was briefly diagnosed in Wagner, 1964, p. 846 (*Compte rendu 5th Carboniferous Congress, Paris, 1963*): "Leaf verticils characterized by rather slender, deeply incised leaves with almost straight lateral sides and long, pointed teeth on the distal side. The leaves are usually about 7 to 10 mm long and about 3 to 4 mm wide on the distal border." Comparison was made with *Sphenophyllum cuneifolium* forma *saxifragaefolium* Germar. Only a single specimen (holotype) was figured at the time. It was refigured, $\times 3$, in Wagner and Artieda (1970) as part of a documentation of the Stephanian B flora of the Cifera-Matallana Coalfield, but a truly representative collection of several hundred specimens from a single locality was obtained in later years from the basal coal-measures of the neighbouring La Magdalena area, further west in northern León (NW Spain). This locality (983) yielded the specimen figured in the '*Traité de Paléobotanique*' and in Wagner, 1965, as well as those illustrated by Stockmans and Willièrè, 1965. All the specimens recorded in the present paper are from this locality at La Magdalena. They show the full range of variation as described above.

On the basis of the few specimens illustrated in the literature, Alvarez-Ramis (1975) has suggested that *Sphenophyllum incisum* might represent the basal portions of *Sphenophyllum angustifolium* Germar. This view finds no support from the extensive collection of remains of *Sphenophyllum incisum* reported in the present paper, which does not show a sufficiently wide range of variation for the incorporation of this species in *Sphenophyllum angustifolium*. The specimen from the Tineo Coalfield in western Asturias (North-west Spain) which Alvarez-Ramis (1975, lám. II, fig. 2) figures under the name *Sphenophyllum incisum*, probably does belong to *Sphenophyllum angustifolium* which is a fairly common species at Tineo (compare Wagner, 1965, pp. 142-144, pl. 70).

Remarks on Preservation—The holotype of *Sphenophyllum incisum* Wagner is a black imprint and stain on a dark grey mudstone from the Pastora Formation of the Ciñera-Matallana Coalfield. The rank of coals in this coalfield (12-14% volatiles) seems to preclude the recovery of a cuticle. The specimens from the La Magdalena Coalfield, recorded in the present paper, are preserved as dark carbonaceous stains on rust-coloured imprints on slightly silty mudstone and shale which has been intensely weathered. Both the degree of weathering and the rank of coals in the La Magdalena area preclude the recovery of a cuticle.

Distribution—Ciñera-Matallana Coalfield (province León, north-west Spain): San Francisco to Matallana formations, i.e. throughout the succession in this coalfield, Stephanian B (Wagner, 1971, p. 421).

La Magdalena Coalfield (province León, north-west Spain): loc. 983 (Wagner, 1965, p. 52) in shales above the first thin coal which follows upon the basal breccia in exposures near the road to Villablino, on the northern edge of this coalfield, Stephanian B.

Sphenophyllum nageli Grand'Eury

Pls. 5, 6, figs. 13-19

1890 *Sphenophyllum nageli* n. sp., Grand'Eury, *Géologie et Paléontologie du Bassin houiller du Gard*, p. 230, pl. 17, fig. 20.

Description—Slender axes with widely spaced verticils of entire leaves, six to a whorl. Dimensions of leaves quite variable,

TABLE 2—DIMENSIONS OF LEAVES IN INDIVIDUAL SPECIMENS OF *SPHENOPHYLLUM NAGELI* GRAND'EURY FROM THREE LOCALITIES IN ZONE 2 (PANISSIÈRE) IN THE CÉVENNES COALFIELD OF SOUTHERN FRANCE

Length	Breadth
9	5
8	5
8	3
7.5	2.5
7	2.5
6	2
5	2

even in the limited number of specimens collected (Table 2); length ranging from 5 to 9 mm, width from 2 to 5 mm; length-breadth ratio ranging from 1.6 to 3; lateral borders straight and distal borders convex, with short rounded teeth which may not always be apparent where preservation is slightly defective; nervation fairly close and consisting of a single initial vein splitting rapidly and dichotomising into numerous ultimate veins each of which corresponds to a rounded tooth on the distal border.

Remarks on Figured Material—The specimens figured on Pl. 5, figs. 13-15 and Pl. 6, figs. 19, 19a, are all from the Cévennes in southern France, which is the type area for *Sphenophyllum nageli* Grand'Eury. Pl. 5, figs. 14, 14a depicts the specimen that corresponds most closely to the original type as figured by Grand'Eury (1890, pl. 17, fig. 20) from the Cévennes. Like the type it shows a longitudinal compression of leaves along the axes which tends to favour the narrower leaves and which may make it difficult to observe correctly the base of the leaves and their insertion. This may explain some parts of the original description of the species as provided by Grand'Eury and which are at variance with the description given in the present paper, as based on the more abundant material collected more recently by Bouroz, Gras and Wagner (1970) from the Cévennes Coalfield. Grand'Eury (1890, p. 230) described *Sphenophyllum nageli* as follows: "Cependant je ne saurais confondre avec aucune des formes possibles du *Sph. Schlotheimii* le *Sphenophyllum* (pl. 17, fig. 20) trouvé seulement dans le bassin Nord, à Gagnières, Souhot, Mazel, dans les schistes

stériles et au Souterrain; aussi dans la bacnure de Brissac sous la Fanode, il se distingue par des verticilles de six feuilles rigides, dressées, oblongues, spathuliformes, à bord arrondi, toujours entier, limbe coriace; nervures peu apparentes réduites à deux à la base; tige pointillée par des écailles cétaées, faibles sillons correspondant à la séparation des feuilles."

Grand'Eury did not provide dimensions which is perfectly reasonable since the longitudinal compression of the type specimen makes the proper observation of the dimensions of the leaves rather difficult. It is quite probable that Grand'Eury's mention of two veins entering the base of each leaf is also due to the difficulties of observing properly the insertion of the leaves in longitudinal compression. Grand'Eury did not mention the somewhat crenulate border of the leaves as collected more recently. Indeed, not every specimen shows this character clearly, since the teeth on the distal border are very short and rounded, thus requiring a nearly perfect preservation for this character to become apparent. The mention of scales on the stems or branches may refer to imperfect preservation as well.

The newly collected material (Bouroz, Gras & Wagner, 1970), as reported in the present paper, is obviously most important for the description of *Sphenophyllum nageli* Grand'Eury. The specimens figured here from the Cévennes show a fairly wide range in size and length-breadth ratio of the leaves, despite the fact that only a relatively small number of specimens have been recorded. The single holotype figured by Grand'Eury was obviously insufficient for any range in variation to become apparent.

With the new material from the Cévennes in France a number of specimens comparable to *Sphenophyllum nageli* are figured from strata of a similar age in northern Spain. The latter (Pl. 5, fig. 16; Pl. 6, figs. 17-18) also possess six leaves per whorl and they show the convex distal border with short, rounded teeth that helps to characterize this species. However, their leaves are marginally more truncate than those of *Sphenophyllum nageli* from the Cévennes. In fact, they may be regarded as intermediate forms between this species and *Sphenophyllum emarginatum* forma *truncatum* Schimper. This is the form with an entire

distal border, as against the form with a central cleft which constitutes the type of *Sphenophyllum emarginatum* (Brongniart).

Stockmans and Willièrè (1965) figured very similar specimens from north-west Spain under the name *Sphenophyllum truncatum*, and pointed out the relationship with *Sphenophyllum emarginatum*. It does seem possible that the *Sphenophyllum emarginatum* with a central cleft passes into the forma *truncatum* in the higher Westphalian D strata, and that this form shows a transition into *Sphenophyllum nageli* of Cantabrian age. The transition form may be distinguished by the more convex distal border which is, however, not quite as convex as that of *Sphenophyllum nageli* proper. Both *Sphenophyllum emarginatum* forma *truncatum* and *Sphenophyllum nageli* show the veins ending entirely on the distal border, and although the lateral borders in the latter seem to merge gradually into the distal border, there is no case of a total merging with the veins ending on both the lateral and distal borders as occurs in the group of *Sphenophyllum thoni* von Mahr.

The transitional forms figured on Pl. 5, fig. 16 and Pl. 6, figs. 16-18 are recorded here as *Sphenophyllum* cf. *nageli* Grand'Eury. Some of these are the same specimens as mentioned as *Sphenophyllum nageli* in Wagner and Varker (1971, p. 598) and in Wagner, Park, Winkler Prins and Lys (1977, pp. 111, 113).

Comparison—The forma *truncatum* of *Sphenophyllum emarginatum* (Brongniart) Koenig is also characterized by entire leaves with short, rounded teeth on the distal margin. However, its distal border is either truncate or only slightly convex, whereas it is very rounded in *Sphenophyllum nageli*. The latter thus simulates the merging of lateral and distal borders which is such a pronounced feature of *Sphenophyllum thoni* von Mahr and several other, mainly Permian species.

In fact, the general shape of the leaves in *Sphenophyllum nageli* Grand'Eury is quite similar to that of *Sphenophyllum thoni* var. *minor* Sterzel, a late Stephanian B form with entire leaves (as against the fringed leaves of *Sphenophyllum thoni* proper). There is, however, a fundamental difference in that some of the veins end on the lateral borders in *Sphenophyllum thoni* var. *minor*, whereas they all terminate on the distal

border in *Sphenophyllum nageli*. The leaves also tend to be a little larger in *Sphenophyllum thoni* var. *minor*, but it must be noted that the size variation in this species overlaps with that of *Sphenophyllum nageli*. The small crenulations that appear on the distal border of *Sphenophyllum nageli* are apparently absent in *Sphenophyllum thoni* var. *minor*.

Comparison can be made also with *Sphenophyllum crenulatum* Knight which has entire leaves with rounded tops showing bluntly acute teeth becoming slender and awl-like in some cases. This is a species of the group of *Sphenophyllum thoni* and thus shows the presence of vein endings on both the lateral and distal borders which are fully merged into one another. Also, Knight's species seems to show generally larger leaves than occur in *Sphenophyllum nageli* Grand'Eury.

Sphenophyllum verticillatum (von Schlottheim) Zeiller is very closely similar to *Sphenophyllum nageli*. It also shows all the veins ending on the distal margin which is convex and set with small, rounded teeth. The size and length-breadth ratios of the leaves are also comparable and the two species could well be confused if *Sphenophyllum verticillatum* had not shown the extreme dimorphism recorded for this species which possesses deeply incised leaves on the main axes. This dimorphism is unknown for *Sphenophyllum nageli*, even though it should be noted that the number of specimens is still rather small and its full range of variation possibly unknown as yet.

Distribution — Undoubted specimens of *Sphenophyllum nageli* Grand'Eury are known only from the type region, i.e. the Cévennes in southern France. Recent collection (Bouroz, Gras & Wagner, 1970) has shown its presence in Zone 2 (Panissière), of middle to late Cantabrian age: Loc. 2015 — old tips at Le Mazel, seams III, IV and V of Zone 2 in its lower part, near the Bannelle Fault; Loc. 2016 — tip of Le Souterrain, Ruisseau de la Combe de Banne, Zone 2 in its middle part.

Specimens comparable to *Sphenophyllum nageli* and apparently transitional to *Sphenophyllum emarginatum* forma *truncatum* Schimper occur in middle Cantabrian and Stephanian A strata of north-west Spain: Loc. 1784 — old tip on the path to Petrita,

near Mercedes in the Barruelo Coalfield (province Palencia), Barruelo Formation, Calero Member, early Stephanian A; Loc. 2208 — tip of San Francisco Mine (Sanfesa Company), south of San Salvador de Cantamuda (province Palencia), Salvador Formation, middle Cantabrian.

REMARKS ON SOME OTHER SPECIES OF *SPHENOPHYLLUM* FROM THE STEPHANIAN

An alphabetical order is followed for some brief remarks on several other species of *Sphenophyllum* from the Stephanian of western Europe, and the same order is followed for the accompanying range chart (Table 3).

Sphenophyllum alatifolium Renault, a species with rather large and broad leaves with straight lateral borders and a truncate distal margin set with short, rounded teeth, has often been confused with *Sphenophyllum costae* Sterzel which may be distinguished by its somewhat convex distal border. These two species are possibly synonymous (as was proposed by Doubinger & Vetter, 1954), and in this case *Sphenophyllum alatifolium* has priority (see comments in Wagner, 1965, pp. 140-142).

There are no problems attached to the identification of *Sphenophyllum angustifolium* Germar which is easily recognized on its rather slender leaves with 2 to 4 elongate, pointed teeth. This species is a reliable index for Stephanian C and Autunian. An American species, *Sphenophyllum tenuifolium* Fontaine & White, which shows similar characteristics, has sometimes been recorded mistakenly from Europe after specimens belonging to *Sphenophyllum angustifolium* Germar.

One of the two species recently introduced by Knight (1975), *Sphenophyllum casetasense*, has somewhat flaring, dissected leaves with a sharply toothed distal border, a length-breadth ratio of 1.25 to 2 (ranging in length from 4 to 10 mm) and only a certain amount of dimorphism. Comparison has been made primarily with *Sphenophyllum kidstoni* Hemingway, which has similar leaf types, but which shows tetrasporangiate clusters amongst whorls of ordinary leaves, whereas *Sphenophyllum casetasense* bore small strobili on ultimate branches. The latter has been described from Stephanian B

TABLE 3—STRATIGRAPHIC RANGES OF THE DIFFERENT SPECIES OF *SPHENOPHYLLUM* IN STEPHANIAN ROCKS OF FRANCE AND SPAIN (STEPHANIAN SERIES CONSISTING OF FOUR STAGES CANTABRIAN, STEPHANIAN A, STEPHANIAN B, STEPHANIAN C).

	CANTAB.	St. A	St. B	St. C	AUTUN.
<i>S. alatifolium</i> Renault			—		
<i>S. angustifolium</i> Germar				—	—
<i>S. casetasense</i> Knight			—		
<i>S. crenulatum</i> Knight			—		
<i>S. costae</i> Sterzel			—		
<i>S. emarginatum</i> forma <i>truncatum</i> Schimper	—	—	—		
<i>S. galeanoi</i> Broutin					—
<i>S. guerreiroi</i> Teixeira	—				
<i>S. incisum</i> Wagner			—		
<i>S. longifolium</i> Germar	—		—		—
<i>S. miravallis</i> Vetter			—	—	—
<i>S. nageli</i> Grand'Eury	—	—?			
<i>S. oblongifolium</i> (Germar & Kaulfuss)	—	—	—		
<i>S. thoni</i> von Mahr				—	—
<i>S. thoni</i> var. <i>minor</i> Sterzel			—	—	
<i>S. verticillatum</i> (von Schlotheim)			—	—	—

strata in the Sabero Coalfield of north-west Spain, whereas *Sphenophyllum kidstoni* occurs in Westphalian B.

Sphenophyllum crenulatum Knight is another Stephanian B element from the Sabero Coalfield, but it also occurs in the late Stephanian B of Saarland (Germany). It was illustrated from Saarland by Germar, Kneuper and Wagner (1968) under the name *Sphenophyllum* nov. sp. aff. *thoni* von Mahr, and by Germar (1971) as *Sphenophyllum miravallis* Vetter. *Sphenophyllum crenulatum* is a species in the group of *Sphenophyllum thoni* with which it agrees in showing leaves with the distal border merging gradually into the lateral borders, and the veins ending partly on the lateral margins. *Sphenophyllum crenulatum* is further characterized by its bluntly acuminate teeth, normally with only weak incisions in between but, particularly on the top-lateral margin, the teeth may be slender, awl-like and incised up to 2.5 mm. In this respect it differs markedly from *Sphenophyllum miravallis* which possesses leaves with an entire margin. The size and length-breadth ratios of the leaves are quite similar in both species, but it is also to be noted that *Sphenophyllum miravallis* Vetter shows anisophyllous whorls.

The two species described by Knight (1975) are in an unpublished Ph.D. thesis which is currently in the press.

The very common species *Sphenophyllum emarginatum* (Brongniart) Koenig is mainly recorded from Westphalian C and D, but it persists with large numbers into Cantabrian strata and still occurs sporadically in Stephanian A (Knight, 1975). From late Westphalian D onwards it is the forma *truncatum* Schimper which is present, the typical form with a central cleft being restricted apparently to Westphalian C and early to middle Westphalian D.

Sphenophyllum guerreiroi Teixeira is a form with small leaves (up to 4.5 mm long) which shows a strongly developed median cleft, somewhat convex lateral borders and four pointed teeth on the distal border (Teixeira, 1951, pp. 14-15). It was described originally from the late Westphalian D of Portugal but has been found since in upper Westphalian D and middle Cantabrian rocks of Palencia, north-west Spain.

Sphenophyllum longifolium Germar is a very characteristic species with fairly large, relatively long and dissected leaves. It occurs in Stephanian B and C as well as in the lower Autunian. Storch (1966) has recently figured *Sphenophyllum longifolium* from Westphalian D strata in Saxony, thus showing its range to be appreciably longer. It is generally of rare occurrence and its early appearance in the Zwickau-Lugau-Oelsnitz Coalfield of Saxony may well be linked to considerations of habitat.

Sphenophyllum miravallis Vetter, a rare species of the *Sphenophyllum thoni* group, is characterized by the veins ending on both the lateral and distal borders which merge very gradually. The size of the leaves is fairly large (up to 20 mm long), with a length-breadth ratio of up to 2.5. They possess rounded, entire margins, and the general aspect of this species is not too dissimilar to *Sphenophyllum speciosum* Royle of the Permian of Gondwanaland. The only reliable records of this species are from the Massif Central of France, where Vetter (1968) records its occurrence from Stephanian B to Autunian.

Sphenophyllum oblongifolium (Germar & Kaulfuss) Unger is undisputably the most common species of *Sphenophyllum* in Stephanian strata. It is easily recognized by its convex lateral borders, central cleft and pointed teeth on the distal border. Anisophylly is often a characteristic feature of this species which ranges from middle-late Cantabrian to Autunian.

Broutin (1973) has described a similar species, *Sphenophyllum galeanoi*, from the Autunian rocks of Guadalcanal (province of Sevilla, southern Spain). It differs from *Sphenophyllum oblongifolium* mainly on the basis of cuticle characteristics.

Sphenophyllum thoni von Mahr is a stratigraphically important, well-characterized

species representing the first of a group of mainly Permian *Sphenophyllum* with merging lateral and distal borders. It first appears in upper Stephanian B with the variety *minor* Sterzel which is characterized by somewhat smaller leaves with an entire margin. In the Stephanian C it is joined by the typical form of *Sphenophyllum thoni* which has generally larger leaves with a fringed border.

Sphenophyllum verticillatum (von Schlottheim) Zeiller has smaller leaves with only an apparent merging of lateral and distal borders which possess very short, rounded teeth. This species shows a high degree of polymorphism ranging from the typical form with an entire margin to highly dissected leaves. It occurs from Stephanian B onwards and ranges into the Autunian.

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EXPLANATION OF PLATES

(All figures natural size unless indicated otherwise)

PLATE 1

(Sphenophyllum incisum Wagner)

1, 2. Longitudinal compression of leaf whorls showing the standard kind of deeply incised leaf (figs. 1a & 2a 3).

3. Longitudinal compression showing partial cross sections of leaves in closely spaced whorls on lateral branch (fig. 3a. × 3).

PLATE 2

(Sphenophyllum incisum Wagner)

4. Part of a strobilus with spiky bracts and axillar sporangia (fig. 4a. × 3).

5, 6. Spread-out leaf verticils showing the long pointed teeth on deeply incised leaves (figs. 5a, 6a. × 3).

7. Longitudinal compression of closely spaced leaf verticils showing mainly cross sections of leaves which thus appear to be simple or only once bifurcate (fig. 7a. × 3).

8. Spread-out leaves showing central cleft and long, pointed teeth.

PLATE 3

(Sphenophyllum incisum Wagner)

5a, 8a. Spread-out, deeply incised leaves. × 3.
9. Spread-out verticil of very deeply incised leaves together with ribbed axis and lateral branch in longitudinal compression (fig. 9a. × 3).

10a. Spread-out leaf verticils. × 3 (natural size on Pl. 4).

PLATE 4

(Sphenophyllum incisum Wagner)

10. Spread-out leaf verticils.
11. Strobilus together with axes showing ordinary leaf verticils. (fig. 11a, strobilus three times enlarged in order to show the alternate arrangement of bracts with axillar sporangia).

12. Longitudinal compression of axes showing cross sections of leaves (on the left a fragment of a strobilus), (fig. 12a. × 3).

N.B. All specimens on Pls. 1-4 from loc. 983 in the La Magdalena Coalfield, Stephanian B,

PLATE 5

(*Sphenophyllum nageli* Grand'Eury) (figs. 13-15) and
S. cf. nageli (fig. 16)

13. Spread-out leaf verticils showing the characteristic shape of leaves with rounded tops (fig. 13a, three times enlarged in order to show the short, rounded teeth on the distal border).

14. Semi-longitudinal compression of axes with slender leaves showing the characteristic rounded tops (fig. 14a, three times enlarged to show venation). This specimen is similar to that figured by Grand'Eury (1890) as the type of *Sphenophyllum nageli*.

15. Exceptionally small leaves in spread-out verticils (fig. 15a. $\times 3$).

16. Semi-longitudinal compression of intermediate form between *S. nageli* and *S. emarginatum* forma *truncatum* Schimper, showing somewhat less rounded tops to the leaves.

N.B. Figs. 13-14 from loc. 2015 in Cévennes Coalfield, middle to upper Cantabrian; fig. 15 from loc. 2016 in Cévennes Coalfield, middle to upper Cantabrian; fig. 16 from loc. 2208 in northern Palencia, middle Cantabrian.

PLATE 6

Sphenophyllum cf. *nageli* Grand'Eury (figs. 16-18),
S. nageli (fig. 19), and *Sphenophyllum incisum*
Wagner (fig. 20)

16a. Semi-longitudinal compression of verticils showing leaves with convex but almost truncate distal margins. $\times 3$ (natural size figured on Pl. 5).

17, 18. Spread-out leaf verticils showing rounded tops set with short, blunt teeth (figs. 17a & 18a. $\times 3$).

19. Spread-out leaf verticils with rather narrow leaves with characteristically rounded tops (fig. 19a. $\times 3$).

20. Longitudinal compression showing cross sections of leaves. $\times 3$.

N.B. Fig. 16a from loc. 2208 in northern Palencia, middle Cantabrian; figs. 17-18 from loc. 1784 in northern Palencia, lower Stephanian A; fig. 19 from loc. 2015 in Cévennes Coalfield, middle to upper Cantabrian; fig. 20 from loc. 983 in La Magdalena Coalfield, Stephanian B. All figured specimens are in the author's collection at the University of Sheffield, England.

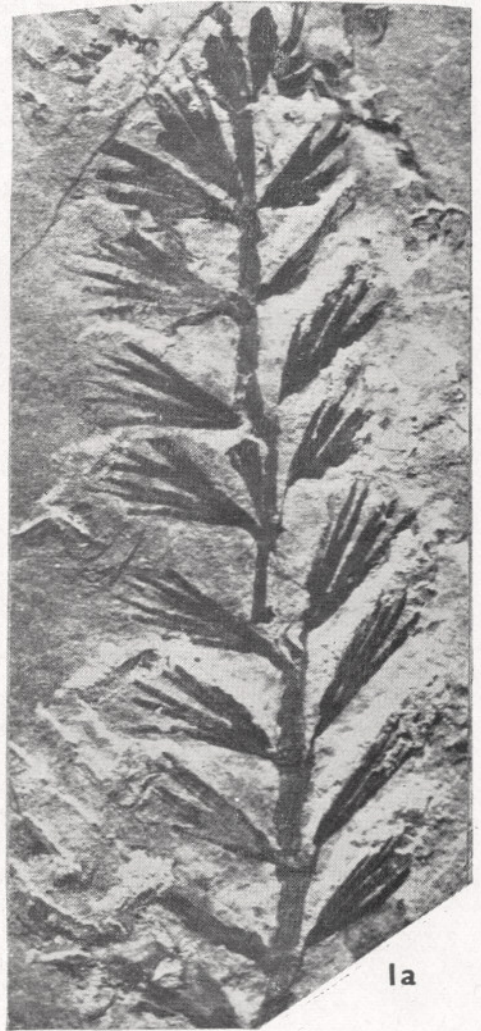
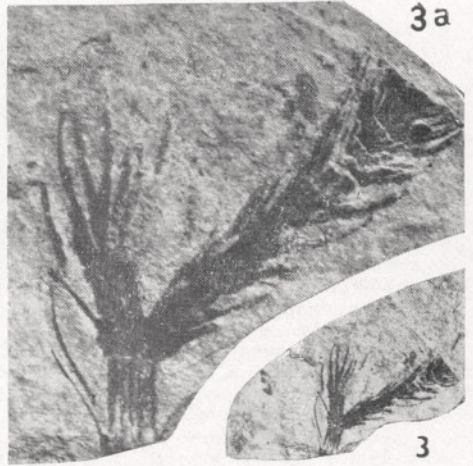
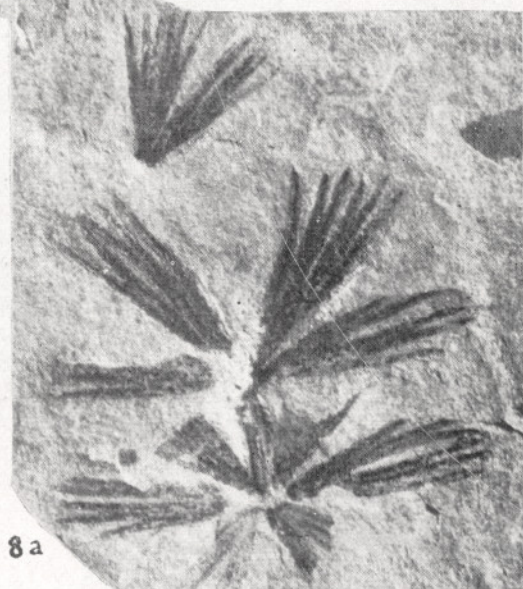
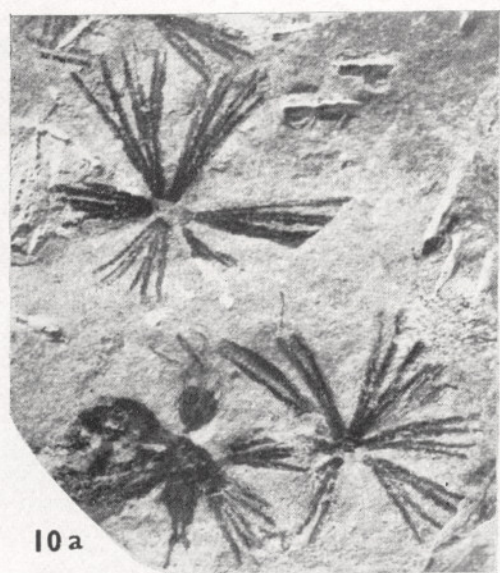
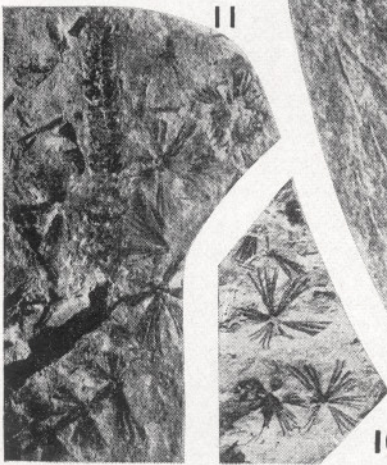
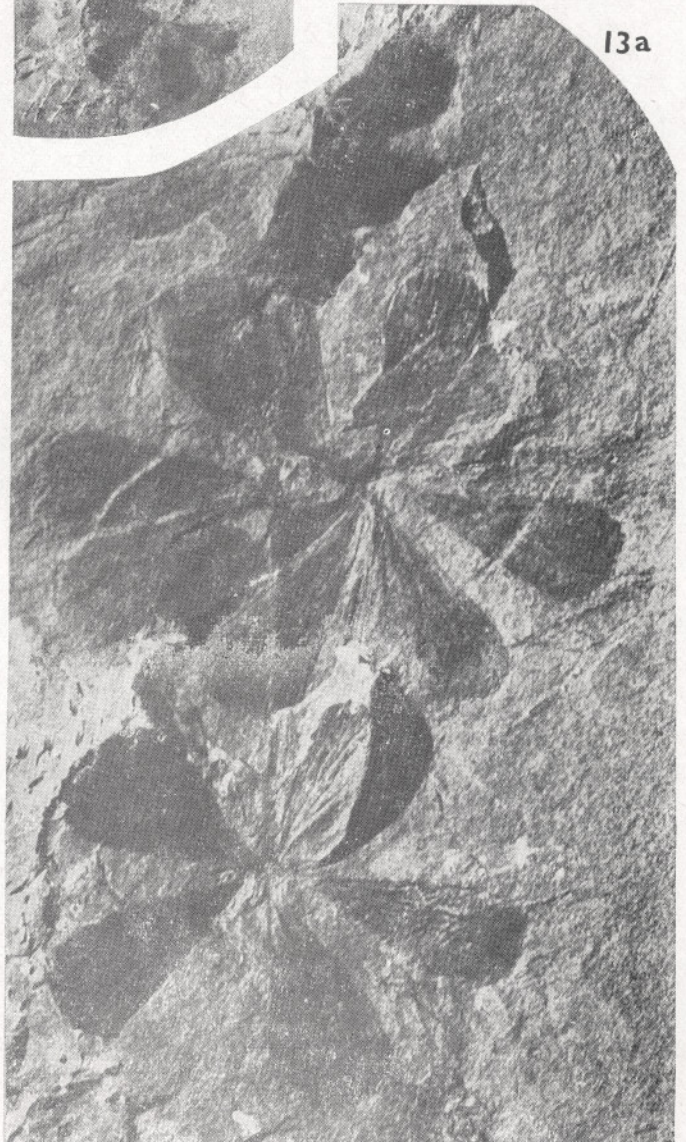
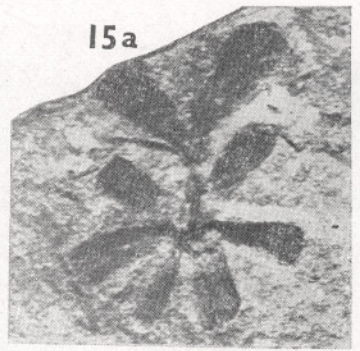




PLATE 2







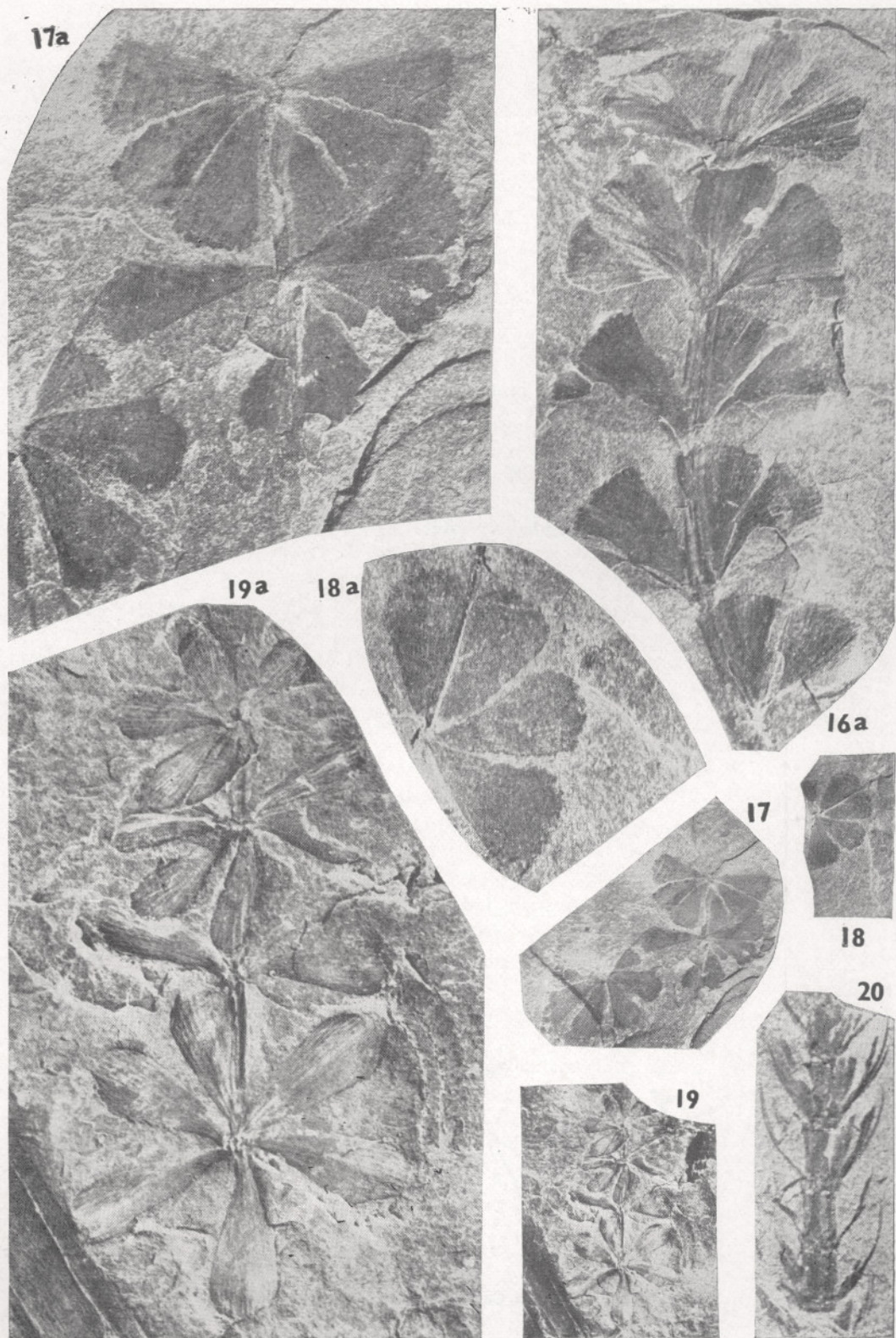


PLATE 6