L.
B.M.
C.b.
9.
52.

THE YORKSHIRE JURASSIC FLORA

IV GINKGOALES AND CZEKANOWSKIALES

BRITISH MUSEUM
GENERAL
20 JAN 1975
LIBRARY
NATURAL HISTORY

BRITISH MUSEUM (NATURAL HISTORY)

THE YORKSHIRE JURASSIC FLORA

IV

1 GINKGOALES

By

THOMAS MAXWELL HARRIS, F.R.S.

Professor of Botany in the University of Reading

and

WENDY MILLINGTON

2 CZEKANOWSKIALES

By

THOMAS MAXWELL HARRIS, F.R.S.

and

JOSÉ MILLER

With eight plates
and forty-one figures in the text

LONDON
TRUSTEES OF THE BRITISH MUSEUM (NATURAL HISTORY)
1974

© Trustees of the British Museum (Natural History) 1974

Publication number 724

ISBN 0 565 00724 6

Printed in England by Staples Printers Limited at The George Press, Kettering Northamptonshire.

This volume is dedicated to Professor C. A. Arnold

CONTENTS

	Page
INTRODUCTION	1
SYSTEMATIC DESCRIPTIONS	2
1. GINKGOALES	2
Key to the genera of Yorkshire Ginkgoales	3
Key to the Yorkshire species of *Ginkgo*	3
GINKGO Linnaeus	4
Ginkgo digitata (Brongniart)	5
Ginkgo huttoni (Sternberg)	11
Ginkgo sp. cf. *sibirica* Heer	17
Ginkgo longifolius (Phillips) Harris comb. nov.	21
Ginkgo whitbiensis Harris	27
BAIERA F. Braun	29
Baiera furcata (L. & H.)	30
Baiera gracilis Bunbury	30
SPHENOBAIERA Florin	39
Sphenobaiera pecten Harris	40
Sphenobaiera longifolia (Pomel)	43
Sphenobaiera ophioglossum sp. nov.	48
Sphenobaiera gyron sp. nov.	53
ERETMOPHYLLUM Thomas	56
Key to the Yorkshire species of *Eretmophyllum*	57
Eretmophyllum pubescens Thomas	57
Eretmophyllum whitbiense Thomas	62
PSEUDOTORELLIA Florin	66
Pseudotorellia tibia sp. nov.	67
REPRODUCTIVE ORGANS OF THE GINKGOALES	71
Seeds attributed to *Ginkgo huttoni* (Sternb.)	72
Bud scales attributed to *Ginkgo huttoni* (Sternb.)	74
Seeds attributed to *Baiera furcata* (L. & H.)	74
Male cone attributed to *Ginkgo huttoni* (Sternb.)	76
2. CZEKANOWSKIALES	79
Provisional list of characters	80

Generic key to the Czekanowskiales 83
Key to the Yorkshire species of Czekanowskiales . . 84
Relationships of the Czekanowskiales 84

SOLENITES Lindley & Hutton 86
Solenites vimineus (Phillips) 87

CZEKANOWSKIA Heer 92
Czekanowskia furcula sp. nov. 92
Czekanowskia microphylla (Phillips) 97
Czekanowskia thomasi sp. nov. 100
Czekanowskia blacki sp. nov. 102
General comparison of the Yorkshire species of *Czekanowskia* 106
Czekanowskia sp. A 108
Czekanowskia sp. B 109
Czekanowskia sp. C 109
Czekanowskia sp. D 110
Czekanowskia sp. E 110

SPHENARION gen. nov. 110
Sphenarion muiriae sp. nov. 111

LEPTOSTROBUS Heer 114
Leptostrobus cancer Harris 114
Attribution of *Leptostrobus* to *Czekanowskia* and *Solenites* . 124

IXOSTROBUS Raciborski 126
Ixostrobus whitbiensis sp. nov. 131

DESMIOPHYLLUM Lesquereux 134
Desmiophyllum gramineum sp. nov. 135

REFERENCES 139

INDEX 147

PLATES 151

INTRODUCTION

THE laboratory work of this volume was assisted by the Natural Environment Research Council. The Council supported my research assistants, Mrs Wendy Millington, B.Sc. (for the Ginkgoales) and Miss José Miller, B.Sc. (for the Czekanowskiales). These workers made nearly all the laboratory observations while the text was prepared jointly. Neither was however able to complete her part and the conclusion of the section on Ginkgoales, dealing with reproductive organs, was by me alone.

The final version of the manuscript of this work was delivered to the British Museum (Natural History) in July 1972. Publication has been unavoidably delayed, but references later than 1970 have generally not been added.

The manuscript was edited by Mr. F. M. Wonnacott to whom I am deeply grateful.

TOM M. HARRIS

SYSTEMATIC DESCRIPTIONS

1. Ginkgoales

In this volume we divide the leaves which have been conventionally included in the Ginkgoales into two main classes. In the Ginkgoales in the strict sense, there are only those leaves which are found preserved separately having been shed from a clean cut leaf base. In the Czekanowskiales there are the leaves which are persistently retained in a group on a dwarf shoot, the dwarf shoot itself being shed as a unit. In each class there are also a few isolated reproductive organs thought to belong to the same species as certain leaves. The leaves of both classes are constructed on the same general plan of repeated dichotomy of the veins, followed as a rule, but at a long or short interval, by dichotomy of the lamina. The veins end separately in the distal margin. The stomata are haplocheilic and of a typical Gymnospermous appearance.

The leaves of these two classes are divided into genera by a few obvious characters. They are thus of the kind called form or artificial genera, but whether they will ultimately prove to correspond with natural genera is pure surmise. For convenience we have followed previous authors (in particular Florin) in the scope of these form-genera as closely as we can, merely dropping one (*Ginkgoites*) because it is ill-defined and seems unnecessary, at any rate for the Yorkshire species.

To some extent our taxonomic work, at least at the specific level, has proved disappointing. At the outset we knew of a good many described species of *Ginkgo*, *Baiera* and *Sphenobaiera* in Yorkshire and we were sure our collection would disclose others. The earlier described species had no microscopic details and few were based on numerous or well localized leaves. With the help of the form and cuticles of many localized specimens we had hoped to provide species with sharp distinctions, even though we were sure that each species would show a considerable range of variability.

The way our results worked out was not at all like this. Rather we found local populations with slightly different characters from other local populations. (It is noticeable that Ginkgoalean leaves though met rather seldom in the Yorkshire flora are often gregarious when they are met.) We felt certain that these local populations were homogeneous units but we were unsure about the slight differences in many sorts of variable characters between one local population and another. The differences, whatever their cause, are statistically significant, and sometimes, as with *Baiera furcata* and *B. gracilis*, there seemed to be a trend with age. But 'significance' does not always make differences taxonomically practical and the treatment adopted here, which much reduces the number of possible species, is merely the last of a number of attempts.

Difficulties of this kind have not been reported by other workers in their floras though all have recognized that the leaves of a Ginkgoalean species vary in form. It may be that no such difficulties occur elsewhere or even that in Yorkshire we have somehow made them, but we incline strongly to the belief that similar difficulties may be widespread or even general and that the reason we have met them is that we have closely examined an unusual number of specimens from very many localities. We consider that many of the described species based on the study of just a few specimens are not better characterized than some of those Yorkshire ones which we have merged and eliminated. For instance the Yorkshire *Baiera canaliculata* and *B. scalbiensis* were each based on just a few leaves, apparently with rather striking distinguishing characters. We do not merge the species of other floras where we have not studied the specimens, but there is no reason to think they are more securely based than these two. Specific distinctions in this family are difficult.

We thus think that in addition to thoroughly different species in the Ginkgoales, there are also species which produce local assemblages of leaves differing just perceptibly in character from other local assemblages and we have felt this many times. Such differences could arise from a slight peculiarity of the genetic balance of the population of trees (or even individual tree) shedding the leaves we find, or it might be caused by environment. These local peculiarities deserve notice, as we notice them here. But we think that to treat such local assemblages as different species would be as disastrous an error as to pick out peculiar specimens and to make them species. Either would load taxonomy with endless species and make it quite impossible for anyone with just a small number of leaves from a locality to place them. We have therefore ended by favouring broadly-defined species with a wide range of form though this by no means eliminates difficulty for the next worker.

Current terms have been used for describing our leaves and cuticles but one needs explanation. All figures for the thickness of a cuticle refer to the apparent thickness in a fold produced at the time of compression. Such folds or wrinkles are common and easily measured. We think this measurement gives the original thickness but that during compression substance has been lost from all parts of a fossil leaf including the cuticle, and so a thin section of the cuticle gives a measurement which is much too small.

Key to the genera of Yorkshire Ginkgoales

(1)	Leaves shed singly	2
	Leaves remaining attached in groups to caducous short shoots	Czekanowskiales, p. 79
(2)	Lamina lanceolate, undivided	3
	Lamina wedge- or fan-shaped (usually lobed or divided)	4
(3)	Lamina over 100 mm × 10 mm	*Eretmophyllum*
	Lamina under 100 mm × 10 mm	*Pseudotorellia*
(4)	Leaf as a whole wedge-shaped (no distinction between lamina and petiole)	*Sphenobaiera*
	Leaf with a petiole abruptly enlarging into the lamina	5
(5)	Lamina lobed or coarsely divided (over 4 veins per segment)	*Ginkgo*
	Lamina finely divided (4 veins or less per segment)	*Baiera*

Key to the Yorkshire species of *Ginkgo*

All species produce a few small leaves of unusual form and these are not included.

(1)	Lamina under 25 mm in radius	*G. whitbiensis*

	Lamina over 25 mm in radius	2
(2)	Basal angle of lamina under 100° (segments long, narrow)	*G. longifolius*
	Basal angle of lamina over 100° (segments rarely over 40 mm long, usually broad)	3
(3)	Lamina divisions very shallow (basal angle often over 180°)	*G. digitata*
	Lamina divisions nearly to petiole (basal angle under 180°)	4
(4)	Lamina substance and cuticle delicate	*G.* cf. *sibirica*
	Lamina substance and cuticle robust	*G. huttoni*

This key uses characters which vary a good deal in each species, the radius of the lamina, the depth of segmentation, number of segments and the basal angle of the lamina. Certain leaves would be wrongly placed by the key, but where there are many leaves found together, it should place the normal ones.

Genus GINKGO Linnaeus

TYPE SPECIES. *Ginkgo biloba* L.

Characteristics of fossil *Ginkgo* leaves

Leaf with petiole falling from stem at maturity. Petiole distinct, enlarging abruptly at its top to form lamina. Upper surface of petiole hollowed, hollow extending on to base of lamina. Lamina as a whole with straight lateral margins and a terminal margin forming an arc of a circle. Terminal margin usually incised, incisions shallow (forming lamina lobes) or deep and almost to petiole (forming lamina segments). Petiole possessing two veins, both veins forking at base of lamina and afterwards forking repeatedly (but not anastomosing). Primary division of lamina median. Main lamina divisions corresponding to early divisions of veins; divisions of veins and of lamina equal, or outer part stronger and subsequently more divided than inner part. Segments or lobes of lamina always fairly broad and at no level having fewer than four veins; usually having more. Resin, if present, occurring in short or fusiform cavities between veins.

Cuticle present; stomata on both sides or confined to lower. Stomata mainly between veins, orientation varied, not as a rule placed regularly in files. Guard cells sunken, thinly cutinized, surrounded and usually overhung by a ring of haplocheilic subsidiary cells. Ring usually irregular; lateral subsidiary cells at least often having encircling cells. Epidermal cells with straight or slightly sinuous walls; surface flat or papillate. Trichomes absent or simple and unicellular.

The genus *Ginkgoites* Seward is here dropped. It has been used in three different ways. Seward (1919, p. 10) proposed it as a convenient name for all fossil species that resembled *Ginkgo* but were only known in the fossil state and thus lacked full information (about reproductive organs). *Ginkgoites* had no morphological distinction. A good many authors followed this use until Florin (1936, p. 105) deliberately abandoned the convention of Seward but still used *Ginkgoites* for some species. He used it for two groups of fossils: those species which he judged differed too much from *Ginkgo* to be included, and those species which were too imperfectly known, mostly because their cuticles were uninvestigated. The first use is based on morphological distinctions but these are undefined; the second is a pure convention, but not the same as that of Seward. Many authors have since followed Florin rather than Seward

in the way they have used *Ginkgoites* but others have dropped it and called all the fossils *Ginkgo* as did Heer (1876). Recently Tralau (1968) proposed yet another distinction between *Ginkgo* and *Ginkgoites*:

'Leaves divided into two or more lobes by shallow notches which never reach the basal part of the lamina' *Ginkgo* (and *Ginkgodium*);

'Leaves deeply and symmetrically divided into narrow segments' *Ginkgoites* (and *Baiera*).

These distinctions have the merit of being morphological but we are unable to apply them. Half the leaves of *Ginkgo huttoni* from the Type locality are divided right to the petiole and some have rather narrow segments. They would fall into *Ginkgoites*. Again certain trees of *Ginkgo biloba* produce many deeply divided leaves and on our reading of Tralau's definition would also fall into *Ginkgoites*. If the fossil *Ginkgo*-like leaves are to be divided some other morphological basis must be found and it must be one that is clearly defined. And a name should be found that is less loaded than is *Ginkgoites* with alternative meanings.

Ginkgo differs from *Baiera* (as emended by Florin) in a single character. The lamina in *Baiera* is more divided and the segments are narrow enough to have at some levels no more than four veins. This distinction might be expected to fail many times because, in a single species, more divided leaves would show narrow and less divided ones, broad segments or lobes. Such overlap does occur (see for example *Ginkgo longifolius*) but so few leaves are intermediate in this respect that almost all species are easy to place.

Florin (1936, p. 106) gives a useful list of fossil species of *Ginkgo* and *Ginkgoites*.

Ginkgo digitata (Brongniart) Heer

Text-fig. 1

Yorkshire specimens:

1830 *Cyclopteris digitata* Brongniart, p. 219, pl. 61 bis.
1869 *Baiera digitata* (Brongniart) Schimper, p. 423, pl. 44, fig. 1. (Good leaf)
1876 *Ginkgo digitata* (Brongniart) Heer, p. 40. (Name)
1884 *Salisburia digitata* (Brongniart) Saporta, p. 294, pl. 160, fig. 1. (? Figs. 2–5 Siberian leaves)
1900 *Ginkgo digitata* (Brongn.): Seward, p. 254, pl. 9, figs. 1, 9 only. (Figs. 2, 4, 10 *G. huttoni* and text-fig. 45 *Caytonanthus*)
1900 *Ginkgo whitbiensis* Nathorst: Seward, p. 261, pl. 9, fig. 8.
1900 *Ginkgo digitata* (Brongn.): Seward & Gowan, pl. 9, fig. 46; pl. 10, fig. 54. (Same specimen as Harris 1948, text-fig. 7 C and present Text-fig. 1 C)
1900*a* *Ginkgo digitata* (Brongn.): Seward, p. 23, pl. 2, fig. 5.
1910 *Ginkgo digitata* (Brongn.): Lane, p. 206. (Name and photograph only)
1919 *Ginkgo digitata* (Brongn.): Seward, p. 14, text-fig. 637 only.
1936 *Ginkgo digitata* (Brongn.): Florin, p. 106. (Name in revision)
1948 *Ginkgo digitata* (Brongn.): Harris, p. 207, text-figs. 7 A-D, 8. (Figures repeated here)

Similar looking leaves from other regions are listed on p. 9.

DIAGNOSIS. Radius of lamina typically 30 mm, basal angle 200°. Petiole slender, upper surface grooved. Divisions of lamina shallow, seldom extending more than one-third from the margin to the base, occasionally very shallow indeed. Lobes about 6–9, each deeply notched, or margin with about 12 nearly equal lobes. Lamina seldom showing an especially deep primary division into two halves. Apices of lobes rounded or irregularly truncate. Leaf

substance thin. Veins usually conspicuous, numerous—about 16 per cm half-way up lamina, arising from two in the petiole, branching throughout and showing little tendency to form strong marginal veins. Small resin bodies, 0·1 mm × 0·1 mm to 0·1 mm × 0·4 mm, frequent between veins.

Cuticles very delicate, upper about 1μ thick, lower about 0·5μ. Upper cuticle lacking stomata. Veins only obscurely marked by a few rows of slightly more elongated cells. Cells between veins isodiametric or slightly elongated. Lateral walls more or less broad but not prominent, straight or almost straight, with exceedingly fine sinuosity, sometimes slightly interrupted, as if by pits. Cell surfaces flat, unsculptured, no median papillae but with occasional trichomes resembling those of lower side.

Lower cuticle with numerous stomata between veins. Cells along veins elongated and crushed at sides of vein. Zones between veins about three times as wide as zones along veins. Cells between veins isodiametric, not in rows. Lateral walls inconspicuous, often very ill-marked, straight or almost straight, with very fine sinuosity. Cell surfaces flat, unsculptured, no median papilla. Trichomes frequent along veins, occasional between veins. Each trichome consisting of a cell of ordinary size, with rather thickened surface raised in the middle, forming a bulge or cylinder of fairly thick cuticle about 20μ wide, up to 30μ long but rather longer on leaf margins.

Stomata scattered between veins, irregularly orientated but often longitudinal. Stomatal pit elongated, guard cells only slightly sunken, poles reaching the surface. Subsidiary cells forming rather ill-defined ring, lateral ones usually quite unspecialized, occasionally with slight surface thickening, and with band of thickening at side of pit, never bearing distinct papillae. Terminal subsidiary cells unthickened, encircling cells rarely present.

Discussion. If the exceptional specimens mentioned below are included, it would follow that the leaf lamina can be divided almost to the base into probably at least two, possibly more, lobes each of which is shallowly divided again. The veins can be as few as 9 per cm. The cuticle can show small papillae on some ordinary epidermal cells, and some stomata at least can have most of their subsidiary cells each showing a distinct papilla.

Ginkgo digitata, though long known, seems rather rare. Most of the leaves examined agree closely in form with the one shown in Text-fig. 1 B. There are a few much smaller leaves with rather irregular lobing but they are associated with typical ones. Thus V.25855 from Gristhorpe is of 9·5 mm radius. Its divisions are shallow. The leaf shown in Text-fig. 1 B is almost exactly like Brongniart's holotype as are those shown in Seward (1900*a*, pl. 2, fig. 5, 1900; pl. 9, fig. 1), Seward & Gowan (1900, pl. 9, fig. 46) and Schimper (1869, pl. 44, fig. 1). There are, however, specimens which range from the almost entire leaf shown in Text-fig. 1 C, to the fairly deeply divided leaf shown in Text-fig. 1 A. The almost entire leaf agrees with the Tertiary *Ginkgo adiantoides* (Unger) in outline, but is distinguished from it by the lack of a stronger marginal vein, by having smaller resin bodies and by differences in cuticle. The small leaf figured by Seward (1900) as *G. whitbiensis* is deltoid in shape and deeply divided into rather narrow lobes with tapering apices, but its cuticle, prepared by W. N. Croft, agrees with that of normal *G. digitata*. One of the leaves from Haiburn Wyke is bilobed to half-way from the margin, but the venation, lobing of each half, and basal angle, are normal. Unfortunately a satisfactory cuticle preparation could not be obtained.

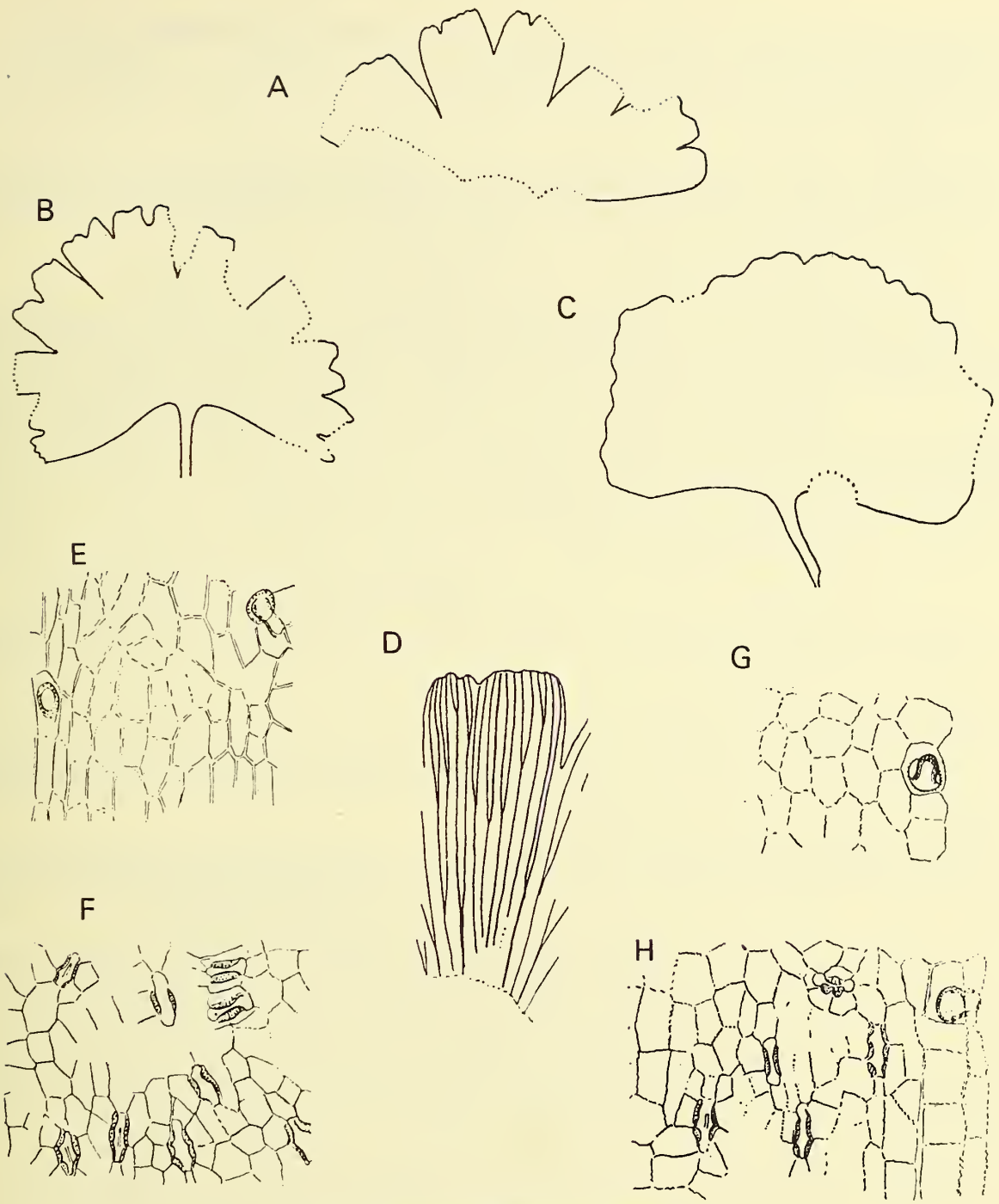


Fig. 1. **Ginkgo digitata** (Brongniart)

A, deeply divided leaf, actual size. B, leaf of normal type, actual size. C, almost entire leaf, actual size. D, veins of one lobe of specimen shown in A, magnification ×2. E, upper cuticle with vein on extreme left, V.27507, magnification ×200. F, lower cuticle with numerous stomata, V.27507, magnification ×200. G, upper cuticle showing small trichome, V.27506, magnification ×200. H, lower cuticle showing trichome on a vein, and five stomata, V.27506, magnification ×200.

C is possibly from Haiburn Wyke, the rest are from the Gristhorpe Bed. A–D are in the Yorkshire Museum. All the figures are from Harris (1948, text-figs. 7, 8).

The following characters vary more or less independently of one another:
(1) Basal angle, present range 110°–260°;
(2) Lamina radius, present range 22 mm–47 mm;
(3) Depth of lobing.

In addition to the material described above, we include, with some doubt, the following few specimens. Only those features which differ from the normal form are mentioned, for instance resin bodies were not seen in any of these leaves.

(1) *From the Gristhorpe Bed, Gristhorpe Series, Middle Deltaic*

A block collected by H. H. Thomas shows fragments of at least four very similar leaves, and a second block has one leaf which seems similar. The leaf lamina is deeply divided into perhaps two, or possibly more, broad lobes, each slightly divided again (no whole leaf exists). The veins are rather widely spaced, 12 (9–15) per cm, and the subsidiary cells of many stomata have small but distinct papillae, although others have none. A few ordinary epidermal cells on the lower side also have small papillae.

A leaf (V.28515) with normal venation also has papillate stomata. There are a few leaves with distant veins and unknown cuticles.

(2) *From Cloughton Wyke, 2ft 6in Drifted Plant Bed, Gristhorpe Series, Middle Deltaic*

A single broad fragment showing a slightly lobed margin has a cuticle with distinct papillae on some of the subsidiary cells.

(3) *From Marske Quarry, Lower Deltaic*

A single fragment collected by H. H. Thomas is almost exactly like the Cloughton specimen, but in addition to having some papillate subsidiary cells, some of the ordinary epidermal cells of the lower surface have small papillae.

Lane's specimen from Marske Quarry (1910, p. 206) appears to be more deeply divided than normal *G. digitata*, but not so deeply as the exceptional Gristhorpe leaves. No description is given, nor any details of the exact stratum of the leaf's occurrence.

The occurrence of some papillate subsidiary cells on all of the above mentioned leaves, and the presence of some papillate ordinary epidermal cells on the Marske Quarry and exceptional Gristhorpe leaves, are slight variations in the direction of *Ginkgo huttoni*. The leaf lobing of the Gristhorpe specimens also renders them slightly further in the direction of *G. huttoni*. However, we have grouped all this material with *G. digitata* because the general appearance of their delicate cuticles with fine cell walls, and the lobing of the fragments from Marske and Cloughton, are much more like *G. digitata* in character than *G. huttoni*.

Attention is drawn to a few specimens from Whitestone Point, nr. Whitby, which are grouped with *G. huttoni* as an unusual form of that species, and have features in the direction of *G. digitata*. They are rather shallowly lobed but their cuticles are more like those of *G. huttoni*. Thus, where there appears to be a discrepancy between cuticle and leaf shape, as with the Gristhorpe leaves and those from Whitestone Point, we have put more weight on the overall character of the cuticle. Possibly we are dealing with more than two species with very similar leaves, but with scanty material we prefer to group the unusual specimens with the two described species.

Comparison. *Ginkgo digitata* has been much confused with *Ginkgo huttoni* since Seward (1900) united the two species. However, although there are a few specimens of intermediate character, such as those described immediately above, typical leaves of these species differ very markedly from each other in their cuticles and gross form. *G. digitata* is usually distinguished by a much wider basal angle, more numerous and much shorter lobes, and the occurrence of vein dichotomies throughout the lamina. The cuticle differs in being much thinner, with ill-marked, often minutely sinuous cell outlines, and in lacking papillae on both ordinary epidermal cells and subsidiary cells.

The cuticle of the Yorkshire leaf called *Ginkgo* sp. cf. *sibirica* is somewhat similar to that of *G. digitata* in being at least as delicate, with equally faint cell outlines and some similar stomata but it differs in the cell outlines being straight. The whole leaf may be almost as wide as *G. digitata* but differs in always being deeply divided almost to the petiole. Other Yorkshire species differ from *G. digitata* more considerably, and no confusion is likely.

A leaf figured by Seward (1919, text-fig. 633) from Helmsdale, Scotland, is rather similar in form both to the exceptional leaves from Gristhorpe and to *G. huttoni*. Florin's photographs show the cuticle of the Helmsdale leaf to be more like those of the Gristhorpe leaves in lacking the large well-developed papillae and trichomes of *G. huttoni*, but the cell walls are less sinuous and the guard cells more obscured.

It is impossible to make a useful comparison with the numerous foreign specimens more or less resembling *Ginkgo digitata* where the gross form alone is known. The determination of many of them appears to have been influenced by some specimens of *G. huttoni* which have been confused with *G. digitata*, and by two leaves from the Stonesfield Slate (Bathonian), Gloucestershire, figured by Seward (1904, pl. 11, fig. 3, text-fig. 9) which are deeply bilobed and cannot be confidently compared with any Yorkshire species as their cuticles are not known.

The following are Mesozoic leaves of other floras resembling forms occurring in Yorkshire of *Ginkgo digitata* (Brongn.) and *G. huttoni* (Sternberg). Cuticles are only known where stated. This list is not exhaustive.

1852 *Cyclopteris digitata* Brongn.: Ettingshausen, pl. 4, fig. 2. (Wealden)
1868 *Cyclopteris incisa* Eichwald, pl. 4, fig. 6. (Jurassic; Kamenka, USSR)
1871 *Baiera multipartita* Schimper, pl. 24, figs. 1–4. (Wealden; N. Germany)
1876 *Ginkgo huttoni* (Sternb.): Heer, pl. 5, fig. 16, pl. 10, fig. 8. (Upper Jurassic; Amurland)
1889 *Ginkgodium digitata* (Brongn.) Yokoyama, pl. 13, fig. 2. (Jurassic; Japan)
1894 *Ginkgo digitata* (Brongn.): Bartholin, pl. 4, figs. 11, 11 A. (Liassic; Bornholm)
1905 *Ginkgo digitata* (Brongn.), *G. huttoni* (Sternb.), *G. sibirica* Heer: Fontaine *in* Ward, pl. 30, figs. 1–12, pl. 33, figs. 6, 10. (Jurassic; Oregon)
1905 *Ginkgo digitata* (Brongn.), *G. schmidtiana* Heer cf. *parvifolia* Krasser, pl. 2, figs. 3–6. (Jurassic; Transbaikal)
1907 *Ginkgo digitata* (Brongn.): Stopes, pl. 27, figs. 3–5, text-figs. A, B. (Middle Jurassic; Scotland. More like *Sphenobaiera gyron* than *G. huttoni* in form and cuticle)
1907 *Ginkgo digitata* (Brongn.): Seward, pl. 7, figs. 53–55. (Jurassic; Turkestan)
1910 *Ginkgo digitata* (Brongn.): Kryshtofovich, pl. 3, fig. 1. (Jurassic; Ussuriland)
1911 *Ginkgo digitata* (Brongn.): Seward, pl. 7, fig. 54. (Jurassic; China)
1911 *Ginkgo digitata* (Brongn.): Thomas, pl. 4, fig. 7, pl. 8, fig. 2. (Jurassic; Kamenka)
1912 *Ginkgo digitata* (Brongn.): Seward, pl. 4, fig. 51. (Jurassic; Afghanistan)
1913 *Ginkgo digitata* var. *huttoni* Seward & Bancroft, text-fig. 6. (Upper Jurassic; Helmsdale, Scotland. Figure repeated in Seward 1919. See also Florin 1936)
1914 *Ginkgo digitata* (Brongn.): Knowlton, pl. 6, fig. 5, pl. 7, figs. 3–5. (Jurassic; Alaska)

1917 *Ginkgo autarctica* (Saporta): Walkom, pl. 1, figs. 1, 2. (Trias; Queensland)
1918 *Ginkgo digitata* (Brongn.): Zalessky, pl. 27, fig. 2, pl. 42, figs. 4, 5, pl. 48, figs. 3, 4. (Jurassic; Angara)
1919 *Ginkgo digitata* (Brongn.): Walkom, pl. 1, figs. 3, 4. (Jurassic; Queensland)
1919 *Ginkgo digitata* var. *huttoni* Seward, text-figs. 633, 634, 635 (part), 636 A, B, 637–639. (Various specimens, figures mostly copies, but fig. 636 A, B from a Brora leaf)
1927 *Ginkgoites digitata* (Brongn.): du Toit, text-fig. 16 B. (Middle Trias; S. Africa)
1927 *Ginkgoites digitata* (Brongn.): Chapman, pl. 11, fig. 29. (Triassic; Victoria, Australia)
1927 *Ginkgo digitata* (Brongn.): Kryshtofovich, pl. 34, fig. 5. (Jurassic; Central Siberia)
1929 *Ginkgo digitata* (Brongn.): Khaklov, text-figs. 18–20. (Jurassic; Kuznetsk, Siberia)
1930 *Ginkgoites huttoni* (Sternb.): Turutanova-Ketova, pl. 1, fig. 6. (Jurassic; Kirghiz)
1930 *Ginkgo digitata* (Brongn.): Hollick, pl. 11, figs. 2–7 A, 8. (Upper Cretaceous; Alaska)
1931 *Ginkgoites digitata* (Brongn.) var. *huttoni* Seward: Oishi, pl. 18, fig. 4. (Mesozoic; Japan)
1932 *Ginkgoites digitata* (Brongn.) var. *huttoni* Seward: Oishi, p. 64, pl. 10, fig. 9. (Rhaetic; Japan)
1933 *Ginkgo* cf. *hermelini* (Hartz): Sze, pl. 7, fig. 6. (Jurassic; China)
1935 *Ginkgo digitata* (Brongn.): Toyama & Oishi, pl. 3, figs. 4, 5. (Jurassic; Manchuria)
1936 *Ginkgo pleuripartita* (Schimper): Florin, pl. 3, figs. 1–4. (Wealden; Germany. Cuticles, see also Schimper 1871)
1936 *Ginkgo digitata* (Brongn.): Florin, pl. 3, figs. 5–10. (Upper Jurassic; Helmsdale, Scotland. See also Seward & Bancroft 1913)
1936 *Ginkgo huttoni* (Sternb.): Turutanova-Ketova, pl. 1, fig. 6. (Jurassic; Kazakhstan)
1939 *Ginkgoites sibirica* Heer: Kawasaki, pl. 13, figs. 49–52. (Lias; Korea)
1940 *Ginkgoites digitata* (Brongn.): Oishi, pl. 38, figs. 7–9. (Jurassic; Japan)
1957 *Ginkgo digitata* (Brongn.): Stanislavsky, pl. 12, figs. 1–5, pl. 13, figs. 1, 2. (Callovian; Donetz)
1958 *Ginkgo adiantoides* (Unger): Vachrameev, pl. 25, figs. 2, 3. (L. Cretaceous or U. Jurassic; Eastern Siberia)
1958 *Ginkgo huttoni* (Sternb.): Vachrameev, pl. 25, figs. 4, 5. (L. Cretaceous or U. Jurassic; Eastern Siberia)
1959 *Ginkgo digitata* (Brongn.): Delle, pl. 1, figs. 1, 2. (Jurassic; Transcaucasia)
1959 *Ginkgoites digitata* (Brongn.) var. *huttoni*: Kimura, pl. 2, fig. 6. (Lias; Japan)
1960 *Ginkgo adiantoides* (Unger), *G. digitata* (Brongn.) and *G. huttoni* (Sternb.): Vasilevskaya, pls. 1–4. (L. Cretaceous; R. Lena)
1960 *Ginkgo digitata* (Brongn.): Teslenko, pl. 18, fig. 5. (Middle Jurassic; Krasnoyarsk)
1961 *Ginkgo* ex. gr. *huttoni* (Sternb.): Vachrameev & Doludenko, pl. 47, figs. 2, 3, 5, 6, pl. 48, figs. 1–5. (Upper Jurassic; Eastern Siberia. Good leaves and cuticles)
1963 *Ginkgo digitata* (Brongn.): Genkina, pl. 40, figs. 3–5. (Middle Jurassic; Urals)
1963 *Ginkgo adiantoides* (Unger): Samylina, pl. 22, figs. 8, 9. (Lower Cretaceous; Aldan R., Siberia)
1963 *Ginkgo digitata* (Brongn.), *G. huttoni* (Sternb.): Vasilevskaya & Pavlov, pl. 8, fig. 3, pl. 13, figs. 2, 4, pl. 26, figs. 2, 3, pl. 36, fig. 5. (Cretaceous; USSR)
1965 *Ginkgo digitata* (Brongn.): Lebedev, pl. 26, figs. 1–5, text-fig. 33. (Jurassic; Zeia R.)
1966 *Ginkgo huttoni* (Sternb.): Genkina, pl. 43, figs. 1, 2. (Jurassic; Khirgiz)
1966 *Ginkgo digitata* (Brongn.): Prosvirjakova, pl. 20, fig. 1. (Jurassic; Central Asia)
1967 *Ginkgo digitata* (Brongn.): Delle, pl. 23, fig. 8, pl. 24, figs. 3–8. (Middle Jurassic; Transcaucasia)
1967 *Ginkgo paradiantoides* Samylina, pls. 2–4. (Jurassic; Kolyma R. Form like *G. digitata* but papillose cuticle different)
1968 *Ginkgo huttoni* (Sternb.): Tralau, text-figs. 2 A-D. (Upper Jurassic; Scotland. Cuticles)
1968 *Ginkgo pluripartita* (Schimper): Tralau, text-figs. 5 A-D. (Wealden; N. Germany. Cuticles)

Stanislavsky (1957) includes specimens named *Ginkgo integriuscula*, *G. reniformis* and *G. polaris* from Russia and Siberia.

Samylina (1967) describes several Tertiary species of *Ginkgo*, in particular *G. pilifera*, which are very like *G. huttoni* in both form and cuticle.

Occurrence

Typical material

Middle Deltaic Gristhorpe Series . . . Gristhorpe Bed.

Atypical or otherwise doubtful material

Middle Deltaic Gristhorpe Series. Cloughton Wyke according to Leckenby 1864 (no details).
Cloughton Wyke, 2′ 6″ Drifted Plant Bed at 54° 20′ 50″ N (see p. 8).
Gristhorpe Bed (see p. 8).

Lower Deltaic. Haiburn Wyke Plant Bed (cuticle not studied)
Marske Quarry, Lane 1910 (photograph of leaf only)
Marske Quarry (see p. 8)

Ginkgo huttoni (Sternberg) Heer

Text-figs. 2–4

The following are all Yorkshire specimens:

1829 *Sphenopteris latifolia* Phillips, p. 148, pl. 7, fig. 18. (Imperfect figure)
1833 *Cyclopteris digitata* (Brongn.): Lindley & Hutton, p. 179, pl. 64. (Good leaves)
1833 *Cyclopteris huttoni* Sternberg, p. 66.
1841 *Cyclopteris huttoni* Sternberg: Goeppert, p. 92, pl. 4, pl. 5, figs. 17–19. (Good leaves)
1875 *Cyclopteris digitata* (Brongn.): Phillips, p. 200, pl. 7, fig. 18. (Poor figures)
1876 *Ginkgo huttoni* (Sternberg) Heer, p. 59. (Name)
1884 *Salisburia huttoni* (Sternberg) Saporta, p. 299, pl. 31, figs. 4, 5, pl. 32, fig. 8. (Fairly good leaves)
1900 *Ginkgo digitata* forma *huttoni* Seward, p. 254 (part), pl. 9, figs. 2, 10 only. (Good leaves)
1900 *Baiera phillipsi* Nathorst: Seward, p. 270 (part), pl. 9, fig. 4 only.
1929 *Ginkgoites huttoni* (Sternberg) Black, p. 431, text-figs. 17–19. (Leaf, stomata and trichome)
1929 *Ginkgoites scarburgensis* Black, p. 433, text-figs. 20–22. (Description, leaves and stoma)
1929 *Baiera spectabilis* Nathorst: Black, p. 427, text-fig. 15. (Description and stoma only)
1929 *Eretmophyllum pubescens* Thomas: Black, p. 435. (Cuticle)
1948 *Ginkgo huttoni* (Sternb.): Harris, p. 192, text-figs. 4 A-L, 5 A, B, 6 I-L, 7 E. Refigured in present work. (Description, leaves and cuticles)

For leaves of similar form in other floras, see list on p. 9. The most fully similar of these are the specimens of *Ginkgo* ex. gr. *huttoni* of Vachrameev & Doludenko (1961) and *Ginkgo pluripartita* from N. Germany (Tralau 1968).

Diagnosis. Leaf typically with slender petiole, lamina 30 mm radius, basal angle 120°, more or less deeply divided into six slightly contracted lobes, apices rounded, irregularly truncate or notched. Veins slender, inconspicuous, rather crowded, about 25 per cm half-way up lamina, branching in lower parts of lobes only. Round or oval resin masses, about 150μ wide, fairly numerous between veins.

Cuticles thick, upper about 5μ, lower 2–3μ. Upper cuticle with very few evenly scattered stomata between veins. Vein areas narrow, rather ill-marked by longitudinal rows of slightly elongated, more or less rectangular cells. Between veins epidermal cells usually irregular. Encircling cells frequent but unspecialized, rarely with papillae contributing to protection of stomatal pit.

Holotype. Specimen figured by Lindley & Hutton 1833, p. 179, pl. 64.
Seeds, a male cone and bud-scales of *G. huttoni* are described on pp. 72–74.

Discussion. *Ginkgo huttoni* is a very variable leaf, both in form and cuticle, but the most common values of the measured characters occur at or near the mean as would be expected within a single species, and these values are termed here as normal or typical.

The variation in lobing of the lamina at the Type locality is shown in Text-figs. 2 A, C, E, G,

H; about half the specimens closely approach the normal form shown in Text-fig. 2 H. The range in size and form is rather similar at other localities except at Yons Nab, Gristhorpe Bay,

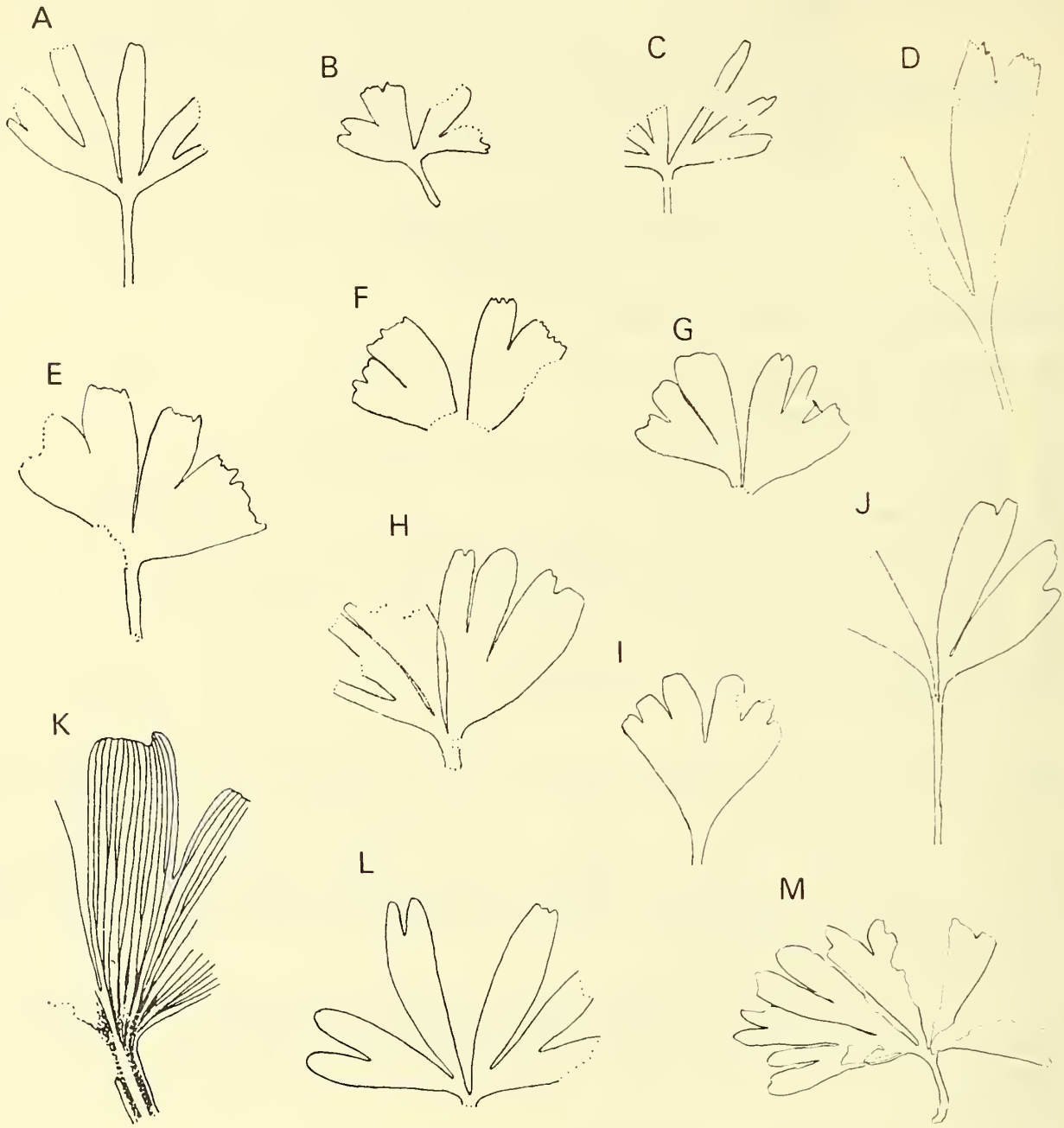


Fig. 2. **Ginkgo huttoni** (Sternberg)

A, C, E, Yorkshire Museum specimen labelled 'Y' 'Upper Shale Scarborough' (no doubt from Scalby Ness). B, F, small leaves from R. Derwent, North Plant Bed, V.27492. D, leaf from Brown Rigg Beck *Ginkgo* Bed, V.27491. G, H, two leaves on Yorkshire Museum specimen from Scalby, labelled '*Sphenopteris latifolia*'. I, Manchester Museum specimen, unlocalized. J, Leaf from R. Derwent, V.27493. K, veins of leaf shown in E, magnification ×2. L, Yorkshire Museum, unlocalized specimen. M, Hancock Museum, unlocalized specimen on a block with many similar leaves (see p. 13).

All figures except K are of natural size. Figs. A–L are from Harris (1948, text-figs. 4, 7).

and the River Derwent '*Ginkgo* Bed' where the leaves are often slightly larger than normal, about 40 mm radius.

The cuticle varies somewhat in thickness but could never be described as thin. The typical form of cuticle is shown in Text-figs. 3 C, E and is closely approached by the majority of the present specimens. Certain leaves are more papillose than normal, such as Black's '*Baiera spectabilis*' and the cuticle shown in Text-fig. 4 A, where almost all of the cells of both surfaces, and most of the subsidiary cells, have well developed papillae; but trichomes are neither more numerous nor larger than usual. A leaf from Bloody Beck and the many leaves on an unlocalized block from the Hancock Museum are also much more papillose than is normal, see Text-fig. 4 A. The Hancock Museum leaves also have more lobes than usual, up to twelve, but they agree with typical material otherwise. On the other hand, specimens collected by H. H. Thomas from White Nab, and described by Black (1929) as *Ginkgoites scarburgensis*, have very few ordinary cell papillae on either surface, and a large proportion of subsidiary cells lack papillae and have thickening which forms only a flattened wavy rim round the stomatal pit. They do have some papillate subsidiary cells, however, and also occasional trichomes of normal size but rather thinly cutinized. Leaves with still smoother cuticles occur, for instance the one shown in Text-fig. 3 D, but even here a few trichomes occur on both sides.

The following characters and groups of characters appear to vary independently of one another:

Basal angle: 40°–220°
Lamina radius: 13 mm–45 mm
Number of lobes: 2–12
Depth of lobing: lateral divisions $\frac{1}{3}$ to $\frac{9}{10}$
Form of apices: truncate-rounded
Density of veins: 15–40 per 10 mm
Distance between veins: 210μ–520μ
Width of veins: 115μ–175μ
Tendency of cells to form longitudinal rows
Cell wall width and degree of interruption as if by pits
Tendency of cells to form transverse bars by late division
Frequency of trichomes along veins
Length of trichomes
Development of papillae on ordinary cells of upper and lower epidermis and on subsidiary cells
Stomatal density on upper side: 1 in 5 mm^2–10 in 1 mm^2
Stomatal density between veins on lower side: 50–90 per mm^2

There are three rather unusual leaves, two on one block and one on a second block, from Whitestone Point. The lamina is divided into two by a division to 10 mm from the base and each half is itself rather shallowly lobed, see Text-figs. 3 A, B. The form of these leaves is somewhat like that of the occasional specimens of *Ginkgo digitata* which are more divided than is typical of that species. The Whitestone Point leaves are included in *G. huttoni* because, although their cuticles are slightly thinner than usual, with fewer and less well developed papillae on the ordinary and subsidiary cells than normal, the cuticles are more unlike those of

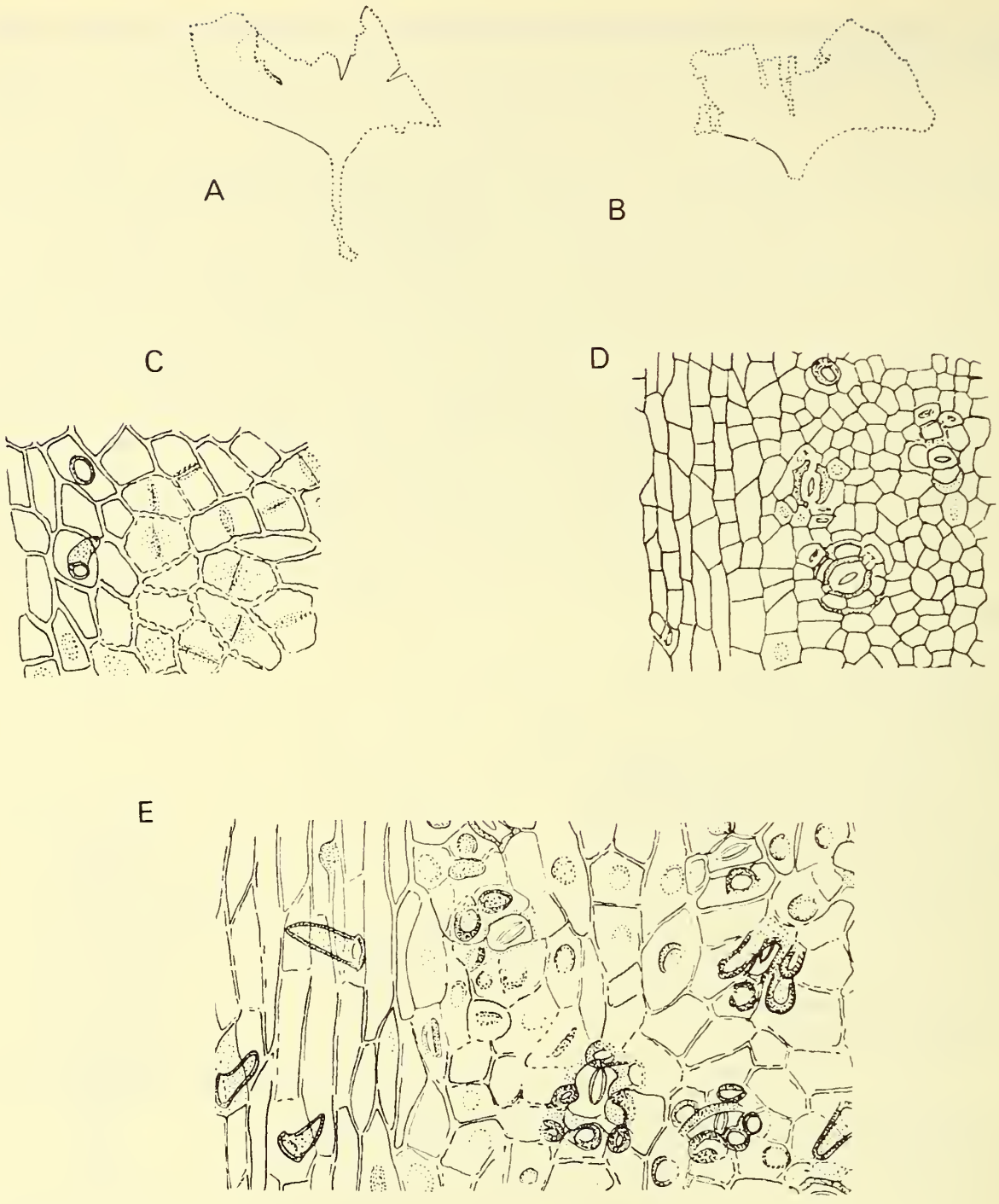


Fig. 3. **Ginkgo huttoni** (Sternberg)

A, B, shallowly divided leaves from Whitestone Point, actual size. V.56444. C, upper cuticle of normal type, magnification ×200, from same leaf as E. D, lower cuticle of smoother leaf from Penny Holme, magnification ×200, V.27505. E, lower cuticle of normal type, magnification ×200, original of Black's text-figs. 18A, B. Sedgwick Museum specimen K.832.

G. digitata which differ in being much more delicate, with slightly sinuous cell outlines and in lacking papillae.

Comparison. *Ginkgo huttoni* has been much confused with *Ginkgo digitata* but its more deeply divided leaf of fewer, longer lobes, with vein dichotomies in the lower parts only, and its thicker cuticle with straight cell walls and papillate subsidiary cells usually serve to distinguish them. (*Ginkgo* sp. A, mentioned below, may be an extreme form of *G. huttoni* but the cuticle fragments obtained have not been large enough to identify it.) *Ginkgo longifolius* matches occasional specimens of *G. huttoni* in the form of its lobes but is distinguished by its less crowded veins, thinner cuticle and lack of trichomes. Some leaves of *Ginkgo* sp. cf. *sibirica* also match a few of *G. huttoni* but their cuticles are much thinner, lack well developed papillae on the ordinary epidermal cells and have no trichomes. *Ginkgo whitbiensis* resembles a small leaf of *G. huttoni* but differs in having many more stomata on the upper side, and in lacking trichomes and well developed papillae on ordinary epidermal cells. Some leaves of *Sphenobaiera gyron* closely resemble bilobed forms of *G. huttoni* but they are usually larger, with fewer veins per cm and a much smoother cuticle without trichomes.

There are many leaves figured from other regions which are very like *G. huttoni* in form, but where their cuticles are unknown it is impossible to identify them with certainty, for list see p. 9. Leaves figured by Vachrameev & Doludenko (1961) of Upper Jurassic age, as *Ginkgo* ex. gr. *huttoni*, have very similar cuticles to those of *G. huttoni* with well developed papillae on the ordinary epidermal cells of both sides, and on the subsidiary cells, and they also have trichomes, although some of the leaves are rather larger than typical *G. huttoni*.

Another leaf very like *G. huttoni* is *G. pluripartita* from the Wealden of N. Germany; for form see Schimper (1869), Schenk (1871) and Heer (1881); for cuticle see Florin (1936). We can recognize no differences, though the age differs considerably from the Yorkshire specimens.

Ginkgo sp. A was figured by Seward as *G. digitata* (1900, p. 254, pl. 9, fig. 2).

Two leaves, the second like the figured one, on an unlocalized block (possibly from the Gristhorpe Bed) resemble the unusual specimens of *G. digitata* from the Gristhorpe Bed described on p. 8 but are well distinguished by the cuticle which is much thicker. The figured specimen has been varnished, and only minute bits of cuticle could be obtained, perhaps of one side only. The thickness of the cuticle looks similar to that of *G. huttoni*. The cell walls are slightly sinuous, no central papillae were seen and stomata were not observed with certainty. It is not typical *G. huttoni* because the lamina is too broad, and we exclude these specimens from the morphological range of *G. huttoni*.

Occurrence

Upper Deltaic	30 localities including Scalby Ness, the Type locality
Middle Deltaic Gristhorpe Series	17 localities
Millepore Bed	3 localities
Middle Deltaic Sycarham Series	2 localities
Lower Deltaic	4 localities

None of the specimens from the two Middle Deltaic Sycarham Series localities shows the whole shape of the leaf, but the cuticles are normal for *Ginkgo huttoni*, and at Stainsacre Beck

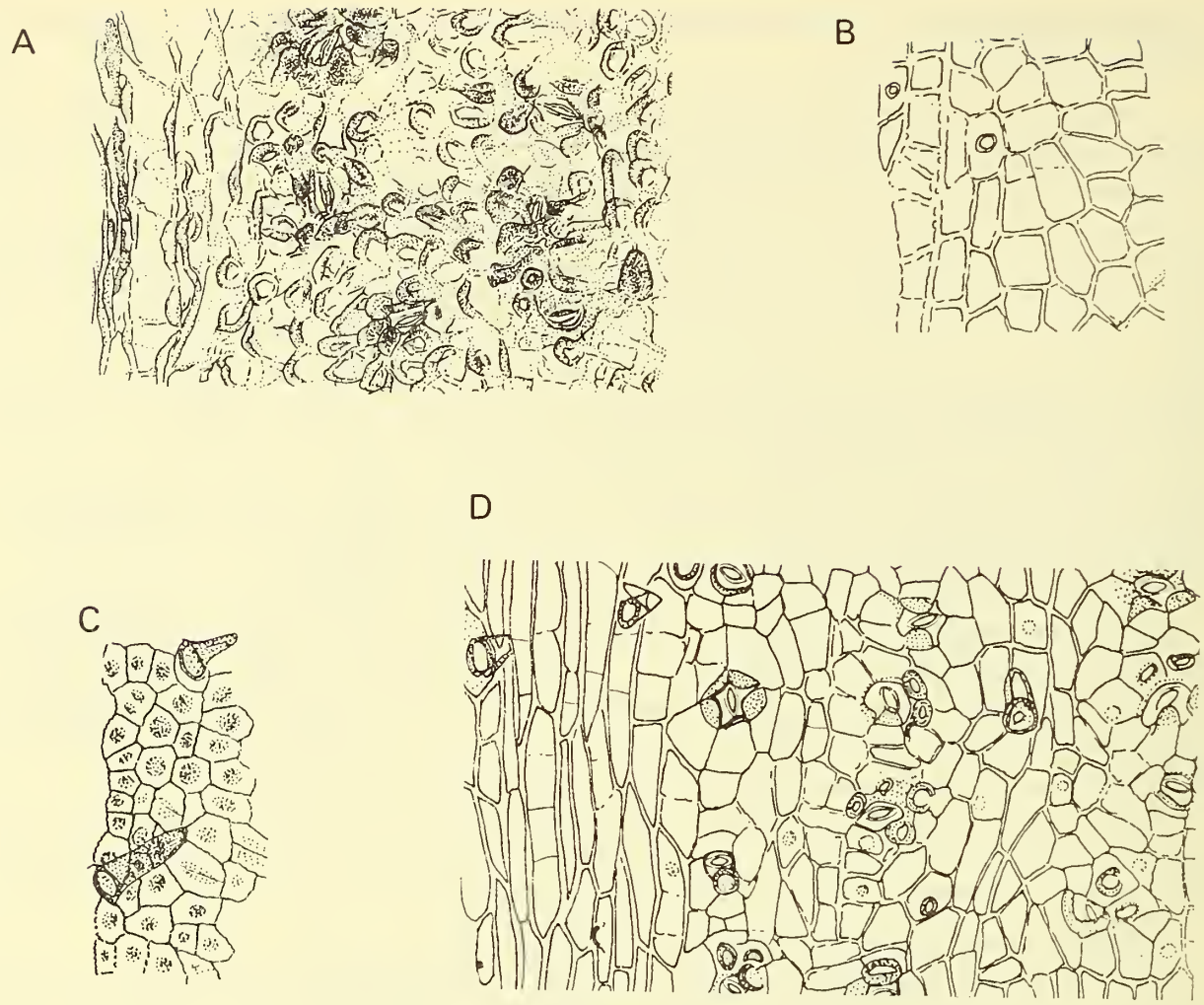


Fig. 4. **Ginkgo huttoni** (Sternberg)

A, very papillose lower cuticle of leaf shown in Fig. 2 M, magnification ×200. B, upper cuticle from Black's slide K.834 in Sedgwick Museum, magnification ×200. Originally determined as *Ginkgo scarburgensis*, possibly same leaf as D and may be the original of Black's text-fig. 22. C, upper cuticle of leaf from Langdale, magnification × 200, V.27496*a*. D, lower cuticle from Black's slide of specimen K.835 in Sedgwick Museum, magnification ×200. Originally determined as *G. scarburgensis*, from White Nab.

the lobes are of typical size. In the Lower Deltaic, Phillips's specimen (J.5025, Oxford Museum) from Haiburn Wyke is poorly preserved and without cuticle, but resembles Text-fig. 2 A in form. Two unlocalized leaves are also thought to be from Haiburn Wyke: the matrix of the specimen shown in Text-fig. 2 L (York Museum) is typical reddish sandstone and its cuticle is normal; the specimen in Text-fig. 2 I (Manchester Museum) has two associated species which suggest Haiburn Wyke.

Cuticle fragments more or less closely resembling *G. huttoni* have been obtained by maceration of rocks from a large number of other localities, in particular of the Upper Deltaic.

Ginkgo sp. cf. *sibirica* Heer

Text-fig. 5

For references see p. 20.

There are two groups of leaves from the Lower Deltaic which are somewhat similar to one another and distinct from other Yorkshire species so far described. The first group is a population of sixteen leaves from Petard Point, and the second comprises twenty-one leaves from Roseberry Topping and two from Hasty Bank. These groups cannot be completely separated or united, nor can they be described as one or two new species, as most of the cuticle preparations have been unsatisfactory because the cuticles are extremely delicate, and the leaf substance breaks up into powder.

Petard Point population. Typical lamina deeply divided into several lobes, central division deeper than others. Each lobe divided once, sometimes twice, resulting in 10 (4–15) ultimate lobes, each 5 mm (2·5 mm–6·5 mm) wide. Lamina radius 30 mm (14–50 mm), basal angle 140° (70°–170°). Apices rounded-obtuse to sub-acute. Petiole slender, about 1 mm (0·8 mm–2·0 mm) wide, longest portion preserved 16 mm. Leaf substance rather thin; veins inconspicuous, typically 7 (4–10) to a lobe, density 14 per cm (16–19 per cm), veins slightly converging towards apex. Vein dichotomies at least to half-way along lamina. Resin often present as small and round, or long and spindle-shaped bodies between veins.

Cuticles delicate, upper slightly thicker than lower. Upper cuticle with isodiametric, polygonal cells between veins; slightly elongated cells along veins. Lateral walls straight or slightly sinuous, occasionally interrupted. Surface walls sometimes with a single median thickening on each cell, but papillae and trichomes absent from ordinary cells. Stomata infrequent, similar to those of lower side.

Lower cuticle with zones of elongated cells along veins; cells between veins with obscure outlines. Lateral walls fine, surface walls without median thickenings or papillae.

Stomata with guard cells more or less exposed, stomatal pit somewhat elongated. Lateral subsidiary cells with strip of thickening, or bulging thickening next to pit, or, very occasionally, each with a thinly cutinized solid papilla projecting over pit.

Roseberry Topping and Hasty Bank leaves. Typically, lamina deeply divided into about six main segments (minimum 4), with deepest division in centre. Each segment often dividing once again, resulting in up to ten ultimate lobes each 8 mm (5 mm–12 mm) wide. Lamina radius up to 54 mm, basal angle about 165° (100°–200°). Petiole 1·5 mm (1·0 mm–2·5 mm) wide, longest portion preserved 60 mm long (but see below). Veins more or less conspicuous, slightly converging towards apex, typically 7 (4–13) per lobe at concentration of 14 (10–20) per cm. Vein dichotomies to at least half-way along lamina. Leaf substance fairly thick, resin not detected.

Cuticles delicate, upper thicker than lower. Upper cuticle with elongated cells along veins; between veins, cells polygonal, sometimes slightly elongated, occasionally in short rows. Lateral walls straight or faintly sinuous, fine, except over veins where longitudinal walls often thicker.

Lower cuticle with obscure cell outlines, lateral walls very fine. Surface walls without any median thickening. Papillae usually absent from ordinary cells of both sides but some trichome bases occurring on lower side. Attached trichomes not known. Stomata seen on lower side

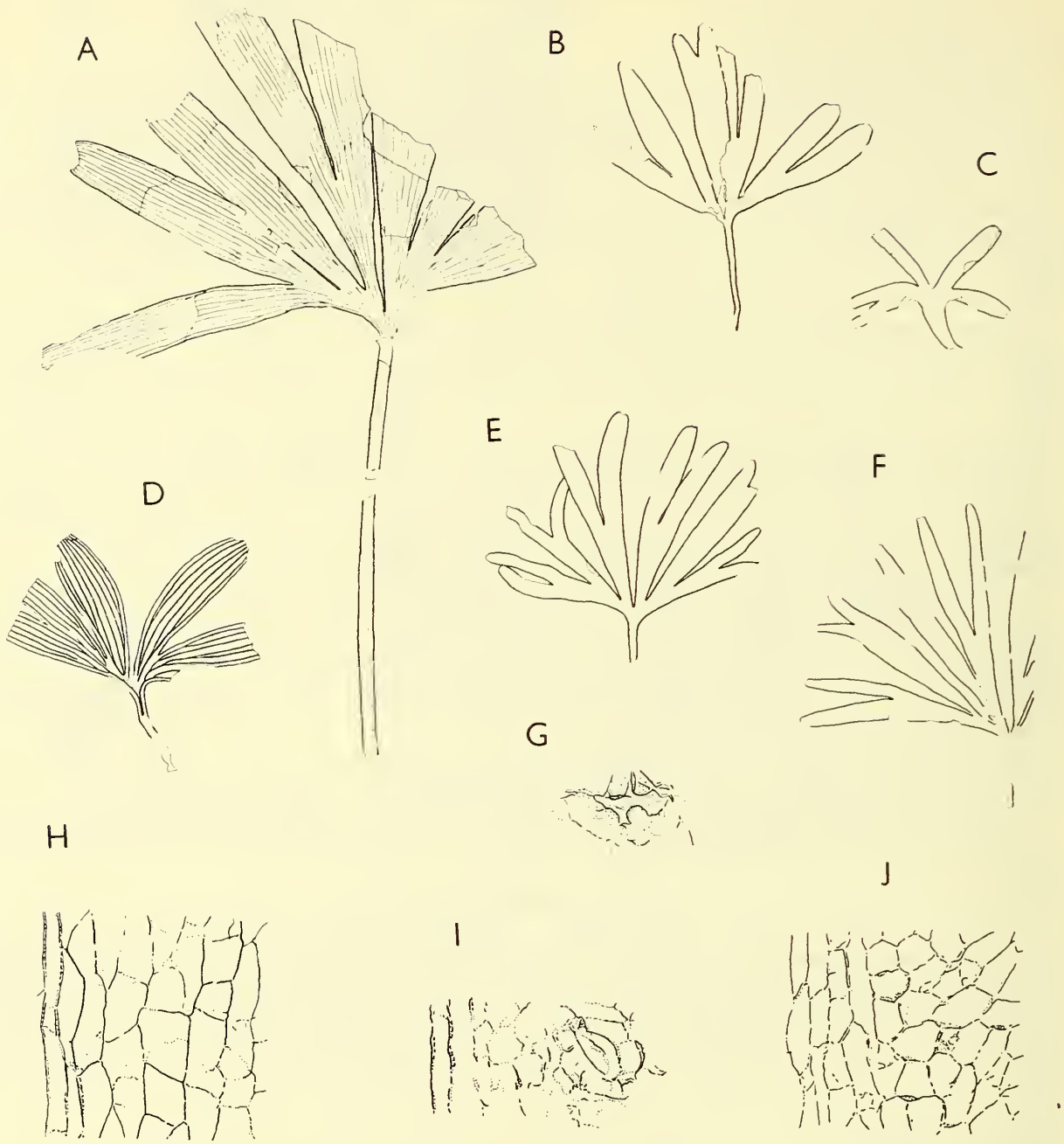


Fig. 5. **Ginkgo** sp. cf. **sibirica** Heer

A, D, leaves from Roseberry Topping, actual size. B, E, F, leaves from Petard Point, actual size. C, specimen intermediate between foliage and scale leaf, from Petard Point, actual size. G, stoma from specimen shown in C, magnification ×400. H, part of upper cuticle, magnification ×200. I, part of lower cuticle with stoma, from specimen shown in A, V.56445, magnification ×200. J, part of upper cuticle, magnification ×200. H, I, J, all have part of a vein on the left. G, J are from Petard Point, H, I from Roseberry Topping.

only. Guard cells exposed; some subsidiary cells unthickened, others with strip of thickening next to stomatal pit.

The 'Petard Point' material was collected by Miss M. W. Kendall in 1947 from the foot of Beast Cliff at about 54° 22′ 19″ N. This precise outcrop has seldom been satisfactorily exposed since. The Roseberry Topping material was collected by H. H. Thomas in 1912 (and listed by him in 1913 as *Ginkgo* sp. cf. *lepida*); one Hasty Bank specimen was collected by H. H. Thomas, and the other by T. M. Harris in 1966.

Discussion. Both groups of leaves include a few very small specimens, which are normal in other respects. The specimen shown in Text-fig. 5 c appears to be intermediate in form between a foliage leaf and a scale leaf. Most of the leaves from all three localities are characterized by delicate cuticles, but a few from Roseberry Topping have thicker upper cuticles with broader cell walls. An ordinary cell bearing a papilla was found on one of these thicker cuticles.

Few stomata were identified with certainty from either group of leaves. Most of the subsidiary cells have a thickened band next to the stomatal pit, but a stoma with completely unthickened subsidiary cells was found on each of two cuticles from Roseberry Topping (see Text-fig. 5 i), and one from Petard Point has well defined papillae on the subsidiary cells (Text-fig. 5 g).

The Petard Point specimens have a thinner leaf substance, more crowded veins, a slightly higher number of narrower lobes, a small basal angle and a slightly more slender petiole than the Roseberry Topping and Hasty Bank leaves. The long petiole shown in Text-fig. 5 a is thought to have been connected with the associated lamina and to have since been sheared in two places. Resin has been found in seven of the sixteen Petard Point leaves, but although none has been detected in the leaves of the other group, there is no conclusive evidence of its absence.

Comparison. Some of the Roseberry Topping leaves are similar in form to *Ginkgo longifolius* but differ in the absence of hollow papillae on the subsidiary cells. The cuticles of both groups of leaves resemble those of *Ginkgo digitata* in their thinness but *G. digitata* is much less deeply divided than any of the present leaves. A few of the smaller leaves from Roseberry Topping are similar in shape to *Ginkgo huttoni* but their cuticles lack papillae and are thinner. Some of the Petard Point leaves with narrow lobes resemble *Baiera furcata* in form but have much thinner cuticle, fewer stomata on the upper surface, and lack conspicuous encircling cells.

The present leaves are similar to Heer's *Ginkgo sibirica* and *Ginkgo lepida*. Unfortunately the cuticles of his material of these two species are not known. The mean values of some leaf characters taken from Heer's figures and from the present leaves are shown in Table 1 below. The figures in brackets show the ranges.

The Roseberry Topping and Hasty Bank leaves differ from *G. sibirica* and *G. lepida* in having rather wider leaf segments. The Petard Point leaves have a somewhat smaller basal angle than either species, and possibly more crowded veins. Despite these differences, the present leaves, taken as a whole, more closely resemble Heer's *Ginkgo sibirica* than they do *G. lepida* or any other species and are therefore called *Ginkgo* sp. cf. *sibirica*. Leaves figured by Johansson (1922) as *Ginkgo* cf. *sibirica* appear to have rather delicate cuticles with fine cell

	Basal angle of lamina	Number of lobes	Width of lobes (mm)	Apices	Radius lamina (mm)
Ginkgo sibirica Hr	165°	8	5	Round	41
	(90°–250°)	(8–11)	(2·5–8·5)	(retuse to acute)	(30–59)
Roseberry Topping	165°	6	8	Blunt	40
and Hasty Bank leaves	(100°–200°)	(4–10)	(5–12)	(retuse to rounded)	(16–54)
Petard Point leaves	140°	10	5	Round	31
				(obtuse to sub-acute)	(14–50)
Ginkgo lepida Hr	195°	10	4	Acute	43
	(100°–300°)	(8–12)	(2–12·5)	(round-acute)	(32–74)

outlines similar to those of the present leaves, but they differ in having more stomata on the upper surface. Lundblad (1959) includes them in *Ginkgo marginatus*. There are many other leaves which resemble *Ginkgo* sp. cf. *sibirica* in form but whose cuticles are unknown. Some leaves of *Ginkgo acosmia*, *G. hermelini* and *G. taeniata* from East Greenland match *Ginkgo* sp. cf. *sibirica* but all their cuticles are thicker than those of the present species and their subsidiary cells are either papillate or form a thickened rim around the stomatal pit.

The leaves described by Yabe & Oishi (1933) and Oishi (1933) are among the few which resemble *G. sibirica* and also have known cuticles. These are evidently delicate but probably thicker than our leaves and they differ in the distinct papillae on the ordinary epidermal cells.

The following leaves from other regions are similar in shape to *Ginkgo* sp. cf. *sibirica*. This list includes some specimens resembling *G. longifolius* and others resembling the *gracilis* form of *Baiera furcata*.

1876 *Ginkgo sibirica* Heer, pl. 7, fig. 6, pl. 9, fig. 5 B, pl. 11, pl. 20, fig. 36, pl. 22, fig. 3. (Upper Jurassic; E. Siberia)
1876 *Ginkgo lepida* Heer, pl. 12, figs. 1–10. (Upper Jurassic; E. Siberia)
1877 *Ginkgo sibirica* Heer: Geyler, pl. 31, fig. 6. (Jurassic; Japan)
1880 *Ginkgo lepida* Heer: Heer, pl. 5, figs. 2, 3 A. (Jurassic; Siberia)
1903 *Ginkgo sibirica* Heer: Möller, pl. 4, fig. 20. (Liassic; Bornholm)
1905 *Ginkgo lepida* Heer: Fontaine *in* Ward, pl. 32, figs. 3–8. (Jurassic; Oregon)
1905 *Ginkgo sibirica* Heer: Fontaine *in* Ward, pl. 33, figs. 1–8, 19. (Jurassic; Oregon)
1905 *Ginkgo schmidtiana parvifolia* Krasser, pl. 2, figs. 4, 5. (Jurassic; Transbaikal)
1906 *Ginkgo lepida* Heer: Yokoyama, pl. 9, fig. 2 B. (Jurassic; China)
1906 *Ginkgo flabellata* Yokoyama, pl. 7, figs. 6–9. (Jurassic; China)
1907 *Ginkgo sibirica* Heer: Seward, pl. 7, fig. 56. (Jurassic; Turkestan)
1908 *Ginkgo lepida* Heer: Yabe, pl. 1, figs. 2 B, 3 D, pl. 2, figs. 4, 5 D. (Jurassic; China)
1908 *Baiera* cf. *gracilis* Bunbury: Yabe, pl. 1, fig. 3 C, pl. 2, fig. 5 C. (Jurassic; China)
1910 *Ginkgo sibirica* Heer: Kryshtofovich, pl. 3, figs. 2–4. (Jurassic; Ussuriland)
1911 *Ginkgo sibirica* Heer: Seward, text-fig. 9 A. (Kimmeridgian; Scotland)
1915 *Baiera longifolia* Heer: Kryshtofovich, pl. 6, figs. 1, 2. (Jurassic; Amurland)
1916 *Ginkgo sibirica* Heer: Kryshtofovich, pl. 10, figs. 6, 7, pl. 11, fig. 1. (Upper Jurassic; Ussuriland)
1919 *Ginkgo sibirica* Heer: Seward, text-fig. 641 A. (Kimmeridgian; Scotland. Same as Seward (1911) text-fig. 9 A)
1922 *Ginkgo sibirica* Heer: Yabe, pl. 4, fig. 10, text-figs. 22–24, pl. 4, fig. 11. (Mesozoic; Korea, Mesozoic; Shantung)
1924 *Ginkgoites sibirica* (Heer): Walkom, pl. 2, fig. 4. (Trias; Queensland)
1925 *Ginkgoites sibirica* (Heer): Kawasaki, pl. 23, figs. 68–71. (Lias; Korea)
1925 *Baiera gracilis* Bunbury: Kawasaki, pl. 25, fig. 72. (Lias; Korea)
1926 *Baiera gracilis* Bunbury: Kawasaki, pl. 9, fig. 25. (Lias; Korea)
1926 *Baiera phillipsi* Nath.: Kawasaki, pl. 27, fig. 80 C. (Lias; Korea)

1928 *Ginkgo* sp., Makarewiczowna, pl. 2, figs. 5, 6. (Lias; Poland)
1928 *Ginkgo sibirica* Heer: Makarewiczowna, pl. 2, fig. 4. (Lias; Poland)
1930 *Ginkgo sibirica* Heer: Turutanova-Ketova, pl. 3, fig. 9. (Jurassic; Khirgiz)
1930 *Ginkgo lepida* Heer: Turutanova-Ketova, pl. 5, figs. 1, 3. (Jurassic; Khirgiz)
1930 *Ginkgoites sibirica* (Heer): Turutanova-Ketova, pl. 5, figs. 1, 3. (Jurassic; Khirgiz)
1931 *Baiera guilhaumati* Sze, pl. 6, figs. 4, 5. (Lias; China)
1931 *Ginkgo sibirica* Heer: Khaklov, text-fig. 22. (Jurassic; Kuznetsk)
1931 *Ginkgo sibirica* Heer: Prinada, pl. 2, fig. 13. (Jurassic; Central Asia)
1932 *Ginkgoites sibirica* (Heer): Oishi, pl. 49, figs. 4, 5. (Rhaetic; Japan)
1933 *Ginkgo* cf. *lepida* Heer: Sze, pl. 10, figs. 1, 2. (Mesozoic; China)
1933 *Ginkgo sibirica* Heer: Kryshtofovich, pl. 12, fig. 6, pl. 16, fig. 4. (Jurassic; Irkutsk, USSR)
1933 *Ginkgo sibirica* Heer: Kryshtofovich & Prinada, pl. 2, fig. 5. (Rhaeto-Triassic; Eastern Urals)
1933 *Ginkgoites* cf. *sibirica* (Heer): Yabe & Oishi, pl. 3, fig. 8, pl. 32, figs. 4–7, 8 B. (Mesozoic; Manchuria)
1933 *Ginkgoites* cf. *sibirica* (Heer): Oishi, pl. 36, figs. 1–7. (Cuticles of above leaves)
1935 *Ginkgoites sibirica* (Heer): Toyama & Oishi, pl. 3, fig. 6, pl. 4, fig. 2. (Jurassic; Manchuria)
1939 *Ginkgoites sibirica* (Heer): Kawasaki, pl. 13, fig. 51. (Middle Jurassic; Korea)
1940 *Ginkgoites sibirica* (Heer): Oishi, pl. 38, fig. 11, pl. 39, fig. 1. (Mesozoic; Japan)
1944 *Ginkgoites sibirica* (Heer): Turutanova-Ketova, text-fig. 4. (Upper Lias; Kazakhstan)
1944 *Ginkgoites lepidus* (Heer): Turutanova-Ketova, pl. 2, fig. 1. (Upper Lias; Kazakhstan)
1953 *Ginkgoites* spp., Sah, pl. 1, figs. 1–10, text-figs. 1-11. (Jurassic; Rajmahal Hills)
1955 *Ginkgoites* sp., Mehta & Sudd, pl. 1, figs. 2, 3. (Jurassic; Rajmahal Hills)
1959 *Ginkgo marginatus* Lundblad, pls. 1, 2, text-figs. 1–4. (Basal Lias; Sweden. Form similar but cuticle different – list of references including *G. hermelini*)
1962 *Ginkgo lepida* Heer: Prinada, pl. 9, fig. 5, pl. 10, figs. 1, 4–7, pl. 11, fig. 5, text-figs. 39–41. (Jurassic; E. Siberia)
1962 *Ginkgo sibirica* Heer: Prinada, pl. 9, figs. 6, 7, pl. 10, figs. 2, 3, pl. 11, fig. 4, pl. 25, fig. 5, text-figs. 37, 38. (Jurassic; E. Siberia)
1963 *Ginkgo sibirica* Heer: Vasilevskaya & Pavlov, pl. 13, fig. 3, pl. 36, fig. 3.
1963 *Ginkgo lepida* Heer: Samylina, pl. 22, fig. 10. (Upper Jurassic-Lower Cretaceous; Aldan R., Siberia)
1963 *Ginkgo sibirica* Heer: Genkina, pl. 37, figs. 3–7. (Middle Jurassic; Urals).
1966 *Ginkgo sibirica* Heer: Prosvirjakova, pl. 20, figs. 2, 7. (Jurassic; Mangyšlak)
1966 *Ginkgo lepida* Heer: Prosvirjakova, pl. 21, fig. 1. (Jurassic; Mangyšlak)

Ginko longifolius (Phillips) Harris comb. nov.

Text-figs. 6–8

1829 *Sphenopteris longifolia* Phillips, p. 148, pl. 7, fig. 17
1864 *Baiera longifolia* (Phillips) Leckenby, p. 76. (Name)
1875 *Cyclopteris longifolia* (Phillips) Phillips, p. 200, pl. 7, fig. 17. (Figure as Phillips 1829)
1880 *Baiera phillipsi* Nathorst, p. 76. (Name)
1900 *Baiera phillipsi* Nathorst: Seward, p. 269, pl. 9, fig. 4, text-fig. 47. (Phillips' type refigured)
1913 *Baiera phillipsi* Nathorst: Krasser, p. 35. (Record of occurrence in Sardinia, but no evidence given)
1936 *Ginkgoites phillipsi* (Nathorst) Florin, p. 107. (Name in review of genus)
1944 *Baiera canaliculata* Harris, p. 680, text-figs. 6 B, C, 7, 8.
1946*a* *Ginkgoites longifolius* (Phillips) Harris, p. 20, text-figs. 6, 7.
1961 *Baiera canaliculata* Harris: Vachrameev & Doludenko, p. 105, pl. 50, figs. 1–8. (Leaf, cuticle. L. Cretaceous; S.E. Siberia)

See also list on p. 20 under *Ginkgo* cf. *sibirica*.

Emended Diagnosis. Leaf petiolate, lamina up to 65 mm long, basal angle typically 90° (60°–120°). Petiole 0·5 mm–2·0 mm wide, up to 40 mm long. Lamina deeply divided into 4–8 segments, each segment simple or forked, resulting in up to sixteen ultimate lobes. Lobes about 3·5 mm (1·5 mm–7·0 mm) wide, with irregularly forked, or rounded to sub-acute

apices. Veins more or less conspicuous, typically 5 (2–10) per lobe, dichotomies up to 45 mm from lamina base; veins slightly converging towards apex. Round or fusiform resin bodies sometimes present. Leaf substance fairly thin, mesophyll sometimes forming transverse bars.

Cuticles of moderate thickness, upper 2–3μ, lower about half as thick. Upper cuticle with veins indistinctly marked by a few rows of narrower, slightly elongated cells. Cells between veins isodiametric, polygonal, becoming somewhat elongated near margins. Cell outlines straight, not very conspicuous. Lateral walls broad, often interrupted. Surface walls of ordinary cells occasionally with a median thickening, transverse bars frequent, but well developed papillae and trichomes absent. Stomata occurring at density of 2 or 3 per mm^2 near lamina base, less frequent or absent throughout rest of lamina. Subsidiary cell papillae less well developed and guard cells more exposed than those on lower surface.

Lower cuticle with fairly distinct vein areas, typically 180μ (105–275μ) wide, areas between veins 570μ (275–905μ) wide. Cells along veins narrow, more or less elongated, often with prominent longitudinal walls. Cells between veins isodiametric, polygonal; rarely rectangular and arranged in short rows. Cell outlines often ill-marked, lateral walls broad, straight, occasionally interrupted. Surface walls of ordinary cells sometimes medianly thickened, sometimes with low, solid or hollow papilla; transverse bars often present. Trichomes absent.

Stomata scattered between veins, rarely in short rows, at density of about 70 (50–85) per mm^2; variously orientated but often longitudinal. Guard cells sunken, partly concealed by subsidiary cell papillae. Subsidiary cells with thickening forming rim around pit, each cell also possessing solid or hollow papilla sometimes pointing upwards, more often flattened, projecting horizontally over guard cells. Encircling cells very rarely present.

Holotype. Specimen figured by Phillips 1829, pl. 7, fig. 17.

Discussion. *Ginkgo longifolius* (Phillips) is different from *Sphenobaiera longifolia* (Pomel) though some of the name combinations are similar. In this account we deal with thirteen undescribed specimens, a small number of leaves previously named *Baiera canaliculata* Harris (1944) and *Ginkgo longifolius* (Phillips) Harris (1946*a*), twelve of which are from the Gristhorpe Bed and one from Marske Quarry. The scope of *G. longifolius* has been enlarged to include all of these, and *B. canaliculata* has been eliminated.

These two species were both based on a very few specimens. None of the present material matches either *B. canaliculata* or Harris's diagnosis of *G. longifolius* perfectly, as indicated below, but they share the various characters which were supposed to distinguish them in varying combinations, and blur all possible distinction. *G. longifolius* becomes a leaf of rather varied form and structure.

The holotype of *B. canaliculata* has segments with most of their margins sharply recurved —a unique character. Not one of the present specimens has this character, all having flat margins, but several match *B. canaliculata* in every other character and all match it in their cuticles. Accordingly we feel that the recurved margins of *B. canaliculata* are not a true specific character but one peculiar to the holotype specimen, possibly an effect of shrivelling after death.

Present specimens matching *G. longifolius* in certain features include five leaves having one or more rather broad segments with more than six veins (and two with ten). One of these and two others including the leaf shown in Text-fig. 6 A have a few resin bodies.

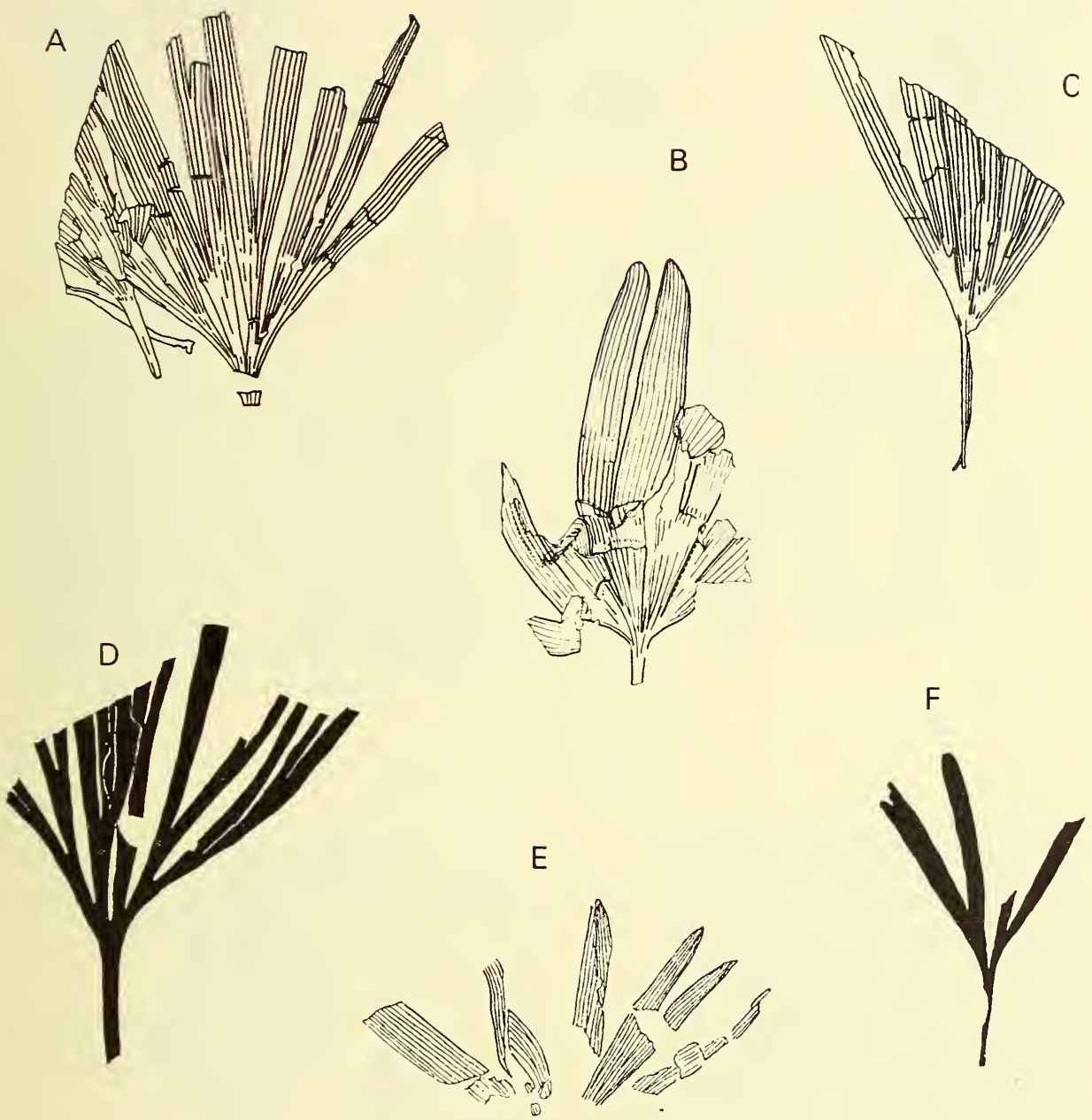


Fig. 6. **Ginkgo longifolius** (Phillips) Harris comb. nov.

A, leaf, interlaced with petioles and basal portions of two other leaves on the left, from part and counterpart. B, lower half of leaf, and leaf segments—two showing an apex, probably detached from the same leaf by sideways shearing; from part and counterpart. C, leaf from part and counterpart. D, holotype specimen of *Baiera canaliculata*, from part and counterpart, V.25854. E, specimen figured by Harris (1946, text-fig. 6 G) as *Ginkgoites longifolius*, V.26952. F, leaf formerly named *B. canaliculata*. All figures are actual size. A–E are from the Gristhorpe Bed, F is labelled 'lower Oolite, Scarborough' with a matrix similar to the Gristhorpe Bed. D, F are from Harris (1944, text-figs. 7 D, E).

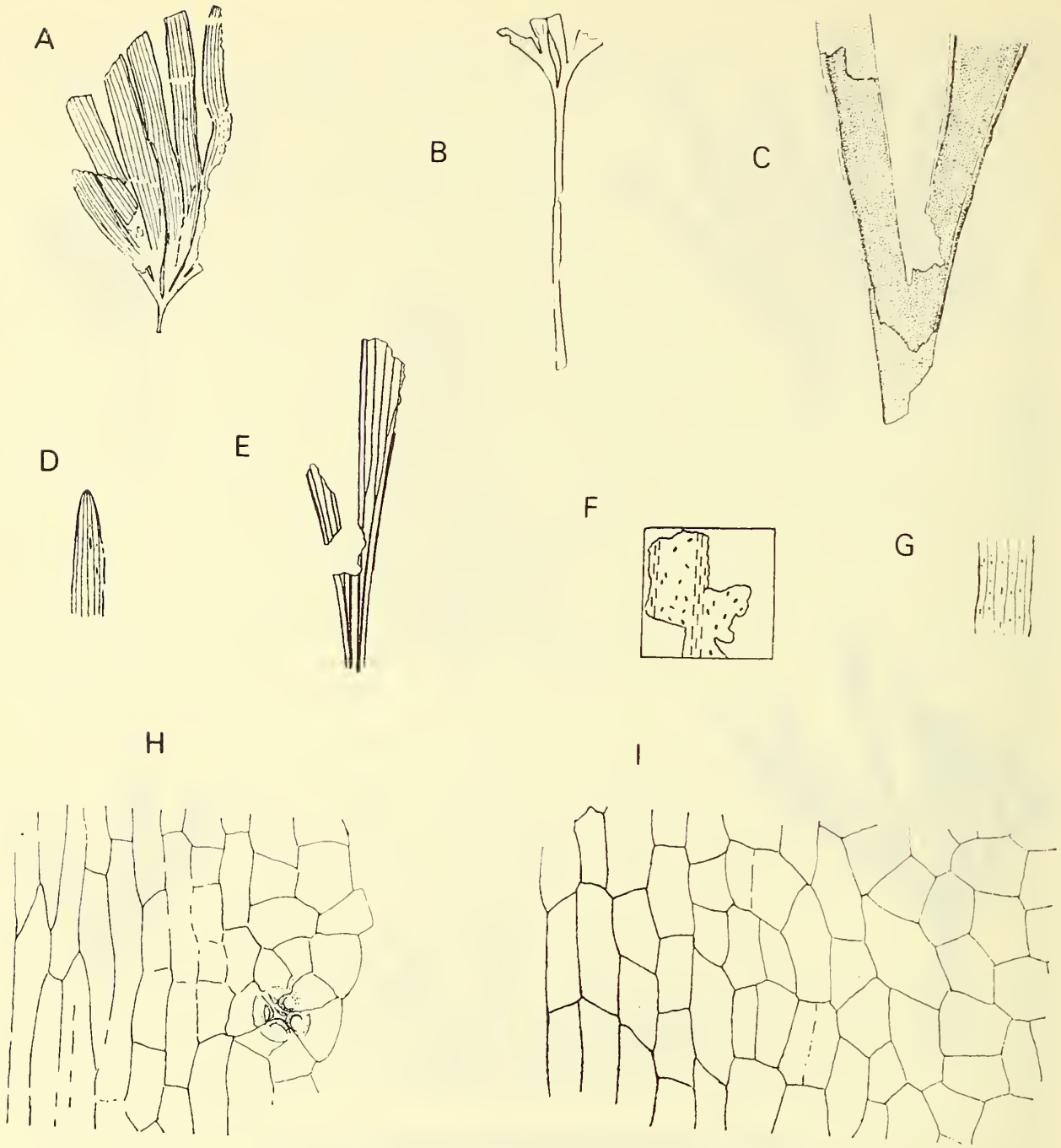


Fig. 7. **Ginkgo longifolius** (Phillips) Harris comb. nov.

A, Phillips's specimen labelled '*Cyclopteris longifolia*'. Two lobes on the left overlap, actual size. B, leaf base and petiole, actual size. C, part of lamina from specimen shown in Fig. 6 D, magnification ×4, showing recurved margins (scarcely indicated at all where the substance has flaked off). D, lobe apex of specimen shown in Fig. 6 E, magnification ×2, by transmitted light to show veins. E, veins of specimen in Fig. 6D. F, fragment of lower cuticle showing two veins and orientation of stomata, the square is 1 mm², from specimen shown in A. G, part of segment of specimen shown in A, showing veins and resin, magnification ×2. H, I, lower and upper cuticles, with rather fine cell outlines, from specimen shown in A, magnification ×200. There is a vein on the left in each. Figs. A, D, F–I are from Harris (1946, text-figs. 6, 7). Figs. C, E are from Harris (1944, text-fig. 7).

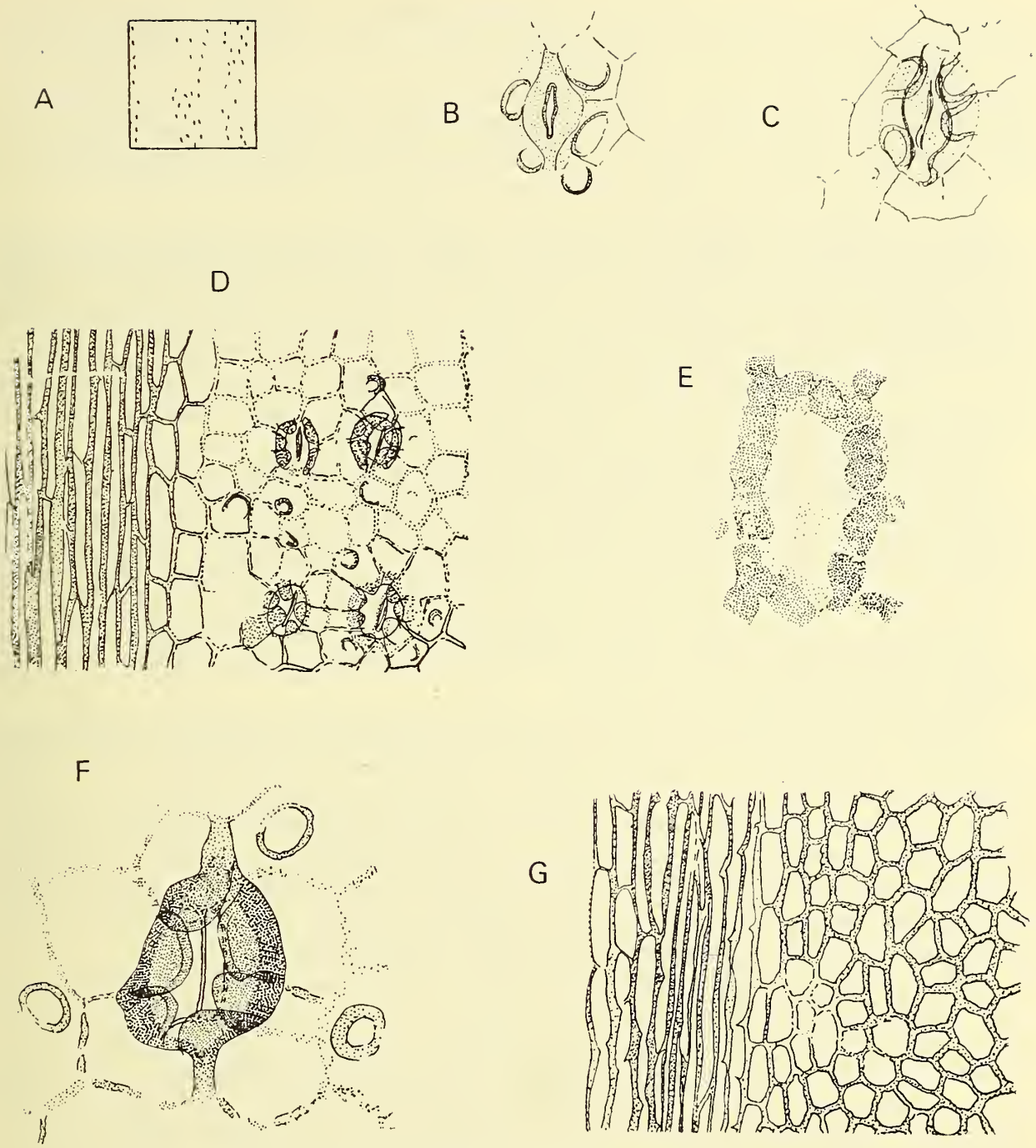


Fig. 8. **Ginkgo longifolius** (Phillips) Harris comb. nov.

A, 1 mm of lower cuticle showing distribution and orientation of stomata. B, C, somewhat exposed stomata, magnification ×400. D, lower cuticle of normal type, magnification ×200. E, cell of upper cuticle to show anticlinal walls, magnification ×800. F, typical stoma, magnification ×800. G, upper cuticle of normal type, magnification ×200. A, D–G are from leaf shown in Fig. 6D, formerly holotype of *B. canaliculata* after Harris (1944, text-figs. 6–8). B, C are from Harris (1946, text-figs. 6A, B).

Unfortunately the upper cuticle of Phillips' holotype of *G. longifolius* in the Yorkshire Museum has been lost, but the lower cuticle is just like those of the present specimens and those figured by Harris as *B. canaliculata*. The cuticles of the two specimens placed in *G. longifolius* by Harris (1946*a*) are rather different in being distinctly thinner with narrower cell outlines, but these leaves are indistinguishable from the present specimens in other features and are therefore regarded as unusual forms of *G. longifolius*, differing from the ordinary form in the aspects of their cuticles mentioned above.

As defined here, *G. longifolius* is unusual in crossing the arbitrary boundary separating *Ginkgo* and *Baiera*. The number of veins per segment, which should provide this distinction (*Baiera* having 4 or fewer, *Ginkgo* more than 4), varies in the present leaves from 2 to 10, the mean being 5, with most counts close to the mean. The width of segments is rather variable, but a histogram of the variation is broadly flat-topped, not binodal; segments 1·5 mm, 3·5 mm and 5·0 mm being almost equally frequent. Resin bodies do occur in small numbers in at least some leaves and the present material does not allow us to say whether they are ever entirely lacking. One specimen has a segment with a microscopically wavy margin.

There are no well developed papillae on the ordinary cells of the upper surface of the leaf, but it is possible that the small, thin, round bodies seen on the upper cuticles of some specimens are ill-defined papillae. Papillae on the ordinary cells of the lower cuticle are rarely numerous and not very heavily cutinized, or they may be absent altogether. The proportion of subsidiary cells bearing a papilla varies, but stomata with no papillate subsidiary cells occur only very rarely.

Fragments of rather shredded leaf segments from the Cloughton *Quinqueloba* Bed have cuticles similar to those of the present leaves and are identified as *G. longifolius*. They add nothing to the knowledge of this species.

Comparison. *Baiera furcata*, *Ginkgo huttoni* and *Ginkgo* sp. cf. *sibirica* each include a few leaves which match *Ginkgo longifolius* in form, but they can be distinguished where their cuticles are known. *B. furcata* has more frequent stomata on the upper cuticle and well marked encircling cells around the stomata on the lower side, *G. huttoni* has trichomes, and both have thicker cuticles than *G. longifolius*. *Ginkgo* sp. cf. *sibirica* is distinguished by its lack of hollow papillae on the subsidiary cells. The specimen figured by Seward (1900, pl. 9, fig. 3) as *Baiera gracilis* forma *münsteriana* is rather similar to both *G. longifolius* and *B. furcata* but cuticle preparations have been too fragmentary for proper identification.

Ginkgo longifolius closely resembles the form of certain foreign specimens; for instance small leaves of *Ginkgoites marginatus* but these have thinner, less exposed guard cells. *G. taeniata* is slightly less similar, having notched lobed apices and less crowded veins (see Lundblad 1959). *Ginkgoites* cf. *sibirica* of Yabe & Oishi (1933) is also of similar form but differs in its strongly marked cell walls on the lower epidermis. The leaves and cuticles figured by Vachrameev & Doludenko (1961) as *Baiera canaliculata*, from the Lower Cretaceous of the Bureya Basin, South Eastern Siberia, match *G. longifolius* almost perfectly and some of the leaves listed under *G.* cf. *sibirica* (p. 20) look similar.

Occurrence

Middle Deltaic Gristhorpe Series	Gristhorpe Bed, Cayton Bay.
	Cloughton Wyke, *Quinqueloba* Bed
Lower Deltaic	Marske Quarry

Ginkgo whitbiensis Harris

Text-fig. 9

1880 *Ginkgo* sp. n., Nathorst, p. 37; 'This species will be called *Ginkgo whitbiensis*', Nathorst, p. 74. (Name and a few notes only), *nomen nudum*
1936 *Ginkgoites whitbiensis* Nathorst: Florin, p. 107 (Name in list)
1951 *Ginkgo whitbiensis* Harris, p. 927, text-fig. 3 A-K, 4 C-G (Figures and description repeated here)

Emended Diagnosis. Leaf very small; petiole typically 10–20 mm long, 2 mm wide. Lamina rather narrow, 10–20 mm wide, basal angle about 90°. Lamina divided into 2 or 4 strap-shaped lobes, each 2–5 mm wide, apices blunt, rounded or slightly lobed but not notched. Veins obscure but probably traversing lamina at density of 15 per cm, 4–6 present in each full-sized lobe. Margins flat, leaf substance dense. Round or fusiform resin bodies, 0·1 mm wide, frequent between veins but only visible after maceration.

Cuticle thick above, rather thin below. Upper cuticle with 10–20 stomata per mm^2, lower with numerous stomata, about 100 per mm^2. Upper cuticle with almost uniform epidermal cells, veins scarcely recognizable. Cells commonly slightly elongated rectangles, up to eight times as long as wide, forming longitudinal rows. Side walls very broad, conspicuous, straight, end walls sometimes broad, sometimes ill-marked. Surface walls flat, unsculptured, without papillae. Trichomes absent. Stomata scattered, resembling those of lower surface, but usually more protected.

Lower cuticle with veins scarcely recognizable. Ordinary epidermal cells more or less isodiametric, polygonal, not usually forming longitudinal rows, but in some specimens a row of rectangular cells occasionally present. Lateral walls rather broad, not prominent, often very indistinct, straight, sometimes rather interrupted. Surface wall almost flat but sometimes with about two very ill-defined thickenings near middle of cell. A few specimens showing an occasional cell with bulging surface. Trichomes absent.

Stomata variously orientated, usually evenly scattered, sometimes forming short longitudinal files, but files very indistinct and many stomata not in any file. Subsidiary cells usually forming a round group of about six very similar cells. Guard cells sunken in pit formed by subsidiary cells. Pit often round, occasionally narrowed. Subsidiary cells thickened next to pit; sometimes forming very prominent ring, and some of them with low, solid or hollow papilla at side of pit. Subsidiary cell surface not specially thickened, but sometimes showing faint mark in middle or near pit. Encircling cells usually absent but unspecialized if present.

Holotype. Specimen figured by Harris 1951, text-figs. 3 D, J, K. (Section for Palaeobotany, Swedish Museum of Natural History, Stockholm Nos. 212, 213).

Discussion. Nathorst's material consists of fifteen leaves and leaf fragments, all of which are small and indicate that this species normally has a very small leaf. In addition to the leaves that Nathorst collected, there are two cuticle fragments, obtained by macerating the coal from the old coal pits at Rosedale Head. Both of these fragments agree in all their characters with *Ginkgo whitbiensis*, but of the very numerous, unassigned, Ginkgoalean cuticle fragments, there are no others agreeing with it; and *Ginkgo whitbiensis* must be regarded as a rare species.

Variable characters include the length to width ratio of the epidermal cells of the upper surface (mean 4:1, range 1:1–8:1), the width of the lateral cell walls of both surfaces, and the

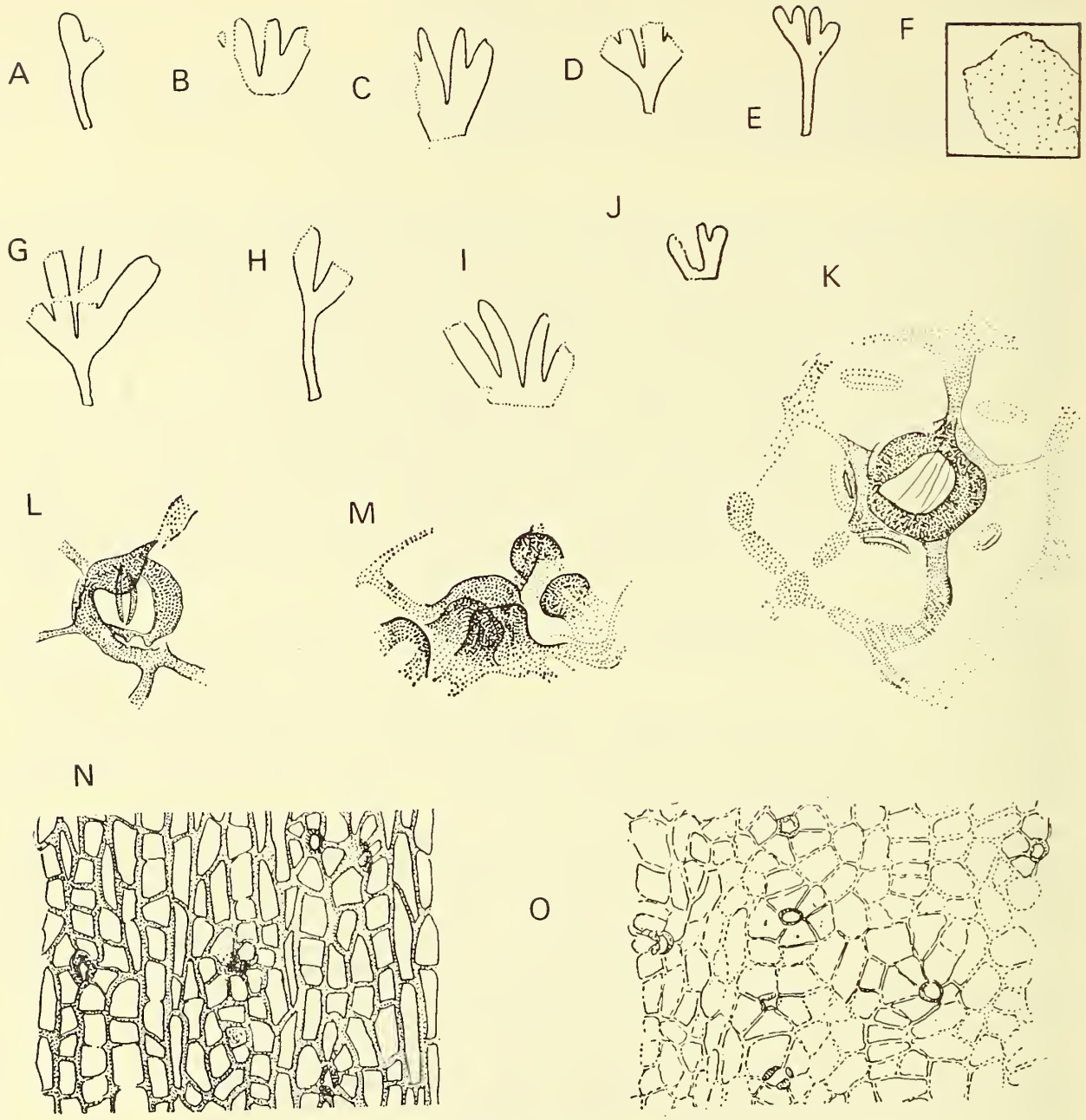


Fig. 9. **Ginkgo whitbiensis** Harris

A–E, G–J, leaf fragments, all actual size. The specimens bear the following numbers: A, 209, B, 214, C, 210, D.218. E (part and counterpart), 206, 207. G (part and counterpart), 208, 216. H (part and counterpart), 212, 213. I, 217, J, 211. F, distribution of stomata in a fragment of epidermis 1 mm square, from 212. K, L, normal stomata. M, stoma with unusually strongly developed papillae. K, L, M, from a specimen on block 212, magnification ×800. N, O, upper and lower cuticles from a second specimen on 212 (not shown in H), magnification ×200. All specimens are in Stockholm Museum. All figures are from Harris (1951, text-figs. 3, 4).

subsidiary cell thickening. Stomata occasionally occur which have one or two of the subsidiary cells lacking a conspicuous thickening next to the pit. Some stomata have guard cells obscured by a rather broad ring of subsidiary cell thickenings or by converging cell papillae as in Text-fig. 9 N.

Comparison. *Ginkgo whitbiensis* agrees in general form with *Ginkgo huttoni* but is far smaller, the leaf being barely half as big, none being as large as a typical leaf of *G. huttoni*. *G. whitbiensis* is distinguished from small leaves of *G. huttoni* by its cuticle which has less well marked veins, less papillose cells, lacks trichomes, has many more stomata on the upper side and there is a greater difference in thickness between the upper and lower cuticles than in *G. huttoni*. Two other Yorkshire species also produce a proportion of small leaves which resemble those of *G. whitbiensis*, but they too can be distinguished by their cuticles. Leaves of both *Ginkgo* sp. cf. *sibirica* and *G. digitata* have much thinner upper cuticles than *G. whitbiensis*, much thinner cell outlines, and no prominent ring of thickening around the stomatal pit.

Very few *Ginkgo* leaves as small as the present ones have been figured from other regions, though no doubt occasional ones must occur in most species. The most similar is *Ginkgo polaris* Nathorst (1900) where the leaf is about the same size though rather more branched. However, Florin (1936, p. 143) described its cuticle, which is quite different, with well developed papillae on the ordinary epidermal cells, and sinuous lateral walls. Some slightly larger leaves described by Heer (1876, 1878) as *G. pusilla* and *G. flabellata* from East Siberia differ in being more branched with fewer veins in a leaf segment, but no microscopic details are known.

Occurrence

Middle Deltaic Gristhorpe Series	Rosedale Head, old coal pits, about 54° 24′ 22″ N, 0° 57′ 11″ W. Cuticle fragments only.
Lower Deltaic	Whitby, 'New Layer'—Type locality.

Genus BAIERA F. Braun emend. Florin 1936

Type Species. *Sphaerococcites muensterianus* Presl.

Diagnosis (freely translated from Florin 1936, p. 105). Leaf as a whole with a clearly differentiated petiole and a lamina with more or less semicircular to broadly triangular outline, lamina deeply divided (over 2/3) into primary lobes arranged in two groups, lobes at least once and usually repeatedly divided to near base. All ultimate lobes narrow and more or less linear, with not more than two to four parallel veins at one level.

Discussion. This definition separates *Baiera* from *Ginkgo* which commonly has more than four and usually more than six veins at one level in a segment, and from *Sphenobaiera* in which the leaf as a whole is wedge-shaped and there is no distinction between petiole and lamina. The venation is fundamentally the same in all three genera and there is general agreement in the frequent presence of resin bodies between the veins and in the character of the cuticles. The only differences are in the gross form of the leaf as a whole. So far as we know *Sphenobaiera* is clearly separated but there are species here included in *Ginkgo* and others

which we include in *Baiera* which transgress the distinction given above. Thus a good many leaves of *Baiera furcata* (*gracilis*) have six veins in some at least of their segments, but most specimens have less. The distinction is arbitrary, but useful as the great majority of species separate readily.

Baiera furcata (L. & H.) Braun
(including ***B. gracilis*** Bunbury)
Pl. 1, figs. 1, 2; Text-figs. 10–13

The following are all Yorkshire specimens:

1837 *Solenites? furcata* Lindley & Hutton, pl. 209. (Good figures)
1843 *Baiera furcata* (L. & H.) Braun, p. 21. (Name only)
1851 *Baiera? gracilis* Bunbury, p. 182, pl. 12, fig. 3. (At least three similar leaves, previously given MS name of *Schizopteris gracilis* by Bean)
1869 *Jeanpaulia lindleyana* Schimper, p. 683. (Name only)
1875 *Solenites furcatus* L. & H.: Phillips, p. 199, Lign 7. (Poor figure)
1884 *Baiera gracilis* Bunbury: Saporta, p. 277, pl. 157, fig. 4; pl. 158, figs. 1–3. (Good leaves)
1900 *Baiera lindleyana* (Schimper) Seward, p. 266, pl. 9, figs. 6, 7. (Good leaf)
?1900 *Baiera gracilis* Bunbury: Seward & Gowan, pl. 10, fig. 68. (Not typical, possibly *G. longifolius*)
?1900 *Baiera gracilis* Bunbury forma *münsteriana* Seward, pl. 9, fig. 3. (Same specimen as Seward & Gowan 1900 but differently drawn)
1900 *Baiera gracilis* Bunbury: Seward, pl. 9, fig. 5. (Good leaf)
1919 *Baiera lindleyana* (Schimper): Seward, p. 49, text-figs. 653 A, B. (Same as Seward 1900, pl. 9, figs. 6, 7, but fig. 6 redrawn here)
1919 *Baiera gracilis* Bunbury: Seward, p. 45, text-fig. 649. (Same as Bunbury 1851, pl. 12, fig. 3), text-fig. 650 (Redrawn from specimen in Seward 1900, pl. 9, fig. 5)
1919 *Baiera gracilis* Bunbury forma *münsteriana* Seward, p. 47, text-fig. 651. (Redrawn from specimen in Seward 1900, pl. 9, fig. 3)
1929 *Baiera gracilis* Bunbury: Black, p. 422, text-figs. 8–12. (Leaf and cuticle)
1929 *Baiera scalbiensis* Black, p. 426, text-figs, 13. 14 A, B. (Figures reproduced here)
1936 *Baiera furcata* (L. & H.): Florin, p. 107. (Name only)
1944 *Baiera gracilis* Bunbury: Harris, p. 674, text-figs. 4, 5, 6 A. (Figures reproduced here)
1945 *Baiera furcata* (L. & H.): Harris, p. 213, text-figs. 1, 2. (Figures reproduced here)

Similar specimens from other floras are mentioned on p. 38. They are less confidently identified with *Baiera furcata*.

Diagnosis. Leaf petiolate, lamina as a whole forming angle of 45°–180°, with radius up to at least 70 mm from first dichotomy. Petiole slender, often as long as lamina. Lamina divided by 2–6 successive dichotomies, usually at angles 20°–30° (rarely 10°–50°), with 4 to at least 24 ultimate lobes. Ultimate leaf segments usually about 1·5 mm wide (extremes 0·5 mm and 4·5 mm), tapering to sub-acute or acute apicies. Lower leaf segments up to 7·5 mm wide. Veins inconspicuous, 2–5 in ultimate lobes, up to at least 7 in lower segments. Numerous small round or oval resin bodies, up to 155μ wide, 215μ long, occurring between veins.

Upper cuticle moderately thick, lower slightly thinner, stomata occurring on both sides. Upper cuticle with veins usually marked by strips about 50μ wide (up to 490μ wide) of more or less elongated cells (up to 10 times as long as wide). Areas between veins about 370μ (140μ–590μ) wide of shorter, rectangular or polygonal cells, often isodiametric near stomata, not

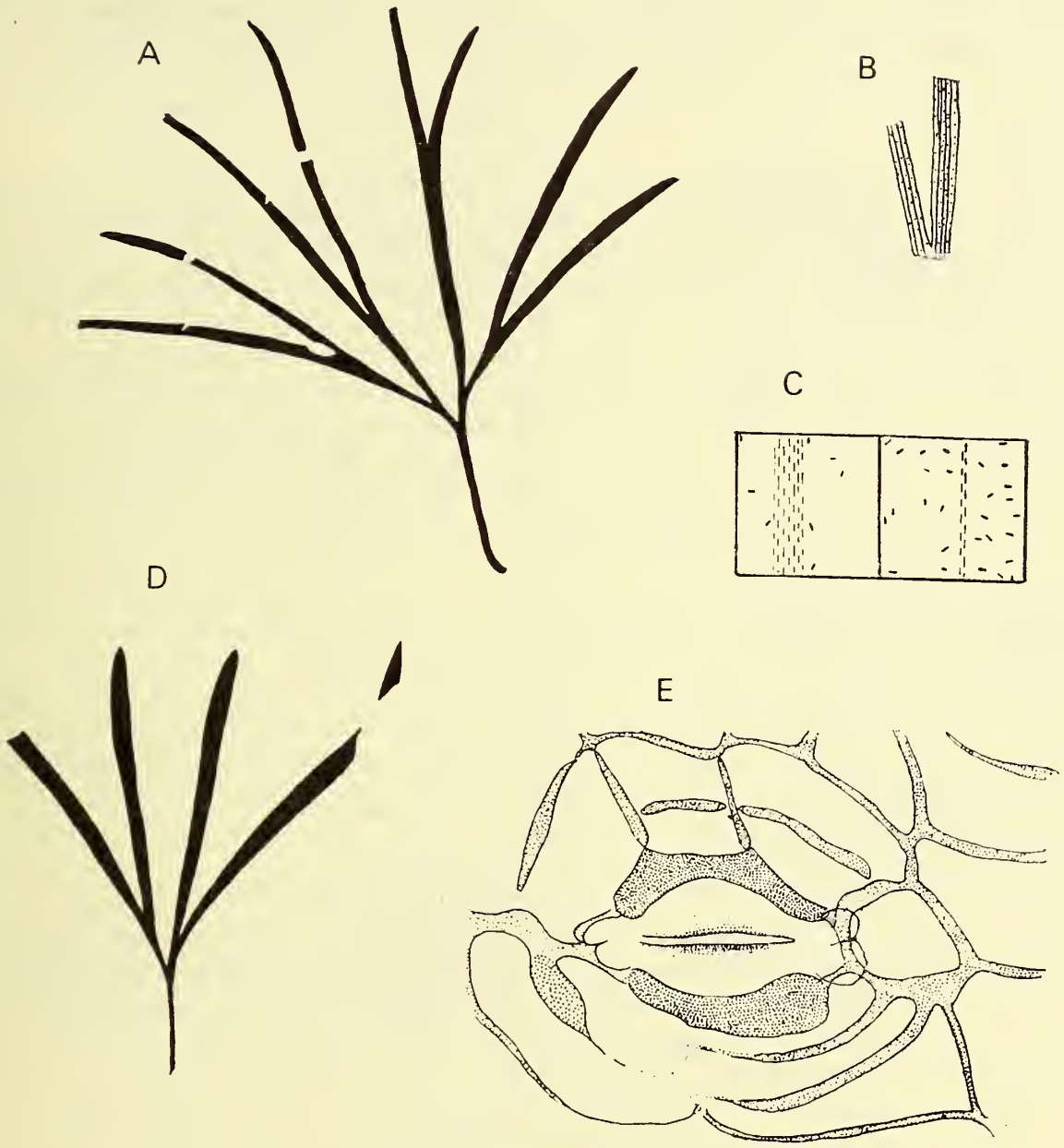


Fig. 10. **Baiera furcata** (L. & H.)

A, V.6475, actual size. B, fragment from V.6475 (slide A), cleared to show veins and resin bodies, magnification ×2. C, 2 mm² of cuticle upper side on left, lower side on right, showing orientation of stomata on either side of vein on each. V.6475*b*. D, 10376, actual size. E, stoma of non-papillate form, V.6475*c*, magnification ×800. All figures from Harris (1944, text-figs. 4, 6).

usually arranged in longitudinal rows. Anticlinal cell walls more or less conspicuous, often prominent, straight, fairly broad, rarely interrupted. Surface walls typically flat, unthickened or rarely with a median thickening or low, solid papilla. Trichomes absent. Stomata occurring between veins, scattered or in short longitudinal files, irregularly orientated, of similar structure to those of lower side though sometimes with narrower pit, and less often with encircling cells.

Lower cuticle with veins indistinguishable, or poorly defined by a few rows of more or less elongated cells devoid of stomata. Cells between veins polygonal, typically isodiametric, occasionally arranged in short longitudinal files. Anticlinal walls more or less conspicuous, straight, of medium width, rarely interrupted. Surface walls flat, unthickened or occasionally bearing a median thickening or low hollow papilla. Trichomes occasionally present. Fairly numerous stomata occurring between veins, scattered, or a few occasionally arranged in short longitudinal file, irregularly orientated. Guard cells with thin surface walls except for thickened strip along aperture. Guard cells surrounded by oval or irregular group of subsidiary cells. Subsidiary cell thickening very varied, but often with band of thickening adjacent to guard cells forming entire rim around stomatal pit, usually broader laterally than at poles, occasionally only lateral subsidiary cells thickened. Rim sometimes bulging, forming papillae projecting upwards, or slightly over guard cells. Surface of subsidiary cells flat, or with a median thickening or small, central, solid papilla in addition to and sometimes fused with bulging rim of thickening around stomatal pit. Unspecialized lateral encircling cells often present, secondary encircling cells occurring only rarely, polar encircling cells absent.

LECTOTYPE. Specimen figured by Lindley & Hutton (1837, pl. 209).

DISCUSSION. It may be pointed out that *Baiera furcata* (L. & H.) is entirely different from *Sphenobaiera furcata* (Heer), a Triassic fossil.

Seeds attributed to *B. furcata* are described on p. 74.

Union of *B. gracilis* and *B. scalbiensis* with *B. furcata.*

We have found the leaves resembling *Baiera gracilis* and *B. furcata* hard to classify. In the early days it may have seemed easy; those leaves with broader segments, about 3 mm or more, were called *B. gracilis*, those with narrower segments, about 1 mm, were called *B. furcata.* There were only a few specimens in all and very few that looked intermediate, but Seward (1919, p. 48) observed that such specimens occur. Localities gave little help (since few of the Museum specimens were localized) and there was no complicating evidence from cuticles. Then in 1929 Black collected leaves he identified as '*gracilis*' from certain Upper Deltaic localities and also leaves with narrower segments which he determined as a new species *B. scalbiensis.* In 1944 Harris described the rather varied cuticles of a few specimens named *B. gracilis* (including the imperfectly localized holotype) and of certain Upper and Lower Deltaic specimens, and also (1945) of the Lower Deltaic *B. furcata* which had a rather different cuticle from *B. scalbiensis.* We thus hoped that when we studied additional well localized specimens, and with preparations of the cuticle of each one of them, we should be able to define some clearly separated species perhaps with zonal value.

What has happened is neither fully satisfactory cleavage into separate species nor fully satisfactory union into one variable species. There are two main sources of material, the Lower

Deltaic Haiburn Wyke Plant Bed where '*gracilis*' and '*furcata*' are both frequent at certain points but absent elsewhere even at this locality and the Upper Deltaic Scalby Wyke Plant Bed (base of the 'Level Bedded Series' of Black) where '*gracilis*' and '*scalbiensis*' occur sparsely

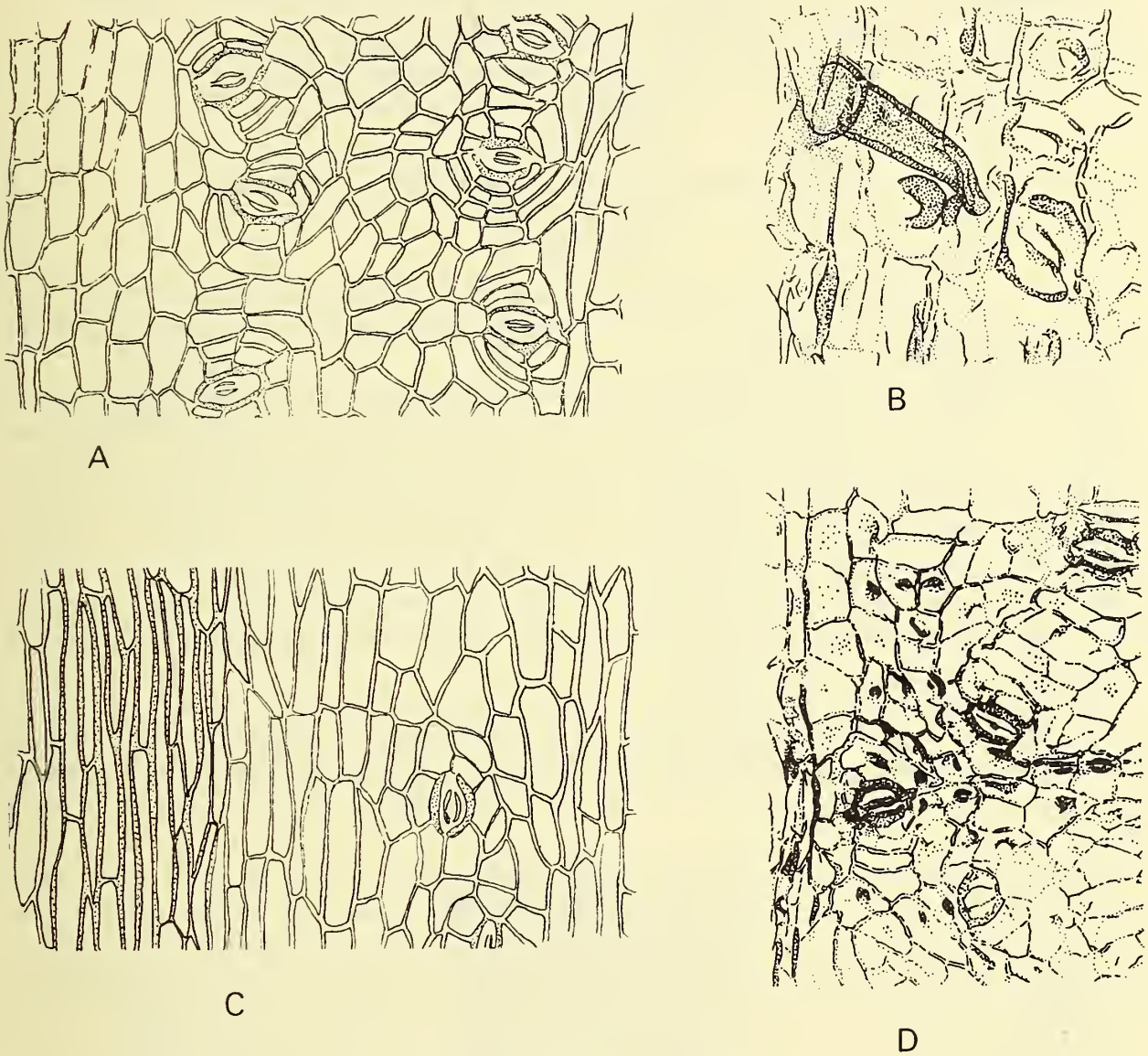


Fig. 11. **Baiera furcata** (L. & H.)

A, lower cuticle, magnification ×200, V.6475*b*. B, lower cuticle showing a trichome, magnification ×400, V.56645. C, upper cuticle, magnification ×200, V.6475*b*. D, lower cuticle of papillate leaf, magnification ×200, V.56646. A vein lies on the left in all cases. A, C, from Harris (1944, text-fig. 4A, B). B, D are from Haiburn Wyke.

as a rule but Nathorst found ample material at some point—his 'Scarborough Nya lagret' (see below). Black found a few similar '*gracilis*' leaves or fragments in some adjacent stream channels. In addition there are cuticle fragments obtained by maceration of rocks at all levels

in the series that agree with '*gracilis*' or '*furcata*' in the broad sense though the shape of the whole leaf is unknown. As indicated, the old Museum specimens are poorly or not at all localized but it is possible to guess that some are from Haiburn and others from Scalby.

The specimens known to be from these two localities can be divided into four groups. The old unlocalized specimens would fall into the same groups.

(1) Lower Deltaic (Haiburn), subsidiary cells mostly lightly cutinized.
Segments broader: '*gracilis*'
Segments narrower: '*furcata*'

(2) Upper Deltaic (Scalby), subsidiary cells mostly strongly cutinized.
Segments broader: '*gracilis*'
Segments narrower: '*scalbiensis*'

It will be seen that while leaves with narrow segments have previously been divided into two species, '*furcata*' and '*scalbiensis*', those with broader segments ('*gracilis*') have not, though this would be equally possible.

Every specimen we have studied from these two localities can be readily separated as Haiburn or Scalby on this stomatal character, provided occasional stomata resembling those of the other locality are discounted as usual. The other Upper Deltaic specimens of Black are just like the Scalby set. There are additional differences, the Upper Deltaic cuticles tend to be thicker and to show the veins on the lower side less distinctly, but these differences are less reliable. We would emphasize that nearly all the leaves, broad and narrow, of one locality have similar cuticles. We could thus make this a primary taxonomic division on cuticle just as we could make segment width a primary division. But there are reasons against both ways of dividing the material.

Division on the microscopic character alone is tiresome and often inapplicable. Moreover it would leave the position of the cuticles of many bulk-maceration fragments of intermediate age in doubt because they are of intermediate appearance. While they may come from leaves of originally different shape there is no evidence for this and we think it wrong to discount these specimens.

Division on segment width is by no means easy. Leaves we first called *B. gracilis* have segments ranging from 6 mm at their widest points down to about 1·5 mm. The different segments of one leaf are by no means equally wide and in the less divided leaves the segments generally are wider than in more divided leaves. The leaves we called *B. furcata* have segments from nearly 2 mm down to about 0·5 mm; there is again variability in one leaf and between different leaves. *B. scalbiensis* has segments 1–2 mm wide. Thus the separation on width is arbitrary and uncertain. Then the field occurrence suggests unity. As indicated, good hand specimens of these leaves are very local. It is a striking fact that a single Haiburn block has two '*gracilis*' and two '*furcata*' leaves and if we may guess the locality of certain old specimens as Haiburn, then several other blocks show both.

In the Upper Deltaic, the specimens are thought to have drifted a considerable distance and are thinly scattered over a wide area and only rarely are leaves with broad and with narrow segments found on the same block. However Nathorst in 1879 collected abundant good specimens from what he called 'Scarborough Nya lagret'. This must be somewhere in M. Black's 'Level Bedded Series'. The leaves are so common just there that even small blocks

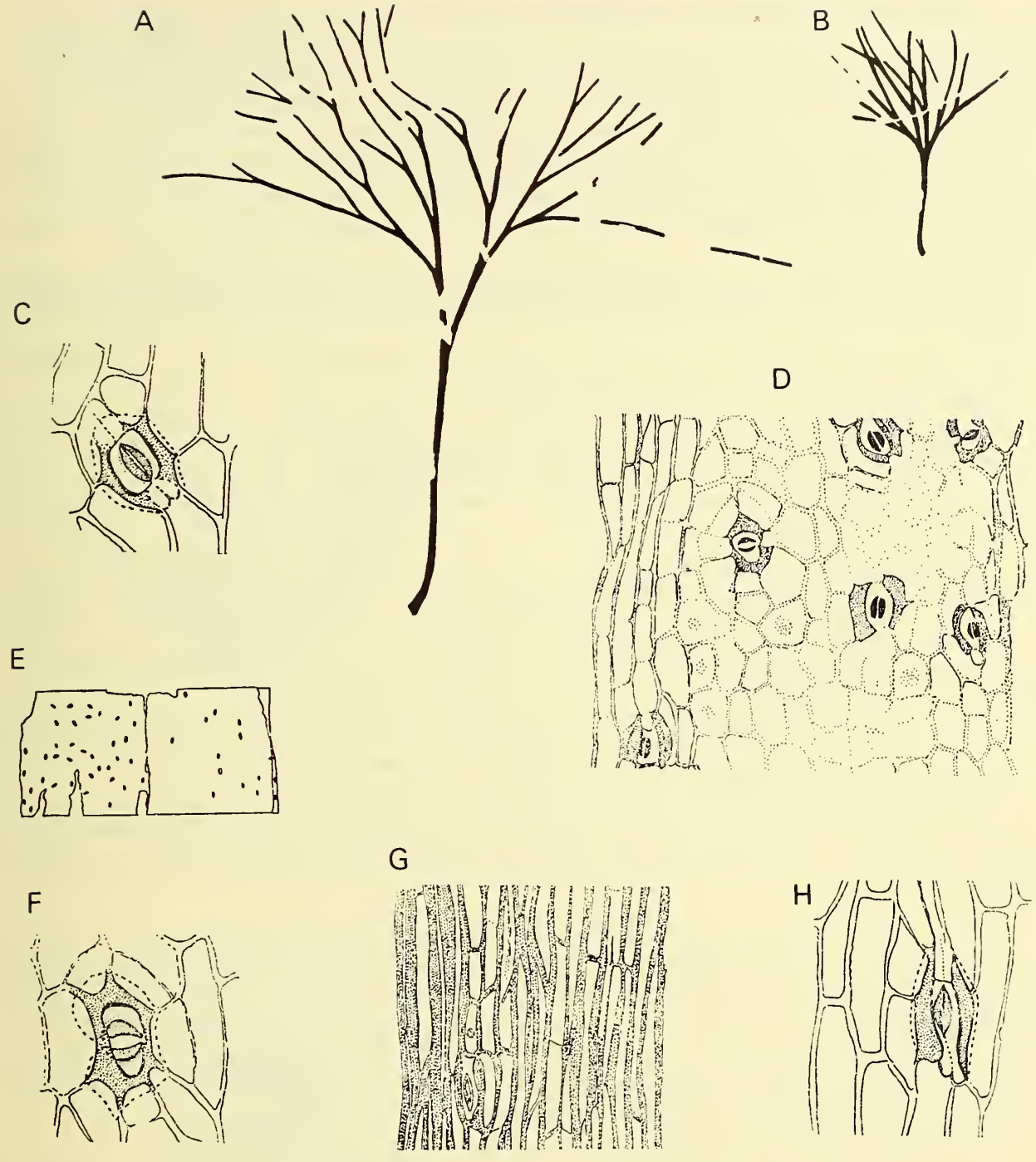


Fig. 12. **Baiera furcata** (L. & H.)

A, V.6475, all lobe apices are missing, actual size. B, small leaf (some lobes damaged), actual size, York Museum. C, F, typical stomata (lower epidermis), magnification ×400. D, lower epidermis, magnification ×200. E, distribution and orientation of stomata in approximately 1 mm² of lamina, lower side left, upper side right, magnification ×20. G, upper epidermis, magnification ×200. H, stoma orientated longitudinally (lower epidermis), magnification ×400. All cuticles figured are from the leaf shown in A. All figures are from Harris (1945, text-figs. 1, 2).

may show several good leaves, and apart from these leaves there is nothing that could be Ginkgoalean. At one extreme are typical *gracilis*-like leaves with just four or six segments which may be 3 mm broad and up to 70 mm long. At the other extreme is a leaf which might be called '*furcata*' or '*scalbiensis*' which in the whole lamina is almost semicircular, of just over 30 mm radius and divided into about 32 ultimate segments. The segments are nearly 1·5 mm wide below and fork at all levels, the width being reduced to 0·75 mm. Most leaves are intermediate and may have 8–12 lobes about 2 mm wide and 40 or 50 mm long, but segments 1–3 mm wide occur in a single leaf. The level at which forking occurs also varies in one leaf.

This fine series gives convincing evidence that the various forms of leaf belong to one species.

It may be well to mention the differences which at an earlier stage of our work we supposed distinguished *B. gracilis*, *B. furcata* and *B. scalbiensis*.

'*B. gracilis*' had 4–6 primary segments, which may fork again, and the segments ranged from 1·5 mm–6 mm broad. They tapered to an acute or obtuse point.

'*B. furcata*' in the strict sense often had more than 12 narrow segments, 0·5–2·0 mm wide, and these tapered gradually to their apices.

'*B. scalbiensis*' had perhaps 30 segments, 1–2 mm wide, which tapered in their apical parts only. The species was based on very few specimens, perhaps only the three described by Black.

'*B. gracilis*' had a rather varied cuticle, the subsidiary cells overhanging the guard cells considerably or only slightly and their inner edges forming a nearly continuous rim, or separate papillae, or intermediate. The veins are most often distinct.

'*B. furcata*' had very indistinct veins, many narrow cells, and often the subsidiary cells were rather elongated, and papillae did not normally occur even on subsidiary cells.

B. scalbiensis (information from Black's figures and his original preparations): most of the preparations show one distinct median strip suggesting a vein, one shows two and others show additional narrow non-stomatal strips of unknown nature. The subsidiary cells often have papillae.

We did however note an Upper Deltaic leaf of '*gracilis*' form but with a cuticle looking just like '*scalbiensis*' in detail and there is a Lower Deltaic leaf from Haiburn Wyke, the Type locality of *B. furcata*, with a cuticle which agrees very well with *B. scalbiensis*. An Upper Deltaic specimen, in the Leeds University Geology Department, of the '*scalbiensis*' form has about 18 segments all about 1·1 mm broad. All may have four veins and round resin bodies and their apices are rounded. There are associated fragments 1·8 mm broad with six veins. The specimen is localized as 'In washout N. of Scalby'.

We conclude that this whole complex of leaves is best treated as a single species. The variation in segment width, though obvious, may not be important, as broad and narrow forms are found together. Perhaps they were borne on different parts of a single tree. The variation in cuticle is possibly more important since there are distinct differences in average form in different localities. Though we cannot be so certain of their determination it looks as though some of the populations of cuticle fragments obtained by maceration of rock in bulk may be of intermediate type as though we had smooth cuticles and non-papillate stomata

predominating in the Lower Deltaic and gradually giving place to slightly papillate leaves with distinctly papillate stomata.

In a particular leaf with narrow segments it was noticed that the stomatal density on the upper side increased towards the apex and that a segment with only 1–2 stomata per mm^2 below had 21 per mm^2 near the apex, nearly as many as the under side (27–37 per mm^2). The epidermal cells are much shorter near the segment apex.

When we refer to the 'veins' we usually mean the dark strands often visible in the lamina of broad segments but more rarely visible in narrow segments. Occasionally surface ridges are seen corresponding to these veins. Cuticle preparations of the segments often show, at least on the lower side, alternate strips of numerous stomata and others (the veins) with very few. However, there are sometimes narrow non-stomatal strips in addition to those we call

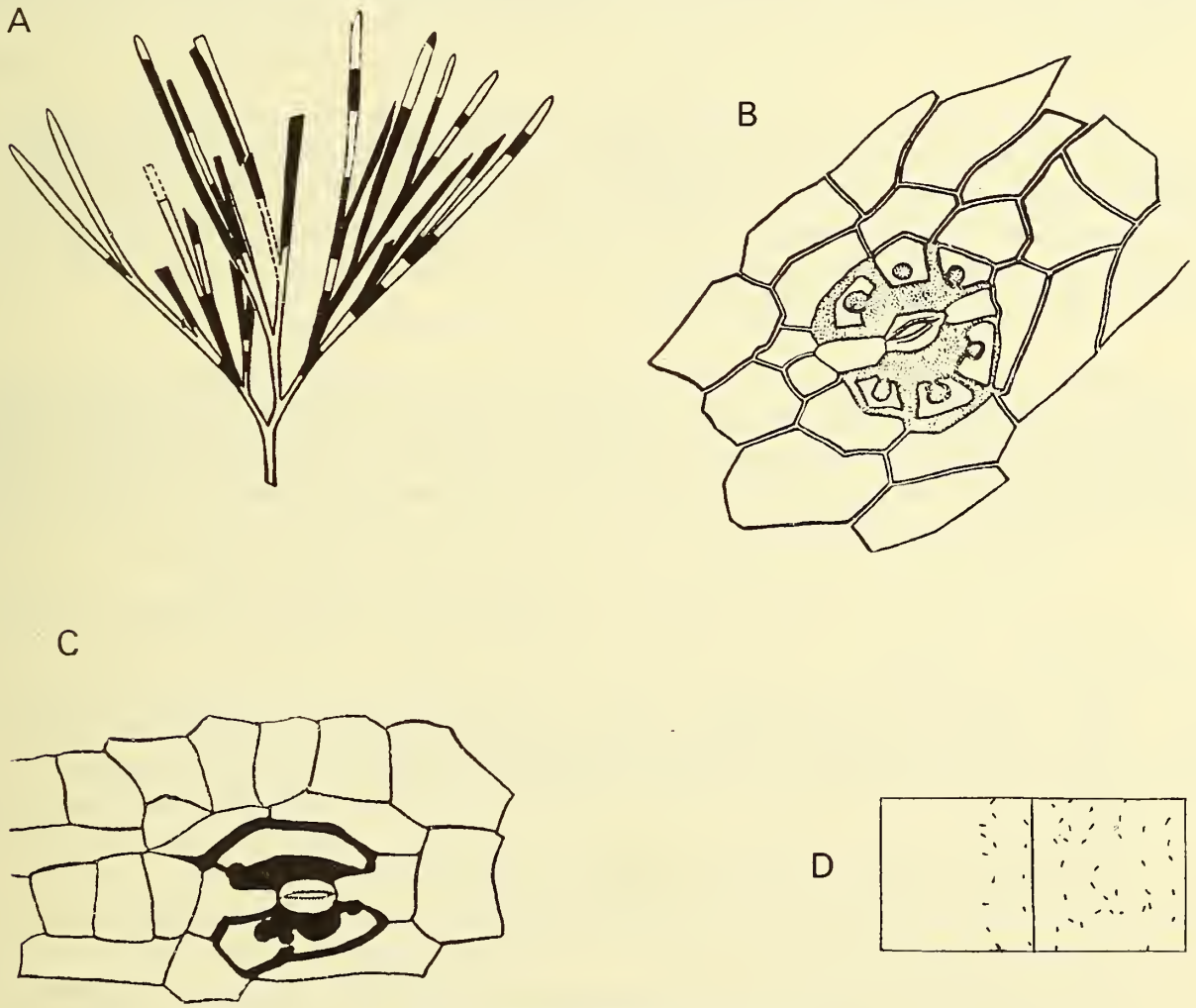


Fig. 13. **Baiera furcata** (L. & H.)

A, Black's holotype of *B. scalbiensis*, actual size, Sedgwick Museum No. 311. B, C, stomata showing fusion of papillae with the thick inner walls of subsidiary cells, magnification ×400. We suppose that the longitudinal axis of the leaf runs diagonally in B and horizontally in C. D, diagram showing distribution and orientation of stomata in 2 mm^2 of cuticle. The upper cuticle is on the left, the lower on the right. B–D are from slide 60 of the holotype. Figs. A–C are from Black (1929, text-figs. 13, 14). Specimens in Sedgwick Museum, Cambridge.

veins. The veins in this species converge on the pointed apex of a segment where they merge; they do not end separately in little teeth. We have not seen the veins in section and have no means of knowing how far a dark strand constitutes a unit vascular bundle.

We often had difficulty in deciding which cuticle in this amphistomatic leaf is the lower. In general the side with a rather thinner cuticle, rather more stomata and better developed papillae and more obvious veins is the one we call the lower, but these differences may be slight. It may be noted that Black interpreted the cuticles of his *B. gracilis* and *B. scalbiensis* the other way from what we do.

A very few trichomes were noted on the undersides of the Lower Deltaic leaves but none on the upper. A single trichome was however seen on the upper side of one Middle Deltaic fragment. The development of trichomes and of papillae on ordinary cells seems independent.

Comparison

1. *Yorkshire. B. furcata* as treated here is easily distinguished from other Yorkshire species. *Ginkgo* sp. cf. *sibirica* though of fairly similar form has an altogether thinner cuticle. *G. longifolius* differs in having very few stomata on the upper side. We are unsure of the identity of the leaf called *B. gracilis* forma *münsteriana* and figured by Seward (1900, pl. 9, fig. 3) as we failed to prepare its cuticle. *Sphenobaiera pecten*, a leaf of very different gross form, differs also in its longitudinally orientated stomata.

2. *Other regions.* Broadening the scope of *B. furcata* by including *B. gracilis* increases the difficulty of comparison with specimens from other regions. A list of very similar looking leaves from the Mesozoic is given below but for most of these we have no microscopic information. Should their cuticles prove to fall within the range of *B. furcata* we feel they should be identified with it even if their origin is distant and their age rather different.

The following leaves from other regions are of similar form to *Baiera furcata*; see also list under *Ginkgo* sp. cf. *sibirica*.

1885 *Salisburia* (*Ginkgo*) *lepida* (Heer) Dawson, p. 8, pl. 2, fig. 2. (Lower Cretaceous; Rocky Mts., Canada)
1905 *Ginkgo lepida* Heer: Krasser, p. 605, pl. 2, fig. 7. (Jurassic; Manchuria)
1922 *Baiera gracilis* Bunbury: Yabe, p. 24, pl. 4, fig. 14 (Mesozoic; Korea), fig. 15 (Mesozoic; China)
1925 *Baiera gracilis* Bunbury: Kawasaki, p. 46, pl. 24, figs. 73, 74; pl. 25, figs. 75–77; pl. 26, figs. 78, 79. (Lias; Korea)
1925 *Baiera lindleyana* Schimper: Kawasaki, pl. 43, fig. 117 B. (Jurassic; Korea)
1928 *Baiera* cf. *asadai* Yabe & Oishi, pl. 21, fig. 4. (Jurassic; China)
1928 cf. *Baiera lindleyana* Schimper: Yabe & Oishi, pl. 21, fig. 3. (Leaf fragment. Jurassic; China)
1933 *Baiera lindleyana* Schimper: Sze, p. 29, pl. 7, fig. 8. (Mesozoic; China)
1933 *Baiera gracilis* Bunbury: Sze, p. 16, pl. 7, figs. 1, 2, ?3, ?4. (Lias; China)
1936 *Baiera* cf. *lindleyana* Schimper: P'An, p. 30, pl. 11, fig. 7; pl. 13, fig. 12. (Good leaves. Lias-Rhaetic; China)
1939 *Baiera gracilis* Bunbury: Kawasaki, pl. 13, fig. 53. (Lias; Korea)
1940 *Baiera gracilis* Bunbury: Oishi, p. 371. (Discussion of certain Asiatic specimens)
1948 *Baiera viannai* Teixeira, pl. 10, figs. 1–3. (Mesozoic; Portugal)
1956 *Baiera gracilis* Bunbury: Boureau, Furon & Roset, p. 233, pl. 6, fig. 30. (*furcata* form. Jurassic; Iran)
1958 *Baiera gracilis* Bunbury: Vachrameev, p. 112, pl. 26, fig. 6; pl. 27, fig. 4. (Upper Jurassic; Siberia)
1964 *Baiera* cf. *gracilis* Bunbury: Benda, text-fig. 23. (Jurassic; Afghanistan)

Occurrence

Hand specimens

Upper Deltaic	Scalby Wyke Drifted Plant Bed
	Burniston Wyke, Black's Channel C
	,, ,, ,, ,, D
	,, ,, 6 ft above footprint bed
	Scarborough, Nathorst's 'New Layer'
Lower Deltaic	Haiburn Wyke (Type locality)

Many specimens are poorly localized and are labelled 'Inferior Oolite, nr. Scarborough'. They may be from some of the above localities.

Cuticle fragments agreeing with *Baiera furcata* were obtained from macerates of shales from many localities, but there is no evidence that the whole leaf agrees:

Upper Deltaic	6 localities
Middle Deltaic Gristhorpe Series	1 locality
Middle Deltaic Sycarham Series	2 localities
Lower Deltaic	12 localities

Genus SPHENOBAIERA Florin 1936: 105

Emended Diagnosis. Leaves shed separately. Leaf as a whole more or less broadly wedge-shaped, without a distant petiole. Lamina forking one or more times to give segments. Veins forking repeatedly, where several in a segment, nearly parallel and ending separately in distal margin.

Cuticle (where known) well developed (of Ginkgoalean type) with stomata scattered or in broad bands, stomata sunken and surrounded by several haplocheilic subsidiary cells.

Type Species. *Baiera spectabilis* Nathorst (1906, p. 4).

Discussion. The above diagnosis differs from that given by Florin mainly by the addition of the words 'Leaves shed separately'. Other differences are trivial. Florin's diagnosis is repeated by Lundblad (1959), who also gives a literal translation into English.

The twenty-two species listed by Florin under *Sphenobaiera* fall into two groups. Most have separate leaves like *S. spectabilis* or else are rather poorly known being represented by a few fragments which do look as though they belonged to separate leaves. All those, we leave alone. But there are three species in which the leaves are borne in bundles on caducous dwarf shoots which look very like those of *Czekanowskia*. No separate leaves of these three with clearly abscissed bases have been described, but there are separate fragments. We consider this character taxonomically important in the large group of leaves placed in the Ginkgoales and Czekanowskiales since it divides them sharply into two and is indeed the only character that does so. This character though recognized from the first has been given but slight value, specific at best, indeed it is often omitted from mention in specific comparison. We on the other hand suspect that it may mark the division between the Ginkgoales and Czekanowskiales but this must await evidence.

It is remarkable that this character has been neglected in a group where characters are urgently needed. Possibly some felt that too many of the species concerned are represented by unsatisfactory fragments which could not be placed, but if so they did not discuss it. Harris (1935) overlooked its possible value. This neglect is the more surprising because we all recognize the taxonomic value of caducous short shoots in the Conifers; it does not indeed distinguish any family but it is the accepted distinction of *Pinus* from all other Abietineae. Meanwhile by restricting *Sphenobaiera* we make a new genus necessary and it is described below under *Sphenarion* gen. nov. Its type species is *Baiera paucipartita* Nathorst whose details have been furnished by Lundblad (1959). *Baiera amalloidea* Harris proves to be a synonym so we have two independent accounts of it.

It is unfortunate that there are no other distinguishing characters at present, the cuticles are of the same general type. We might hope for a difference at the leaf base—two veins or just one—but the evidence is very scanty. Most leaves are too thick and black to show the veins at the base. The only leaf sectioned in the basal part is that of *S. horniana* Florin (1936, p. 148). Florin here found a single vein and he restores the leaf (p. 150, text-fig. 10) as an isolated leaf with a simple basal vein. But his material, as he makes plain, is fragmentary and it is uncertain whether the specimens are fragments of separate leaves or of leaves in bundles. Krassilov (1970) considers this leaf as possibly Czekanowskialean.

Until we know otherwise we may continue to suppose that *Sphenobaiera* as restricted is a natural genus and closely related to *Ginkgo*. But there is some reason to doubt this for a pollen-bearing cone called *Bernettia phialophora* was attributed to *Sphenobaiera spectabilis* by Harris (1935). *B. phialophora* differs considerably from the male cone of *Sphenobaiera furcata* (see Kräusel 1943) and still more from that of *G. biloba* though the difference is not so extreme as to exclude all possibility of relationship.

Sphenobaiera furcata Heer stands apart from other species as there are a number of stems preserved still with their leaves in position (Leuthardt 1903, Kr¨usel 1943). The stems are long ones, unlike the minute dwarf shoots of *Sphenarion*.

Sphenobaiera pecten Harris

Text-fig. 14

1945 *Sphenobaiera pecten* Harris, p. 219, text-figs. 3, 4. (Figures and description reproduced here)

Emended Diagnosis. Leaf wedge-shaped, up to 100 mm long, up to 70 mm wide. Leaf base 2·5 mm wide, becoming slightly narrower above base before widening to up to 4·5 mm wide below first dichotomy. Leaf divided into segments by up to six successive dichotomies at intervals of about 10 mm (5–20 mm), first dichotomy occurring within 20 mm from base. Angle of dichotomies about 10° (5°–20°); segments up to 3·0 mm wide below, becoming narrower above, ultimate segments about 0·7 mm wide tapering to 0·5 mm towards acute apex. Veins not seen in leaf base, obscurely shown as 2–4 broad ridges in lower segments, reduced to single median strand in ultimate segments. Leaf substance thick, resin bodies about 100μ long usually present but not abundant.

Cuticle tough, fairly thick, about 3μ, on both sides, amphistomatic. Upper and lower cuticles alike except in stomata, upper side having stomatal density of about 10 (5–15) per

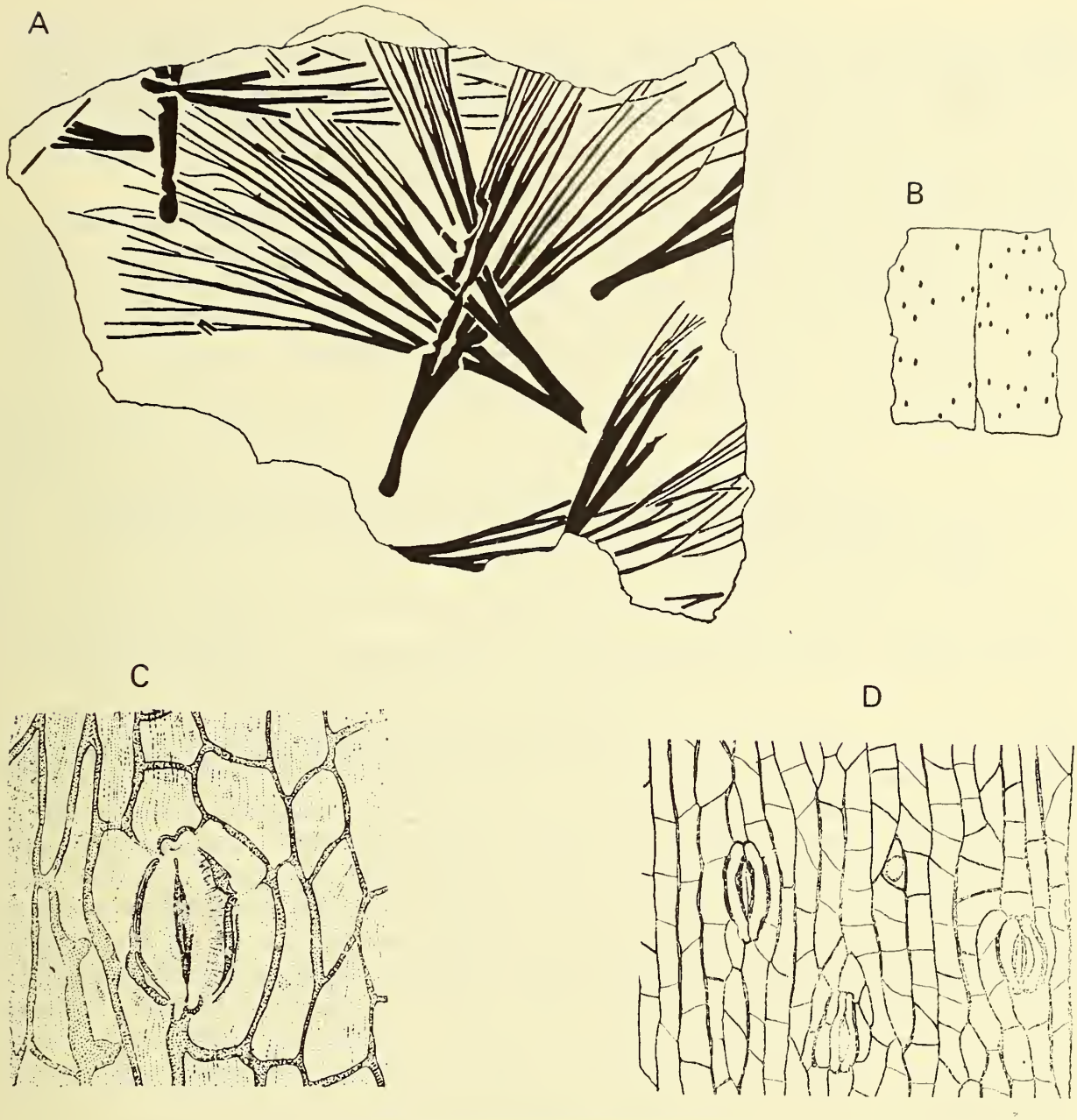


Fig. 14. **Sphenobaiera pecten** Harris

A, slab showing several leaves, all on one bedding plane, actual size. The large leaf pointing upwards and to the left is the holotype. B, both cuticles of an ultimate segment (with small amount missing along outer edges) showing distribution and orientation of stomata, magnification ×20, slide A. The upper part is to the left, the lower to the right. C, stoma and epidermal cells, magnification ×500, slide A. D, lower cuticle showing three stomata and a trichome base, magnification ×200, slide B. All figures from Harris (1945, text-figs. 3, 4). Specimens in Yorkshire Museum.

mm^2 and lower side having stomatal density of about 24 (17–33) per mm^2. Veins indistinctly marked in lower parts of leaf by areas with few or no stomata on either surface, not distinguishable in upper parts of leaf. Epidermal cells forming longitudinal rows, cells isodiametric to

moderately elongated, with longitudinal walls often more conspicuous than end walls. Cell outlines broad, more or less conspicuous, straight, rarely interrupted. Surface walls almost flat, rarely with an ill-defined longitudinal central thickening or low papilla. Surface sculpture often granular or forming fine longitudinal striations. Thin walled sack-like trichomes usually present on both sides of cuticle; trichome bases like ordinary epidermal cells or smaller and thicker, bearing large oval rim surrounding thin area on surface.

Stomata scattered, but few or none in vein strips where these are apparent. Stomata not arranged in well marked longitudinal rows; usually orientated longitudinally (except in area just below dichotomy), the occasional one orientated obliquely. Guard cells only slightly sunken, rather large, surface walls strongly thickened round aperture and along outer lateral edge, intermediate parts and poles thin. Surface of guard cells often showing fine striations radiating from aperture. Subsidiary cells irregular, lateral ones often elongated, terminal ones often apparently absent. Surface of subsidiary cells thinner than ordinary epidermal cell surfaces except for cutinized ridge developed alongside near guard cells but separated from guard cell thickening by thinner strip. Subsidiary cells only occasionally overhanging guard cells, and then only to a small extent, never forming a papilla. Encircling cells absent.

Holotype. Specimen figured by Harris (1945, text-figs. 3, 4); see also Text-fig. 14. Herries Colln., Yorkshire Museum.

Discussion. Three blocks from Haiburn Wyke and two from Ingleby Arncliffe Beacon Scar have provided additional hand specimens. Though damaged, they match the previously described specimens in form and cuticle, though no resin bodies were seen in the lamina.

The width and prominence of cell outlines on the cuticles vary, and sculpturing on the surface of ordinary epidermal cells is not always evident. Trichomes or trichome bases were found on most, but not all, of the specimens. Cuticle fragments from macerated shales from Rosedale Knottside and Snilesworth, River Rye Bed 4 are rather doubtfully included because the leaf segments are narrow and the cuticles match *Sphenobaiera pecten* very closely, although there is a tendency for both the upper and lower cuticles to be conspicuously papillate.

Comparison. *Sphenobaiera pecten* differs from all other Yorkshire species of *Sphenobaiera* in having more numerous and much more slender leaf segments. The other species of the genus, however, have fundamentally similar cuticles and resin. *Sphenobaiera ophioglossum* is similar to *S. pecten* in having exposed guard cells and thin surfaced subsidiary cells, but its leaf segments are never so narrow as those of *S. pecten*. Fragments of *S. pecten* may be confused with narrow fragments of *Baiera furcata* and with *Czekanowskia* species or *Solenites* but they are easily distinguished by their cuticles and in particular by the stomata.

We do not know of any foreign specimens whose leaf shape agrees closely with *Sphenobaiera pecten*.

Occurrence

Hand specimens

Lower Deltaic	Haiburn Wyke
	Beast Cliff, Petard Point (*Sphenobaiera pecten* Bed)
	Ingleby Arncliffe Beacon Scar
	Gnipe Howe, Hawsker

The holotype is unlocalized.

Cuticles

Fragments agreeing with *Sphenobaiera pecten* are widespread in the Lower Deltaic and are known from the following additional localities

Middle Deltaic	2 localities
Lower Deltaic	18 localities

Cuticle fragments from four other Lower Deltaic localities which were formerly determined as *S. pecten*, are now identified as *Sphenobaiera ophioglossum*.

Sphenobaiera longifolia (Pomel) Florin

Pl. 1, figs. 3–5; Text-fig. 15

Selected references; see also p. 47.

1849 *Dicropteris longifolia* Pomel, p. 339. (Name and description only. Corallian; France)
1873 *Jeanpaulia longifolia* (Pomel) Saporta, p. 464, pl. 67, fig. 1. (Pomel's specimen figured)
1913 *Baiera longifolia* (Pomel) Thomas, p. 243, pl. 25, figs. 3, 4; text-fig. 5. (Yorkshire leaves and cuticles)
1919 *Baiera longifolia* (Pomel): Seward, p. 40, text-fig. 647 C, D. (Thomas's figures of cuticle repeated)
1936 *Sphenobaiera longifolia* (Pomel) Florin, p. 108. (Name, see p. 44 below)
1956 *Sphenobaiera longifolia* (Pomel): Samylina, p. 538, pl. 3, figs. 3–5. (Leaves and cuticles. Lower Cretaceous; Aldan R., Siberia)
1959 *Sphenobaiera longifolia* (Pomel): Lundblad, p. 30. (Discussion of Samylina's (1956) specimens; attribution of species to Heer, see p. 44 below)
1963 *Sphenobaiera longifolia* (Pomel): Samylina, p. 101, pl. 27, figs. 1–3; pl. 28, figs. 1–4. (Leaves and cuticles. Lower Cretaceous; Aldan R., Siberia. As 1956 but fuller)
1967 *Sphenobaiera longifolia* (Pomel): Samylina, p. 144, pl. 5, figs. 8–11. (Leaves and cuticles. Jurassic; Kolyma R.)

Emended Diagnosis. Typical leaf wedge-shaped, at least 130 mm long, divided by as many as four successive dichotomies into narrow ultimate segments. Basal, undivided, portion of leaf at least 30 mm long and up to 70 mm long, 1–2 mm wide at base, gradually widening upwards to 10 mm wide below first dichotomy. Basal angle of leaf 30°–55°, angle of branching about 15° (5°–25°). Dichotomies at intervals of 15 mm–50 mm. Leaf segments 1·0 mm–6·0 mm wide, contracted at their base, gradually increasing in width upwards, at maximum width immediately below dichotomy. Veins obscure (in Yorkshire specimens), probably four in a segment 1·5 mm wide, but about seven in a segment 2·5 mm wide, or eleven in a segment 4·5 mm wide (Saporta 1873). Upper part of segment tapering for about 30 mm towards rounded apex. Resin bodies usually absent, if present, oval, 110–170μ wide × 135–255μ long.

Cuticle usually amphistomatic, thick, upper about 6μ thick, lower about 3μ thick. Upper cuticle not showing distinct vein strips, showing isodiametric, polygonal cell outlines. Longitudinal rows of rectangular, isodiametric or elongated cells often present near margin and sometimes a few such longitudinal rows, 1–2 cells wide, occurring on surface of segment. Outline of hypodermal cells frequently visible under rows of rectangular cells, occasionally elsewhere. Hypodermal cells somewhat elongated, rectangular, with their longitudinal axis parallel to that of leaf. Epidermal cell outlines conspicuous, prominent, usually broad, straight, occasionally interrupted, sometimes with oblique extension on to surface wall, sometimes outlines more prominent at cell angles. Surface walls either unthickened or with low papilla or with irregular patches of thickening or thickened all over except for median, radiating thin

area. Trichomes absent. Stomata irregularly orientated, generally distributed, not usually in longitudinal files. Density about 7 (0–17) per mm^2. Stomata similar to those on lower cuticle.

Lower cuticle divided into longitudinal strips with stomata and strips without stomata, but non-stomatal strips probably not always representing veins. Stomatal strips of extremely varied width (180μ–610μ), even in one part of leaf, with isodiametric, polygonal cells sometimes arranged in longitudinal rows. Non-stomatal strips 60μ–550μ wide, of longitudinal rows of isodiametric, rectangular or polygonal cells. Anticlinal walls conspicuous, prominent, straight, less broad than on upper cuticle. Surface walls with granular sculpture, or concentric or radial striations. Ordinary cells usually bearing small solid or large, thick-walled, hollow papilla up to 27μ high. Sometimes adjacent papillae fusing with each other, forming short, longitudinal ridges. Trichomes absent.

Stomata irregularly orientated, scattered in areas bounded by non-stomatal strips, at density of about 30 (15–50) per mm^2. Guard cells sunken in irregularly shaped stomatal pit surrounded by six subsidiary cells. Guard cell surface walls thin except for narrow transverse ridge at either end of aperture. Guard cell poles extending beneath subsidiary cells. Surface walls of subsidiary cells often more heavily cutinized than those of ordinary cells, with ridge of thickening next to guard cells, and usually bearing solid papilla projecting towards stomatal pit. Subsidiary cells occasionally lacking papilla but thickened over whole surface wall except for median thin area. Encircling cells absent.

Discussion. Lundblad (1959, p. 30) considered Heer rather than Pomel as the author of the specific name *longifolia* because Pomel (1849) gave no figure. However Pomel was working with the rules of 1849 which required a latin diagnosis for a new species but not a figure and this was for a fossil plant as for a Recent one. Our present rules require a figure for a fossil, but they do not work backwards to illegitimize what was formerly legitimate. It might be held that Pomel's diagnosis is inadequate but in that case Saporta's (1873) diagnosis of Pomel's specimen with a figure would be the origin of the name. Saporta's figure was what Heer (1876) used when he identified his Siberian material.

Apart from this matter of authorship, there is the question of identity. Pomel's specimen preserved in limestone has presumably no cuticle, nor as we understand have those of Heer. Thomas (1913) was the first to describe the cuticle, from Yorkshire, and then Samylina (1956, 1963), from Siberia. These cuticles and those described here seem to agree moderately well but not perfectly and we mention it below.

The present material, comprising nineteen specimens from Marske, twenty-three from Roseberry Topping, two fragments from Hasty Bank and six leaves from Whitby, is identified with confidence with the Yorkshire material described by Thomas (1913, see Text-fig. 15 A). They are identified with the Type material figured by Saporta (1873) from the French Corallian, with which Thomas identified his specimens, because the leaves look similar in form. There is however no information about the cuticle of the Type material and we recognize that when this is described the Yorkshire leaves may prove distinct.

None of the Yorkshire specimens is complete and the range of variation in leaf shape and size is not known, the longest specimen, shown in Text-fig. 15 A (after Thomas, 1913, pl. 25, fig. 3) is 130 mm long. The leaf segments vary from 1–10 mm wide, the average being 2·5 mm while segments 1·5 mm wide are the most common. Because all the specimens are broken, it is

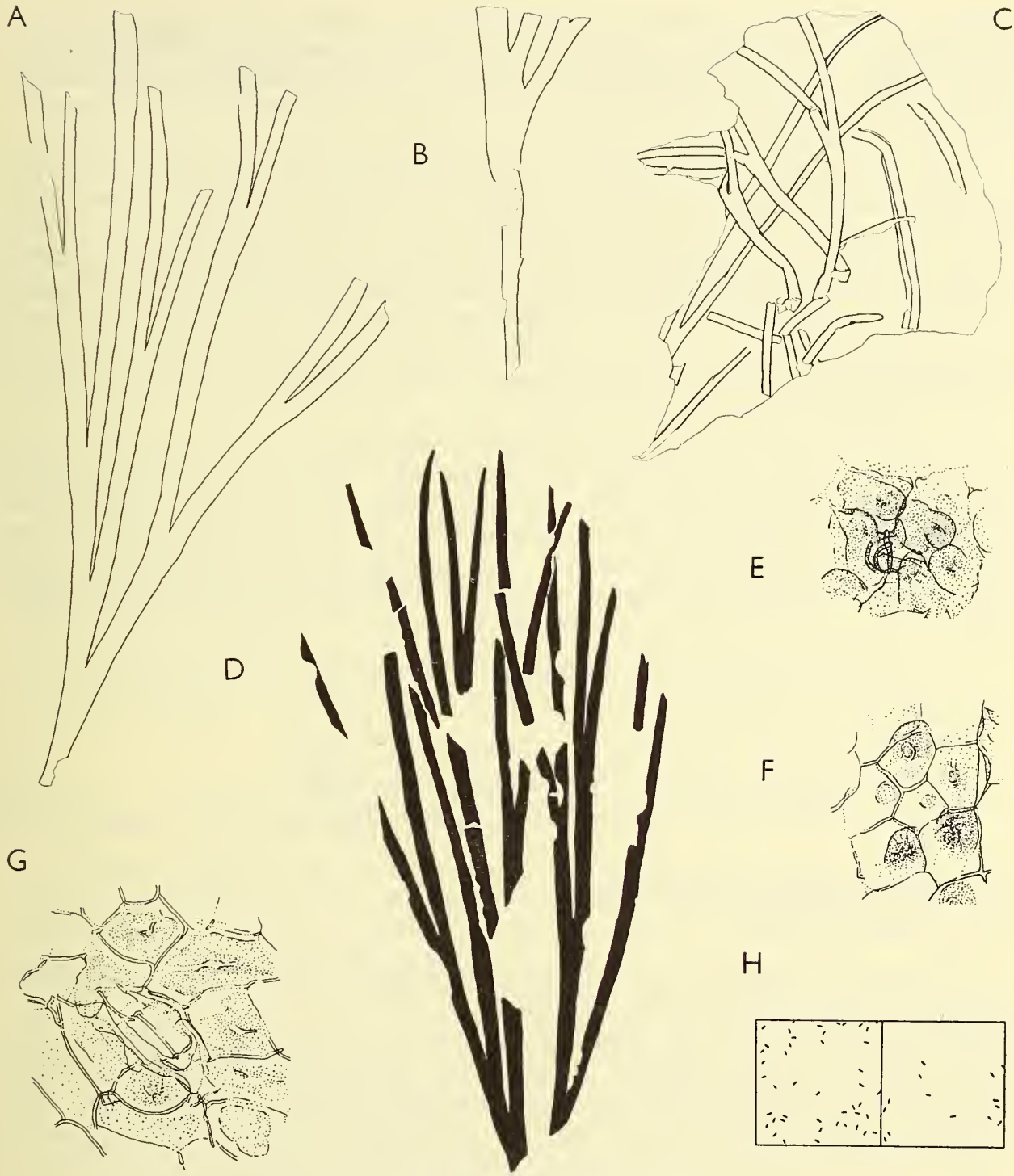


Fig. 15. **Sphenobiaera longifolia** (Pomel)

A, leaf, V.12856, actual size, redrawn. Figured by Thomas (1913, pl. 25, fig. 3). B, leaf base, actual size, redrawn. Figured by Thomas (1913, pl. 25, fig. 4). C, leaves on uppermost layer of block from Roseberry Topping, actual size. D, leaf in Saunders Collection, Middlesbrough Museum, actual size. E, typical stoma from lower cuticle, seen from inner side, magnification ×400, V.56641. The thickening on left side of guard cell aperture has been displaced at one end. F, lower cuticle, magnification ×400, V.56642, showing common kinds of cell surface thickening. G, unusually exposed stoma from upper cuticle, magnification ×400, V.56643. H, stomatal distribution and orientation in 2 mm² of cuticle, the lower on left side, the upper on right, V.56644.

All except Fig. C are from Marske Quarry.

uncertain how much the variation in segment width is a reflection of varying leaf size and dissection rather than of distance from the leaf base. Leaf segments may be undivided for a length of up to 50 mm. They dichotomize at angles not usually exceeding 30°, and an angle of 70° shown by the two leaves from Roseberry Topping is exceptional. Other dichotomies in these specimens are normal.

Saporta's pl. 67, fig. 1*a* of differently preserved material, shows well marked veins in the leaf segments but none of the Yorkshire leaves shows conspicuous veins. Thomas (1913) mentions that three or four parallel ridges can sometimes be seen on the Marske leaves, and a fragment just over 1 mm wide from Roseberry Topping shows four, narrow, longitudinal striations. Cuticle preparations from the lower leaf surface show one or more longitudinal non-stomatal strips, but it is uncertain whether these mark veins as they occasionally vanish when traced longitudinally, they are of variable width and may be separated from one another by only a single row of stomata. Resin bodies have only been found in four leaves from Roseberry Topping and two leaves from Whitby.

There is usually a small proportion of papillate ordinary cells on the upper leaf surface, but papillate cells may be absent altogether and are rarely as frequent as in Thomas's text-fig. 5*a* of the upper cuticle (Thomas 1913, p. 244). The ordinary cells of the lower epidermis show types of surface thickening similar to the cells of the upper epidermis, but papillae are very much more frequent. Four leaves from Roseberry Topping and one from Marske are unusual in having very few papillate ordinary cells on the lower side, and Thomas's text-fig. 5*b* shows fewer, smaller, papillae than are normally present.

The following characters vary independently of one another:

Frequency of resin bodies

Prominence of cell outlines on upper cuticle

Width of stomatal and non-stomatal strips on lower cuticle

Papillae on lower cuticle separate and well defined, or broader and running into one another

Stomatal density on upper cuticle

Length of papillae

The variation in the first four of these characters shows a similar range at each locality (though for some we have but little material).

However, in addition to this general variability we have local populations which to some extent differ from other populations in the last two above-mentioned characters. Stomatal density on the upper epidermis is lower in the leaves from Roseberry Topping (0–5 per mm^2) than in those from Marske (6–17 per mm^2). The leaves from Whitby are unlike those from other localities in having a greater frequency of long papillae (25μ–37μ) with broad bases, which present a very confusing appearance. Also there are four leaves from Roseberry Topping which have resin bodies, very prominent cell outlines on the upper cuticle (see Pl. 1, fig. 4), and very few ordinary cell papillae and wide stomatal strips on the lower cuticle—a combination of characters not found elsewhere. Other leaves with a more typical combination of characters also occur at Roseberry Topping.

COMPARISON. *Sphenobaiera longifolia* has fewer, much wider leaf segments than *Sphenobaiera pecten*, and more numerous, often narrower segments than both *Sphenobaiera ophioglossum* and *Sphenobaiera gyron*. The cuticle of *S. longifolia* differs from those of *S. pecten* and *S. ophioglossum* in having guard cells obscured by subsidiary cell papillae and possessing subsidiary cells with a more thickly cutinized surface, and from that of *S. gyron* in lacking distinctly marked veins on the lower cuticle.

Among Yorkshire species isolated leaf segments of *Baiera furcata*, *Ginkgo longifolius* and *Ginkgo* sp. cf. *sibirica* may be of similar width to those of *S. longifolia*, but they can be easily distinguished by their cuticle. *B. furcata* differs from *S. longifolia* in having distinctly marked veins on the upper cuticle, and, among other differences, both *G. longifolius* and *Ginkgo* sp. cf. *sibirica* have much thinner cuticles than *S. longifolia*.

The cuticle of *Eretmophyllum pubescens* is rather similar to that of *S. longifolia* in that the ordinary and subsidiary cells of the lower cuticle frequently bear a conspicuous papilla. However, unlike *S. longifolia*, it has less frequent papillate cells on the upper cuticle.

The leaves figured by Samylina (1956, 1963) from Siberia are not quite like any of the Yorkshire leaves but the differences are small. In the Siberian cuticles papillae are more strongly developed on the upper side than in most of ours. In the strips along the veins on the under side the cells are longer than in the Yorkshire ones, making the veins better marked. On the under side some only of the epidermal cells have conspicuous papillae whereas nearly all the cells of ours have such papillae, though the papillae vary in other details and some of these differences distinguish Yorkshire leaves from different localities a few kilometres apart.

OCCURRENCE. Hand specimens were obtained from the following localities:

Lower Deltaic	Marske Quarry (location of specimens figured by Thomas 1913)
	Hasty Bank
	Whitby Long Bight Plant Bed
	'Whitby Cliffs, lower sandstone and shale', old Museum specimen
	Roseberry Topping

A cuticle fragment of Lower Deltaic age matching the cuticles of typical *Sphenobaiera longifolia* was obtained by bulk maceration of rock from Jump Down Bight, Whitby. Additional specimens from Marske collected by Percy Kendall of Leeds in 1909 and by Halle in 1910 are in the Rijksmuseum, Stockholm.

We list below many foreign specimens which look like *S. longifolia* but are of unknown structure; some such leaves have already been shown to be of different structure, e.g. *Baiera* cf. *longifolia* (Johansson 1922), now *G. marginatus* (Lundblad 1959). We do not in general include slightly narrower leaves (*S. czekanowskiana* and *S. angustifolia*), nor slightly broader ones (*S. ikorfatensis*), but the differences are ill-marked. Some of these have fairly similar cuticles (see Cahoon 1960, Samylina 1963). Prinada (1962) does unite *S. czekanowskiana* and *S. longifolia* but keeps *S. angustifolia* separate.

1876 *Baiera longifolia* (Pomel): Heer, pp. 52–56, pl. 7, figs. 2, 3; pl. 8, fig. 9; pl. 9, figs. 1–11; pl. 10, figs. 6, 7; pl. 13, fig. 16. (Upper Jurassic; Siberia)
1880 *Baiera longifolia* (Pomel): Heer, pl. 2, fig. 5; pl. 4, fig. 1 A. (Jurassic; Siberia)
1926 *Baiera longifolia* (Pomel): Kawasaki, pl. 9, figs. 26, 27; pl. 10, fig. 28; pl. 11, figs. 29, 30. (Mesozoic; Korea)
1931 *Baiera longifolia* (Pomel): Turutanova-Ketova, p. 330, pl. 4, fig. 9. (Mesozoic; Issik-Kul)

1933 *Baiera longifolia* (Pomel) var. *czekanowskiana* Heer: Kryshtofovich, pl. 1, fig. 2. (Mesozoic; Siberia)
1936 *Baiera longifolia* (Pomel): Turutanova-Ketova, p. 100, pl. 1, fig. 10. (Jurassic; Kazakhstan)
1938 *Sphenobaiera longifolia* (Pomel): Prinada, p. 48, pl. 4, fig. 5. (Jurassic; Kolyma R.)
1956 *Sphenobaiera longifolia* (Pomel): Samylina, p. 536, pl. 3, figs. 3–5. (Jurassic; Siberia)
1958 *Sphenobaiera longifolia* (Pomel): Vachrameev, p. 114, pl. 27, fig. 5; pl. 28, fig. 1. (Upper Jurassic; Siberia)
1959 *Sphenobaiera longifolia* (Pomel): Vasylevskaya, p. 63, pl. 4, fig. 4. (Mesozoic; Siberia)
1962 *Sphenobaiera czekanowskiana* Heer: Prinada, pl. 11, figs. 1, 3; pl. 12, figs. 3, 4, 7; text-figs. 46, 47 A, B, V. (*S. longifolia* of many authors included in this species. Jurassic; E. Siberia)
1963 *Sphenobaiera longifolia* (Pomel): Vasylevskaya & Pavlov, pl. 14, fig. 3; pl. 16, fig. 1; pl. 27, fig. 1. (Cretaceous; USSR)
1965 *Sphenobaiera longifolia* (Pomel): Lebedev, pl. 29, fig. 4. (Upper Jurassic; Zeia R.)
1966 *Sphenobaiera longifolia* (Pomel) forma *lata* Vasylevskaya, pl. 4, fig. 3. (Cretaceous Zhigansk)
1967 *Sphenobaiera longifolia* (Pomel): Samylina, p. 44, pl. 5, figs. 8–11. (Mesozoic; Kolyma R.)
1967 *Sphenobaiera longifolia* (Pomel) forma *lata* Vachrameev: Samylina, p. 145, pl. 6, fig. 4*a*. (Mesozoic; Kolyma R.)
1967 *Sphenobaiera* cf. *longifolia* (Pomel): Barnard, text-fig. 5 F. (Lias; N. Iran)

Sphenobaiera ophioglossum sp. nov.

Pl. 2; Text-figs. 16, 17

DIAGNOSIS. Leaf typically bilobed, narrowly wedge-shaped, up to at least 185 mm long. Basal undivided portion of leaf about 70 mm long, 2·5 mm wide at extreme base, becoming slightly narrower above before gradually widening to about 9 mm (6 mm–12 mm) wide just below dichotomy. Lobes diverging at angle of about 12° (8°–30°), up to at least 110 mm long, about 5 mm (2 mm–8 mm) wide, more or less strap-shaped but slightly tapering above for about 20 mm to truncate apex. Veins fairly conspicuous, parallel, about 11 (5–19) per lobe, at a concentration of about 20 (15–29) per mm^2, slightly converging towards apex. Leaf substance thin, resin bodies usually absent.

Cuticle amphistomatic, 1μ–4μ thick, upper usually slightly thicker than lower. Upper cuticle with veins inconspicuously marked by strips, about 250μ (120μ–370μ) wide, lacking stomata, and showing longitudinal rows of elongated, quadrate or polygonal cells, but shorter, more oval cells often bearing trichome or trichome base occasionally occurring. Cuticle often wrinkled by compression along one or both edges of vein strips. Intervenal strips about 300μ (170μ–690μ) wide, showing elongated, quadrate or polygonal cells, often wider and slightly shorter than those in vein strips, occasionally isodiametric towards centre of strip. Cells usually arranged in longitudinal rows. Anticlinal walls fairly conspicuous, of medium width, straight, occasionally interrupted, sometimes appearing double, as two strips of thickening separated by a very narrow thinner strip. Longitudinal walls often slightly wider, more conspicuous than cross walls. Surface walls with faint granular structure or longitudinal striations. Cell surfaces sometimes with area of median thickening or longitudinal strip of thickening or occasionally bearing a small solid or hollow papilla. Cells bearing papilla more frequent between veins than in intervenal strips, but sometimes absent. Trichomes or trichome bases usually occurring in vein strips, at frequency of about 5 per mm (0–10 per mm), rarely present in intervenal strips. Trichomes sac-like; when compressed vertically appearing round or oval, when compressed laterally free part often wider than base. Longest trichome seen 38μ long, widest 37μ wide, with walls up to 5μ thick. Trichomes usually occurring in central

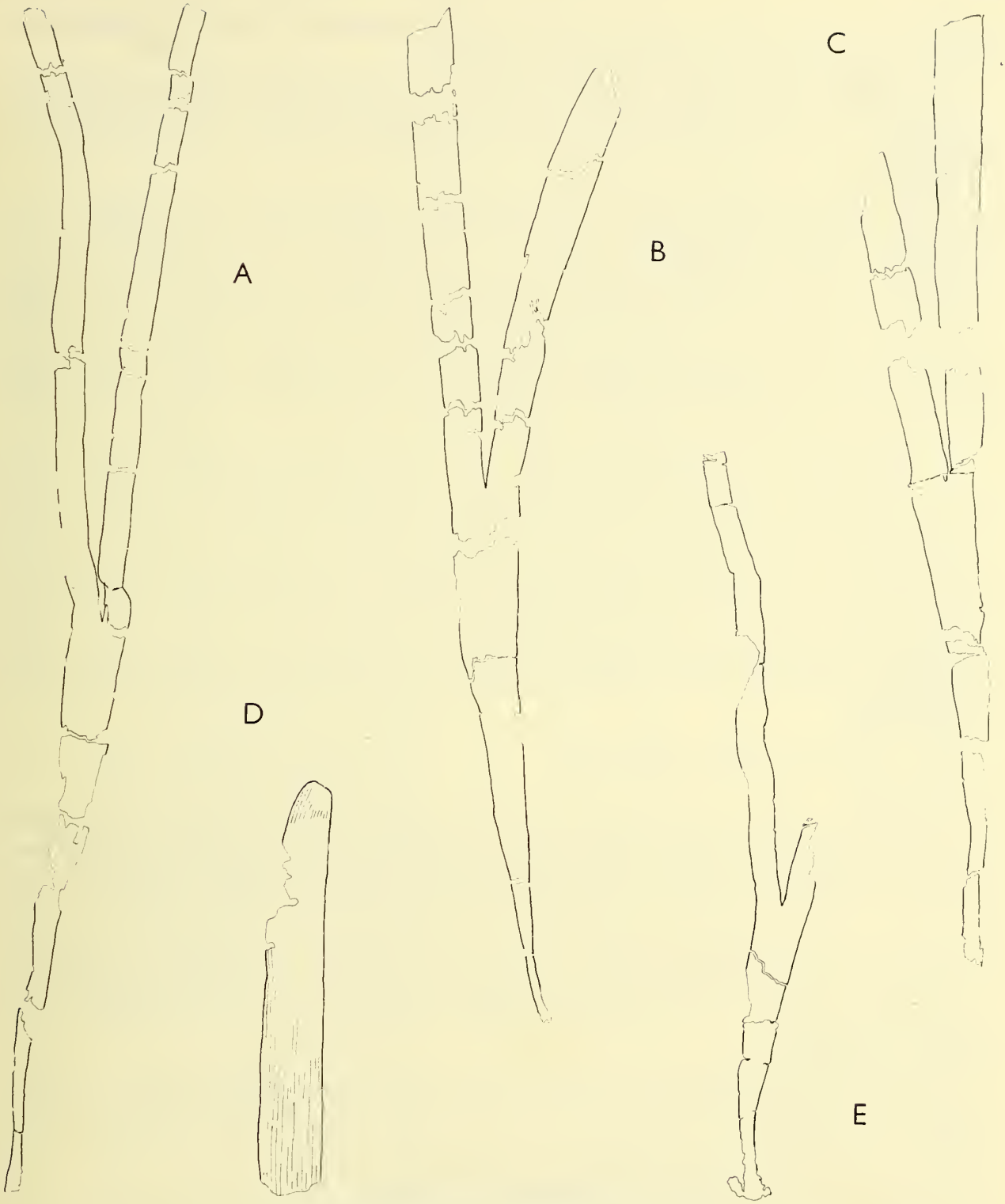


Fig. 16. **Sphenobaiera ophioglossum** sp. nov.

A–C, E, leaves, actual size, V.56466. D, lobe apex, showing veins, magnification ×2. The basal fragment in A may not belong with the upper parts. For discussion of the form of the leaf base in E, see p. 50. All specimens, including the holotype, are on one fallen block from Whitestone Point, Hawsker.

position on surface of short oval cells, or sometimes occurring at one end of an elongated cell. Trichome bases shown as oval pale area on cell surface.

Stomatal density on upper cuticle of lobes about 11 (3–26) per mm^2, below leaf dichotomy about 5 (1–8) per mm^2. Stomata scattered in intervenal strips, usually orientated longitudinally, of similar structure to those of lower cuticle but often with guard cells and subsidiary cells more elongated.

Lower cuticle with veins more or less conspicuously marked by strips, about 80μ (40μ–170μ) wide, of several rows of elongated, quadrate or polygonal cells. Intervenal strips, about 430μ (250μ–780μ) wide, of isodiametric polygonal or rectangular cells, occasionally arranged in longitudinal rows. Anticlinal walls fairly conspicuously marked, of medium width, straight, sometimes interrupted, occasionally more prominent at cell angles. Surface walls usually showing granular sculpture or fine longitudinal striations and frequently with median thickening or one or two longitudinal strips of thickening, cells bearing low solid or hollow papilla or several small patches of thickening often present on leaf lobes, occurring less frequently below dichotomy. Trichomes present in small numbers both on and between veins.

Stomatal density on lower cuticle about 25 (11–42) per mm^2 throughout length of leaf. Stomata scattered between vein strips, irregularly orientated. Guard cells hardly sunken. Guard cell poles usually exposed, surface walls unthickened except next to aperture. Guard cell surfaces sometimes with faint striations radiating from aperture, outer anticlinal wall rather broad. Two to four lateral subsidiary cells present, one or both polar subsidiary cells sometimes absent. Surface walls of lateral subsidiary cells more thinly cutinized than ordinary epidermal cells. Anticlinal walls at right angles to axis of stoma very weakly outlined, walls adjacent to guard cells and to ordinary epidermal cells often fairly broad. Encircling cells rarely present.

HOLOTYPE. V.56466. Text-fig. 16.

DISCUSSION. The material comprises eighteen leaves (sixteen of them on one large block) from Whitestone Point, two specimens from Saltwick, one specimen from Gnipe Howe, numerous fragments on a block from South of Black Nab, three leaves from High Whitby, and one leaf on a block labelled 'Lower Sandstone, Whitby'. A few specimens show the extreme leaf base, and two show a lobe apex, but none of the specimens is complete and the leaf length is unknown. The longest specimen is 18·5 mm long, although the leaf fragments shown in Text-fig. 16 A may have constituted a rather longer specimen, we are not certain that the basal fragment belongs with the upper parts, since there are several other leaves nearby on the same plane of the block.

All the leaves from High Whitby, the old Museum specimen labelled 'Lower Sandstone, Whitby' and one leaf from Whitestone Point which is on a separate block from the others are divided into more than two lobes. The most divided leaf of those shown in Text-fig. 17 B has at least five lobes and is wider just below the first dichotomy (14 mm wide) and has broader lobes (up to 11 mm wide) than typical *Sphenobaiera ophioglossum*. However, the cuticles of this more divided specimen match closely those of the typical bilobed leaves. The variation in the concentration of the veins throughout the material is no greater than is normal within a species. The leaf illustrated in Text-fig. 16 E appears to have short, ill-defined lateral processes

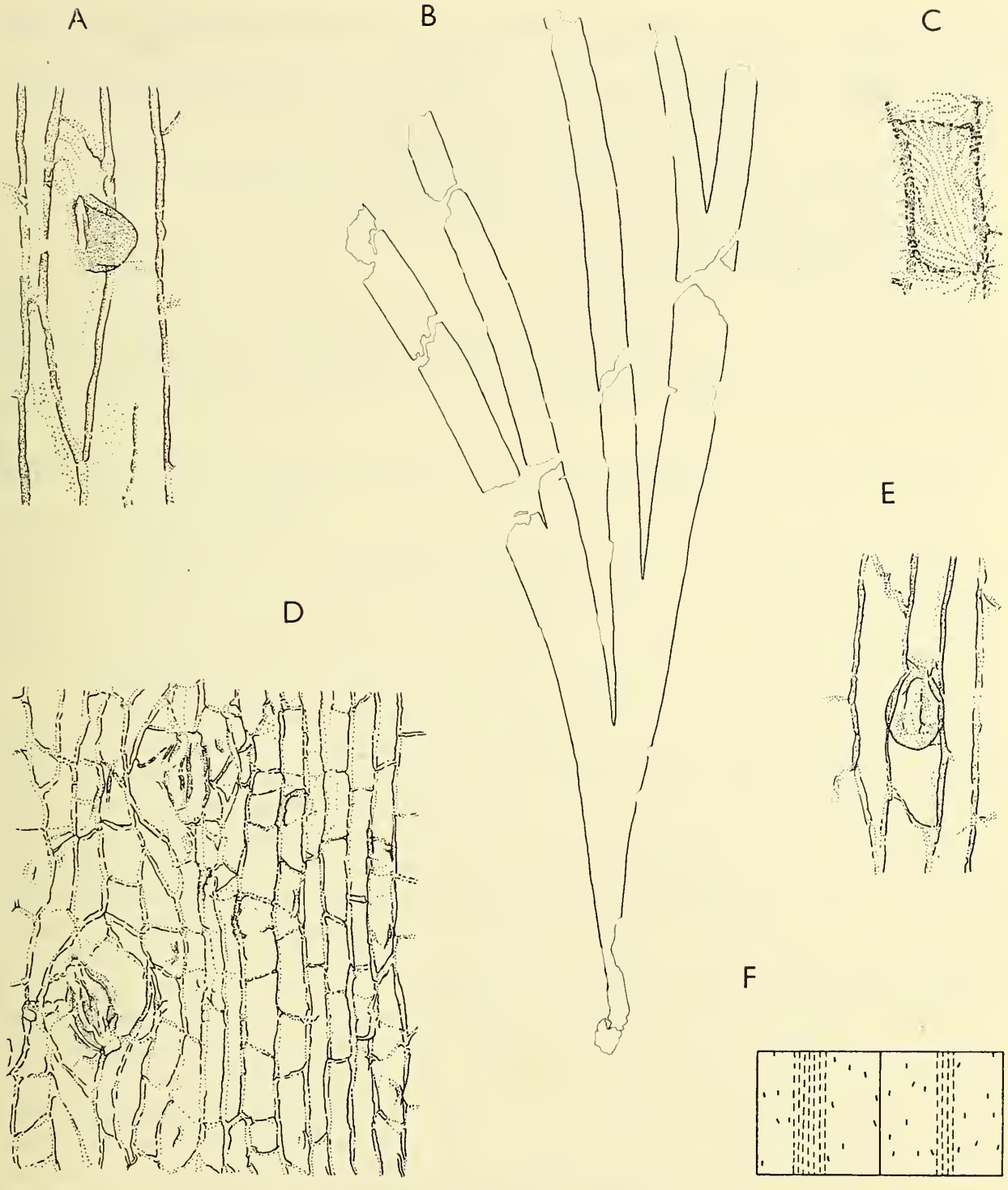


Fig. 17. **Sphenobaiera ophioglossum** sp. nov.

A, laterally compressed trichome on a vein strip of the upper cuticle, magnification ×400, V.56647. B, leaf on fallen block from High Whitby, Hawsker, actual size, V.56475. C, upper cuticle showing surface striations, magnification ×400, V.56648. D, upper cuticle, with part of a vein strip on right, magnification ×200, Cell surface sculpture is not drawn. V.56648. E, vertically compressed trichome on a vein strip of upper cuticle, magnification ×400, V.56647. F, two mm^2 of cuticle showing distribution and orientation of stomata, and vein strips. The upper cuticle is on the right, the lower on the left, V.56649. A, E and F are from Whitestone Point. Hawsker. C, D are from Saltwick.

attached to each side of the extreme base of the leaf. Their nature is unknown and no similar structures have been found on any of the other leaves.

The cuticles show a normal amount of variation between leaves in the following characters which vary more or less independently of one another:

(1) Frequency of papillate ordinary epidermal cells on both surfaces of the leaf.
(2) Width of vein strips on upper and lower cuticles
(3) Width of intervenal strips on upper and lower cuticles
(4) Stomatal density on upper cuticle
(5) Stomatal density on lower cuticle

In a single leaf, two of these characters may also often vary throughout a single leaf, with the distance from the leaf base. The frequency of papillate ordinary epidermal cells on both leaf surfaces often increases distally. Stomatal density on the upper surface is always higher, sometimes more than twice as high on the leaf lobes than it is on the basal, undivided portion of the leaf.

Trichomes or trichome bases are usually present on the vein strips of the upper surface, on only one specimen, from High Whitby, could we find no trichomes on either side.

COMPARISON. *Sphenobaiera ophioglossum* has fewer much wider segments than *Sphenobaiera pecten*, and has fewer segments, diverging at a smaller angle than *Sphenobaiera longifolia*. It differs from the bilobed leaves of *Sphenobaiera gyron* in having a much longer, more tapering base and in having lobes diverging at a smaller angle. Fragments of *S. ophioglossum* can be of similar width to fragments of both *S. longifolia* and *S. gyron* but they differ greatly in cuticle structure, in the leaf substances being thinner and in usually showing crowded veins.

Isolated cuticle fragments of *S. pecten* from the leaf base or just below a dichotomy can be as wide as the extreme base or narrowest lobes of *S. ophioglossum*. The cuticles of these two species are alike in having exposed stomata with very thinly cutinized subsidiary cell surface walls and in having similar trichomes and trichome bases on the upper side. However, the upper and lower cuticles of *S. ophioglossum* differ from each other, whereas in *S. pecten* the two sides are alike in everything but stomatal density. The cuticle of *S. ophioglossum* also differs from that of *S. pecten* in both the upper and lower sides usually showing vein strips, and in the lower cuticle often being more papillate. Cuticle fragments from the extreme leaf base, where the vein strips are occasionally very ill-defined, or from the margin of *S. ophioglossum* may be difficult to distinguish from *S. pecten*.

There are some foreign leaves which resemble *S. ophioglossum* in shape but their cuticles prove that they are merely forms of another species. For instance a leaf of *Sphenobaiera spectabilis* from East Greenland (Harris 1935, text-fig. 12 A) looks just like a leaf of *S. ophioglossum* with four lobes but its cuticle is different and normal for *S. spectabilis*. A leaf of *Sphenobaiera ikorfatensis* (Seward 1926) from the Cretaceous of West Greenland is similar both in form and in cuticle, but the cuticle is incompletely known. *S. ikorfatensis* f. *papillata* from the Lower Cretaceous of Dakota (Cahoon 1960) is very similar but is perhaps a slightly smaller leaf with a shorter base and the epidermal cells are more strongly papillose.

Some of the less divided leaves listed under *Sphenobaiera longifolia*, in particular those figured by Heer (1876), look like the four-lobed ones of *S. ophioglossum*. Its once forked, bilobed form is more unusual. *Baiera cretosa* Schenk (1865, pl. 1, fig. 7) also looks similar.

Leaves from Spitzbergen resembling *S. ophioglossum* in its once-forked form are figured by Sveshnikova & Budantsev (1969) as *Sphenobaiera pulchella* and in its twice forked form as *S. ikorfatensis*. Their cuticles also seem similar except that no stomata are shown on the upper side. Vasilevskaya (1966) has also figured a once forked leaf as *S. pulchella* but its lower cuticle is strongly papillose and its smooth upper cuticle has only a few stomata.

Occurrence. *Sphenobaiera ophioglossum* is confined to the Lower Deltaic and all the hand specimens come from the cliffs just S.E. of Whitby. Apart from an old Museum specimen labelled 'Lower Sandstone, Whitby' which might be a fallen block like ours, they are all in fallen blocks picked up on the beach under the high and unclimbable shale cliff. These blocks were collected on several different occasions over a good many years. They are from Saltwick Bay at about 54° 28′ 59″ N (and from Saltwick also cuticle fragments were obtained by maceration of fixed shale by the waterfall). Other blocks were collected near 54° 28′ 30″ N; near 54° 28′ 50″ N; near 54° 28′ 55″ N and 54° 28′ 0″ N. It is possible that some of these represent parts of a single extensive plant bed but the apparent differences between local leaf populations are perhaps against this. Cuticle fragments were obtained by bulk maceration of shales at three further Lower Deltaic localities: Ravenscar, below Ravenhall Hotel; Bilsdale, Tripsdale Kay Nest; and Farndale Millbank 1.

Sphenobaiera gyron sp. nov.

Text-fig. 18

?1907 *Ginkgo digitata* (Brongn.): Stopes, p. 379, pl. 27, figs. 3–5; text-figs. A, B. (Middle Jurassic; Scotland. Form and cuticle)

Diagnosis. Leaf oblanceolate or deeply bilobed, up to 70 mm long. Lobes about 10 mm (5 mm–15 mm) wide, gradually tapering below to about 1·5 mm wide, up to 15 mm long. Veins inconspicuous, parallel, about 12 (9–19) per cm, branching proximally, slightly converging near obtuse apex. Resin bodies usually absent.

Cuticle fairly thick, upper about 3μ (1μ–5μ) thick, lower slightly thinner. Cuticle usually with stomata present on both upper and lower sides. Upper cuticle with veins obscurely marked by a few rows of slightly elongated, more or less rectangular cells. Cells between veins isodiametric, polygonal, not arranged in longitudinal rows. Some cells divided by transverse bars. Anticlinal walls fairly conspicuous, more or less straight, broad, sometimes interrupted. Surface walls of cells flat, often with single median thickening or very occasionally with indistinct papilla. Trichomes absent. Scattered stomata usually present, about 2 (0–8) per mm^2 in central region of lamina, more numerous in lamina base (up to 15 per mm^2 near petiole). Stomata irregularly orientated, of similar structure to those of lower cuticle. Encircling cells frequently present.

Lower cuticle with vein strips about 270μ (153μ–520μ) wide, distinctly marked by longitudinal rows of elongated (up to 3 times as long as wide), more or less rectangular cells. Strips between veins about 590μ (380μ–810μ) wide with isodiametric, polygonal cells, not arranged in longitudinal rows. Anticlinal walls of cells in vein strips distinct, of even width. Anticlinal walls of cells in intervenal strips often inconspicuous, broad, more or less straight, sometimes interrupted. Surface walls of ordinary cells unthickened, or often with median thickening, or sometimes with low papilla. Transverse bars frequently present. Trichomes absent.

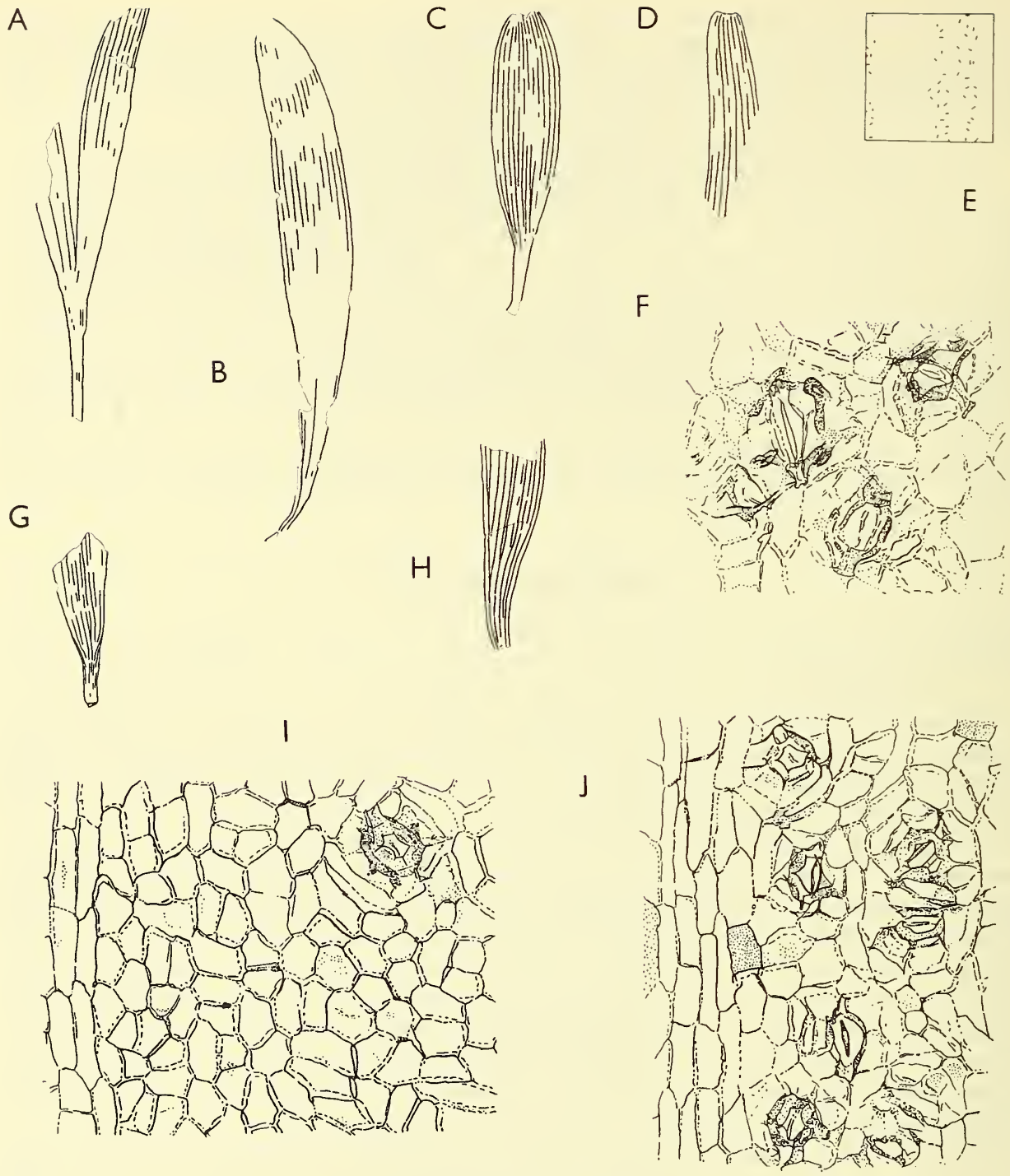


Fig. 18. **Sphenobaiera gyron** sp. nov.

A, bilobed leaf, actual size, V.56458. B, C, entire leaves, actual size, B, V.56459, C, V.56460. D, apex of leaf or lobe showing slightly converging veins, actual size, V.56461. E, diagram of stomatal distribution and orientation on 1 mm^2 of lower cuticle, magnification $\times$20, V.56651. F, lower cuticle showing a few hollow papillae around stomata, magnification $\times$200, V.56650. G, leaf base showing complete petiole, actual size, V.56462. H, base of lamina showing vein dichotomies, actual size, V.56463. I, upper cuticle with part of a vein on left, magnification $\times$200, V.56651. J, lower cuticle with vein on left, from same leaf as E and I, magnification $\times$200. All from Hasty Bank.

Stomata scattered, rarely arranged in short longitudinal rows, between veins, at density of about 51 (28–77) per mm^2. Stomata irregularly orientated. Stomatal pit elongated, or oval, or irregular in shape. Guard cells slightly sunken, but more or less exposed, with their poles sometimes visible. Surface thickening of subsidiary cells variable. Subsidiary cell thickening usually forming rim around pit, occasionally only lateral subsidiary cells with band of thickening next to stomatal pit. Usually some subsidiary cells with small solid papilla projecting towards pit or very occasionally with hollow papilla. Encircling cells frequently present.

The name is from the heraldic word 'gyron' for a narrow triangle. It comes through the French and Italian from a Germanic word for a narrow triangle, as in the English 'gore' of a dress.

Holotype. V.56458. Text-fig. 18 a.

Comparison. The bilobed form of *Sphenobaiera gyron* is rather similar in shape to the bilobed leaves of *Ginkgo huttoni*, but differs from it in usually being larger, in having much less numerous veins, in the smoother cuticle, in lacking trichomes and in usually lacking resin bodies. *G. digitata* of Stopes (1907) looks very similar.

The entire leaf of *S. gyron* shown in Text-fig. 18 b is similar in form to both *Eretmophyllum pubescens* and *E. whitbiense* but is on average narrower, with more numerous veins, and more frequent stomata on the upper cuticle than is typical for either of these *Eretmophyllum* species. The lower cuticle of *S. gyron* differs from that of *E. pubescens* in having far fewer papillate ordinary epidermal cells, and from both *E. pubescens* and *E. whitbiense* in having narrower intervenal strips and stomata with their guard cells more exposed.

Somewhat similar leaves are seen in *Sphenobaiera boeggildiana* (Harris) from the Rhaetic of East Greenland in which the leaf normally has a single shallow division. One difference is in the cell outlines which in *S. boeggildiana* are distinctly jagged instead of being straight.

Some of the varied series of leaves described under the generic name *Ginkgodium* look rather like *S. gyron* but others are very different. The original description (Yokoyama 1889) gave leaves with strong marginal veins from which all other veins arise and these are parallel and unbranched. Between veins are interstitial strands of unknown nature. Oishi (1940) described further Japanese specimens in which some vein dichotomies do occur, near their marginal origin. He mentioned no interstitial strands. Thomas (1911) figured similar leaves from the Middle Jurassic of the Ukraine, but one at least (p. 14, text-fig. 9) where marginal veins are less obvious, looks like *S. gyron*. Stanislavsky (1957) includes varied leaves, some twice lobed and remarkably like *G. huttoni*, while the simple or lobed ones recall *S. gyron*. The veins are not clear. *Ginkgodium nathorsti* (Menendez 1951) from Argentina is like a two-lobed *S. gyron* in its venation which shows the ordinary forking of a *Sphenobaiera*.

Other species are *G. gracile* from Japan (Tateiwa 1929, Oishi 1940), but with marginal veins and shaped like a *Pseudotorellia*. *G. zerauschanicum* (Prinada 1931) from Central Asia is a small simple or forked leaf with veins that fork at the leaf base. There is no marginal vein and the leaf looks like *S. gyron*. *G. amgaensis* (Samylina 1963) is a small wedge-shaped leaf with inconspicuous veins. For none of these species have we cuticles.

G. glandulosum (Samylina 1956, 1963) from the Lower Cretaceous of the Aldan River has well marked marginal veins from which the others arise, interstitial resin cavities and a normal

Ginkgoalean cuticle with strongly developed papillae. This is much the most fully known species.

Ginkgodium ? longifolium Lebedev (1965, p. 116, pl. 25, fig. 3; text-fig. 37) is a rather similar forked leaf. The veins all branch dichotomously.

Kimura & Sekido (1965) figure a remarkable Japanese leaf like a two-lobed *S. gyron* but rather larger, under the name *Ginkgodium nathorsti*. It is still on its stem which is covered with crowded scars of fallen leaves. This stem they properly call a dwarf shoot and it is very like one of the slow growing shoots of *Ginkgo biloba* which produces a fresh crop of leaves each year just behind its apex. Such a shoot is of indeterminate growth and may, if suitably stimulated, change into a long shoot with widely spaced leaves. It is very different from the caducous dwarf shoot of *Czekanowskia* or *Phoenicopsis* which is of strictly determinate growth. In *Pinus* the similar caducous dwarf shoot or spur has a stem apex which aborts before the foliage leaves elongate.

Baiera huangi (Sze 1949) from China is of similar shape but often much larger.

From various authors' treatment it is clear that some distinguish *Ginkgodium* mainly by the simple or lobed shape and others mainly by the marginal vein from which other veins all arise. The two characters vary independently and where there is conflict it is best to distinguish *Ginkgodium* by venation. Thomas (1911) compared his Ukraine specimens with Stopes's (1907) *Ginkgo digitata* from Brora in Scotland but though the outline of Stopes's simple or forked leaves is similar, their venation looks more like that of *Ginkgo huttoni* or *S. gyron*.

Occurrence and Discussion. *Sphenobaiera gyron* is only known from the Lower Deltaic of Hasty Bank where it is rather common in the lower, semi-marine part of the bed. Here the rock is very crumbly so that although many leaves may have been perfect when preserved, the specimens, as collected, nearly all show parts of leaves only and it is often impossible to be sure whether a fragment is of a simple or of a forked leaf. One complete simple leaf is 70 mm long and there is a fragment of a leaf 12 mm wide which may have come from a larger leaf. Certainly both simple and two-lobed leaves occur and simple leaves may be rather commoner. Leaves of different forms agree in other respects including their cuticles.

Genus ERETMOPHYLLUM Thomas 1913*b*, p. 259

Emended Diagnosis. Leaf shed individually by abscission at base of petiole. Leaf entire, oblanceolate to almost linear, symmetrical or slightly falcate. Apex wavy, or retuse, or obtuse or rounded, sometimes asymmetrical. Lamina gradually narrowing below and merging with petiole. Margins of lamina at leaf base often thickened. Veins distant, dichotomizing in basal portion of lamina, parallel above but converging slightly near apex. Veins ending separately at apical margin. Round to spindle-shaped resin bodies often present.

Cuticle amphistomatic or with stomata mostly confined to lower side. Epidermal cells quadrate or polygonal, with straight or wavy anticlinal walls, surface walls flat or with median thickening or papilla. Unicellular trichomes sometimes present. Lower cuticle showing stomatal and non-stomatal strips. Stomata in stomatal strips scattered or arranged in longitudinal rows. Guard cells thinly cutinized, surrounded by ring of regularly arranged haplocheilic subsidiary cells.

Type Species. *Eretmophyllum pubescens* Thomas (1913*b*).

Discussion. *Eretmophyllum* differs from *Ginkgo*, *Baiera* and *Sphenobaiera* in the lamina being entire and usually more linear. *Sphenobaiera gyron* is often similar in shape to *Eretmophyllum*. It is excluded from *Eretmophyllum* because it also includes leaves divided into two lobes.

Eretmophyllum differs from *Pseudotorellia* in its widely spaced veins and irregularly orientated stomata. It is usually a much larger leaf. Several members of the *Phoenicopsis* group described by Florin would be similar if found in isolation, but in good specimens of the *Phoenicopsis* group the leaves are always in a bundle, on a caducous short shoot, and separate leaves with cleanly abscissed bases are unknown. *Eretmophyllum* leaves, on the other hand, are always separate and often show their bases and though many were seen, not one is attached to a dwarf shoot.

Key to the Yorkshire species of *Eretmophyllum*

It is impossible to separate the species on macroscopic characters.

(1) In normal leaves, cells of upper epidermis papillate: *E. pubescens*

(2) Cells of upper epidermis not as a rule papillate: *E. whitbiense*

Other characters which often distinguish *E. pubescens* are distantly wavy anticlinal walls and a thinner cuticle than that of *E. whitbiense*. The papillae of *E. pubescens* can be seen with a binocular microscope in the unmacerated leaf.

Eretmophyllum pubescens Thomas

Pl. 3, fig. 4; Text-fig. 19

Yorkshire leaves:

1900 *Ctenis* sp. Seward, p. 231, text-figs. 42, 43. (Leaf and cuticle)
1900*a* *Ctenis* sp. Seward, p. 21, pl. 2, figs. 3 A, B, 4. (Leaf and cuticle, as Seward 1900)
1913*b* *Eretmophyllum pubescens* Thomas, p. 256, pl. 6. (Leaves and cuticles)
1917 *Ctenis* sp. Seward, p. 583, text-figs. 624, 625 A, B. (Leaf and cuticle, after Seward 1900)
1919 *Eretmophyllum pubescens* Thomas: Seward, p. 59, text-fig. 658 B-D. (Redrawn from Thomas 1913)
1936*a* *Eretmophyllum pubescens* Thomas: Florin, p. 41, pl. 5, fig. 14; pl. 6, figs. 1–4. (Cuticles only)

Emended Diagnosis. Leaf long, oblanceolate, sometimes asymmetrical or slightly falcate, up to at least 145 mm long. Lamina about 14 mm (6 to at least 35 mm) wide at widest part, slightly tapering above to round or retuse, often asymmetrical, apex. Petiole 2–3 mm wide at point of attachment, slightly contracted before widening gradually into lamina. Veins fairly conspicuous, branching near base and up to 60 mm from base of petiole, giving rise to about 12 (6 to at least 21) more or less parallel veins in middle portion of lamina. Veins concentrated at about 8 (5–12) per cm, slightly converging towards apex. Leaf substance rather thick, petiole and margins of lamina base often thicker. Round, oval or spindle-shaped resin bodies usually present, 115μ–1,085μ long, 100μ–400μ wide.

Upper cuticle about 4μ (2μ–6μ) thick, lower about 3μ (1μ–5μ) thick. Stomata mostly on lower side. Upper cuticle with isodiametric or slightly elongated polygonal cells. Cells usually not arranged in longitudinal rows, except occasionally for narrow strips of one or two rows of cells,

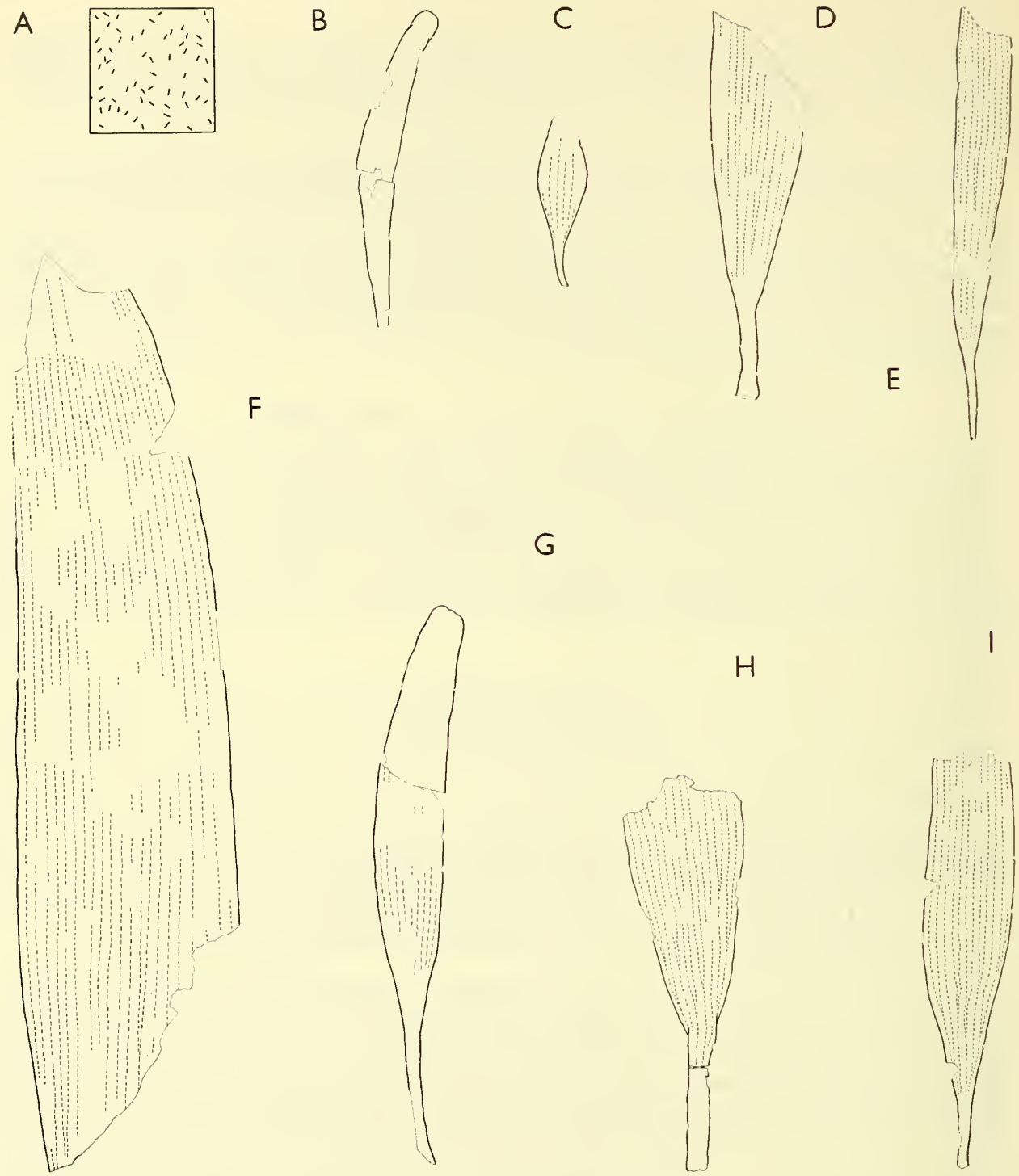


Fig. 19. **Eretmophyllum pubescens** Thomas

A, 1 mm² of lower cuticle showing stomatal distribution and orientation in an intervenal strip, magnification ×20, V.56652. B–I, leaves showing range of variation in size, shape and venation, actual size. B and G also show the leaf apex. H is drawn from four fragments.

All are from the Gristhorpe Bed.

corresponding in position with non-stomatal strips of lower cuticle. Cell outlines fairly conspicuous. Anticlinal walls of medium but irregular width, more or less prominent especially at cell angles. Walls often minutely sinuous, sometimes distantly wavy, sometimes interrupted. Anticlinal walls occasionally composed of two or more strips of thickening separated by narrow, thinner, strips. Surface walls showing faint granular sculpture, usually bearing median thickening or single, fairly small, low, solid papilla, or very occasionally hollow papilla. Trichomes usually absent. Stomata very rarely present in central part of lamina or near apex, but up to 2 per mm^2 in base of lamina. Stomata similar to those of lower side.

Lower cuticle often showing distinct stomatal strips about 1 mm (430μ–1,650μ) wide, between non-stomatal strips about 340μ (150μ–895μ) wide, possibly marking veins, but sometimes non-stomatal strips indistinguishable or discontinuous. Non-stomatal strips with more or less elongated, polygonal or quadrate cells, arranged in longitudinal rows of various lengths. Cells of stomatal strips more or less isodiametric, polygonal, mostly not arranged in longitudinal rows, but a few rows of slightly elongated cells occasionally occurring between rows of stomata. Cell outlines more or less conspicuous, often prominent, especially at cell angles, usually distantly wavy, especially in non-stomatal strips, occasionally minutely sinuous. Anticlinal walls of medium, often irregular, width, occasionally appearing as two strips of thickening separated by narrow thin strip. Surface wall with granular sculpture or occasionally with concentric striations. Some cells with surface wall unthickened, many with median thickening or bearing low, solid papilla, or upright hollow papilla sometimes with separate plug or thickening inside. Isolated short, conical, trichomes occasionally present.

Stomatal density in stomatal strips about 64 (41–107) per mm^2. Stomata irregularly orientated, mostly arranged in longitudinal rows of varying length, but some isolated. Guard cells more or less sunken, poles not exposed. Surface walls of guard cells with strip of thickening adjacent to lateral subsidiary cells, slightly thickened along aperture, often with transverse strip of thickening near poles, 4–7 subsidiary cells surrounding guard cells. Subsidiary cell surfaces usually thicker than ordinary cell surfaces, often very thick except for small, central, radiating, thinner area. Subsidiary cells frequently bearing small solid or hollow papilla pointing vertically or over stomatal pit. Surface walls of polar subsidiary cells sometimes thinner than those of lateral subsidiary cells, less often bearing papilla. Encircling cells absent.

HOLOTYPE. V.27704. Figured Thomas (1913*b*, pl. 6, fig. 2).

DISCUSSION. The present material consists of sixty-four leaves from the Gristhorpe Bed (mostly new specimens) and one from Cloughton Wyke. All agree in leaf shape and variation with Thomas's description of *Eretmophyllum pubescens* and most of the cuticles match closely those he described and those of Florin (1936*a*) but the cuticles of some of the old Museum specimens have not been examined.

None of the present specimens is complete and the length of a full sized leaf is unknown. The almost complete leaf (holotype) shown by Thomas (1913*b*, p.l 6, fig. 2) is about 70 mm long, but most of the present specimens were probably longer than this. The nearly complete leaf in Text-fig. 19c is exceptionally small. There is a wide range of variation in the width of the lamina at the widest part, 6 mm to at least 35 mm, but widths between 10 mm and 16 mm are most frequent. Resin bodies were found in the Cloughton specimen and in all but three

of the Gristhorpe Bed leaves. They occur slightly more frequently in the lamina base than above.

The upper cuticle shows considerable variation in the prominence and width of the anticlinal walls. Two specimens show transverse bars, resulting from the late division of cells already having some surface thickening. Most specimens show a high proportion of cells bearing a median thickening or papilla on their surface wall. In several specimens every cell of the upper surface bears a median thickening or papilla, in only a few specimens are papillae absent and even cells showing slight surface thickening very uncommon. The papillae are usually low and solid and vary in size, very small ones being quite frequent. Larger, hollow papillae rarely occur on the upper cuticle. Median thickenings sometimes project inwards, the outer surface being flat, and in a surface view of the cuticle they appear to be ordinary solid papillae.

Trichomes are uncommon on either surface of the present leaves. One was seen on the upper cuticles of two specimens, and on the lower cuticles of six specimens. In all cases but one, the trichomes on the lower cuticle occur on the non-stomatal strips. Florin (1936*a*) found no trichomes on the lower cuticle, but he described and figured scattered trichome bases on the upper cuticle.

The cell shape shown on both upper and lower cuticles varies slightly. Where the cell outlines are distantly wavy, the cells have the characteristic shapes seen in Pl. 3, fig. 4. Some such cells are usually present, more frequently on the lower side than on the upper, and most frequently in the non-stomatal strips of the lower side. Cells of both surfaces, near the leaf margin, are sometimes more elongated.

We are doubtful if all the non-stomatal strips shown on the lower cuticle mark veins, as although they are distinct in many specimens, in some they are discontinuous, and in eight specimens they are not distinguishable. Where they are distinct, however, they correspond in position to dark strands seen in the leaf after maceration in acid and before treatment with ammonia.

The cells and stomata shown by the lower cuticle in the lamina base are usually narrower and more elongated than those higher up the lamina. They are mostly arranged in longitudinal rows, or at least some stomata are in rows, and only three specimens showed quite scattered stomata. Ordinary epidermal cells bearing a median thickening or papilla on their surfaces are always present on the lower side, although their predominance over cells with an unthickened surface wall varies. In contrast to the upper cuticle, hollow papillae, often with separate internal plugs of thickening, are very common on the lower side. The variation in the frequency of cells bearing a surface papilla (or a median thickening) on the upper side seems unrelated to that on the lower side.

Comparison. *Eretmophyllum pubescens* is very similar to *Eretmophyllum whitbiense* in the shape of the apex and leaf base, in venation, and probably in size. Resin bodies occur in both species, but are more common in *E. pubescens*.

The cuticle of *E. pubescens* differs from that of *E. whitbiense* in being thinner, in usually having narrower cell outlines on both upper and lower cuticles, and in frequently showing a high proportion of cells bearing a surface median thickening or papilla on the upper cuticle. The cuticle of *E. pubescens* often shows distantly wavy anticlinal walls, especially on the lower

cuticle, which render the cells a distinctive shape, and are not present on the cuticle of *E. whitbiense*. The papillae on the lower cuticle of *E. pubescens* are more often solid and low, and occur more frequently on the cells of the non-stomatal strips than those on the lower cuticle of *E. whitbiense*. Non-stomatal strips are always distinguishable on the lower side of *E. whitbiense* but are less frequently distinct in *E. pubescens*. *E. pubescens* also differs from *E. whitbiense* in having slightly more numerous stomata, more often arranged in longitudinal rows in the stomatal strips of the lower side. *E. whitbiense*, however, more frequently has a few stomata on the upper side in the central part of the lamina than has *E. pubescens*.

E. pubescens and *E. whitbiense* are similar in shape to the undivided specimens of *Sphenobaiera gyron* but they are usually wider, with more widely spaced veins, and more often have resin bodies. Both *E. pubescens* and *E. whitbiense* usually have wider stomatal strips on the lower side, and more conspicuous, better developed papillae on the ordinary epidermal cells of the lower side than *S. gyron*. *E. pubescens* also differs from *S. gyron* in having fewer stomata on the upper side, in the ordinary epidermal cells of the upper side frequently bearing a median surface thickening or papilla, and in the distantly wavy cell outlines usually present on the lower cuticle. *E. whitbiense* has broader epidermal cell outlines on both sides, and stomata with the guard cells more obscured by subsidiary cell thickening than those of *S. gyron*.

Isolated leaf fragments of *Ginkgo huttoni*, *Ginkgo longifolius*, *Ginko* sp. cf. *sibirica*, *Sphenobaiera ophioglossom* and *Sphenobaiera longifolia* may be as wide as the smallest leaves of both *E. pubescens* and *E. whitbiense*. However, *G. huttoni*, *G. longifolius* and *S. ophioglossom* have more crowded veins, and *Ginkgo* sp. cf. *sibirica* has a much more delicate cuticle than either of these *Eretmophyllum* species. *S. longifolia* usually has more numerous stomata on the upper surface than *E. pubescens* or *E. whitbiense*. The lower cuticle, especially along the vein strips of *S. longifolia*, is usually more papillate than that of *E. whitbiense* and it lacks the distantly wavy cell outlines seen in *E. pubescens*. The upper cuticle of *S. longifolia* differs from that of *E. pubescens* in lacking frequent ordinary epidermal cells bearing a single conspicuous median surface thickening or papilla.

Foreign leaves of *Eretmophyllum* include *Eretmophyllum lovisatoi* Edwards (1929) from the Jurassic of Sardinia, which is similar in shape to *E. pubescens* and *E. whitbiense* but it is distinct from both in having stomata equally numerous on both upper and lower leaf surfaces. *Eretmophyllum baikonuricum* Orlovskaya (1962, p. 144, pl. 4, fig. 3; text-fig. 3) from the Middle Jurassic of Kazakhstan, is like both *E. pubescens* and *E. whitbiense* in form, venation and in the presence of resin. It is more like *E. whitbiense* in having a few stomata on the upper side and in lacking papillae on the ordinary epidermal cells of the upper surface. However, the veins are more distinctly marked on the upper cuticle than in *E. whitbiense* (the lower cuticle is not described). A leaf fragment, also from Kazakhstan, figured by Orlovskaya (1962, text-fig. 2*b*) as *Eretmophyllum* sp. has more crowded veins than either *E. pubescens* or *E. whitbiense*.

A series of leaves named *E. saighanense* have been described from various floras in Asia see Seward 1912 (Afghanistan), Kryshtofovich 1933 (Ural Mts), and Kawasaki 1933 (Korea). They look equally like *E. pubescens* and *E. whitbiense* (which are macroscopically indistinguishable from one another). Their structure is not known.

E. tetonense Kuriwa & Sekido (1965) from Japan has more crowded veins. The specimen

shows several leaves on a slow growing shoot with crowded leaf scars, a short shoot of unlimited growth, not a determinate shoot as in *Phoenicopsis*.

E. pulchellus (Heer) Nathorst (1919) from the Upper Jurassic of Spitzbergen is a small leaf no larger than a *Pseudotorellia*.

E. baikonuricum Orlovskaya (1962) from Kazakhstan is a rather small leaf with only a few veins.

E. thomasi Doludenko & Svanidze (1969, pls. 79, 80, figs. 1–5) is a smaller leaf with fewer veins. Its cuticle is very like that of *E. whitbiense*.

Occurrence

Middle Deltaic, Gristhorpe Series:	Gristhorpe Bed.
	Cloughton Wyke, *Eretmophyllum* Bed.

Thomas's Type material came from the Gristhorpe Bed at 'adjacent ends of Gristhorpe and Cayton Bays'.

The leaf figured by Seward (1900, 1900*a*, 1917) as *Ctenis* sp., from Cloughton Wyke, is identified as *Eretmophyllum pubescens* (Harris 1964, p. 121). The leaf substance of this specimen had rotted and the fibrous strands had been laterally displaced giving the appearance of anastomosing veins. The cuticle matches that of *E. pubescens* and shows the vein running normally, without anastomoses.

Cuticle fragments more closely resembling *E. pubescens* than any other Yorkshire species are known from the following localities, but are not identified with confidence:

Middle Deltaic, Gristhorpe Series	Leakholm, Hole i' th' Ellers Coalpit.
	Danby, Clitherbeck Coalpits.
	Farndale, Rudland Moor Coalpits.
	Goathland, Darnholm Coalpits.
Sycarham Series	Haiburn Gorse.
	Hagg Beck, Bed D.
Lower Deltaic	Bilsdale, Todhill Beck A.

Eretmophyllum whitbiense Thomas

Pl. 3, figs. 1–3, Pl. 7, fig. 2; Text-fig. 20

Yorkshire leaves:

1913*b* *Eretmophyllum whitbiense* Thomas, p. 259, pl. 7. (Cuticles only)
1964 *Pseudoctenis* sp. A, Harris, p. 87, pl. 3, figs. 5, 6; text-fig. 38 A–D. (Leaf and cuticles)

Emended Diagnosis. Typical leaf paddle-shaped, up to at least 150 mm long, about 17 mm (8 mm–25 mm) wide at widest part, shortly tapering above to rounded or retuse apex. Lamina tapering below, gradually merging into petiole. Petiole about 1·5 mm (1 mm–3·5 mm) wide at narrowest part, slightly wider at extreme base. Leaf substance of medium thickness except for thicker margins of lamina base and petiole. Veins fairly conspicuous, branching in lamina base, becoming more or less parallel above, at about 8 (5–13) per cm, converging

slightly towards apex. Resin bodies often present, most frequent in lamina base, least frequent in apical region. Resin bodies round, oval or needle-shaped, of very varied length, 85μ–1280μ long, about 125μ (50μ–225μ) wide.

Cuticle thick, upper about 6μ (4μ–8μ) thick, lower often slightly thinner. Stomata mostly on lower cuticle. Upper cuticle not showing distinctly marked veins, though ill-defined strips of cells arranged in longitudinal rows, corresponding with vein strips of lower cuticle, occasionally present. Cells isodiametric, polygonal or slightly elongated. Anticlinal walls straight or rarely slightly sinuous, prominent, especially at cell angles, occasionally interrupted. Cell outlines often very distinct, of medium width, sometimes less distinct, broad or of irregular width, occasionally appearing as two or more bands of thickening separated by narrow thin strips. Well developed surface papillae on ordinary epidermal cells absent, cells occasionally present bearing single median thickening or several small patches of thickening or with peripheral band of thickening or thickened over whole surface except for central, narrow, thin strip. Trichomes absent. Stomatal density in lamina base about 2 (0–7) per mm^2, decreasing above, 1 per mm^2 or even less near margin. Stomata scattered, irregularly orientated, though often longitudinal near margins and in lamina base, of similar structure to those of lower cuticle.

Lower cuticle with veins more or less distinctly marked by strips about 400μ (180μ–920μ) wide of slightly elongated, rectangular or polygonal cells arranged in longitudinal rows. Strips between veins about 830μ (260μ–1,390μ) wide, of more or less isodiametric, polygonal cells, not usually arranged in longitudinal rows, but sometimes a few longitudinal rows of cells of similar appearance to those of vein strips present, but of limited length only. Anticlinal walls prominent, more or less straight, of varied width and definition, occasionally appearing as two or more bands of thickening separated by narrow, thinner bands. Surface walls with faint mottled sculpture, or longitudinal or transverse, or concentric striations. Cell surfaces of uniform thickness or with median thickening or longitudinal ridge or several small patches of thickening. Ordinary epidermal cells bearing central hollow papilla, or low, small, solid papilla frequent, often less well developed on cells of vein strips, very rarely absent altogether. Papillae sometimes with separate plug of thickening internally. Cell surfaces occasionally with central well defined oval or round thin area. Trichomes usually absent.

Stomata usually confined to strips between veins, at concentration of about 50 (30–75) per mm^2, increasing slightly towards apex. Stomata scattered or in short longitudinal rows, irregularly orientated. Guard cells sunken, poles not usually exposed. Guard cell surfaces thin except for very narrow band of thickening next to aperture, and narrow transverse band of thickening near poles. Five or six, more or less isodiametric subsidiary cells surrounding guard cells. Lateral subsidiary cells with anticlinal walls adjacent to guard cells thickened, forming rim at sides of stomatal pit. Subsidiary cell surface usually bearing hollow or solid papilla projecting upwards or over stomatal pit. Subsidiary cells occasionally with median surface thickening, or sometimes thickened over whole surface except for central, radiating, thin area. Encircling cells absent.

HOLOTYPE. V.27707. Figured Thomas 1913*b*, pl. 7.

DISCUSSION. The present material, comprising sixty-one specimens from Whitby, one from Beast Cliff and one from Hasty Bank, agrees well with Thomas's description of *Eretmo-*

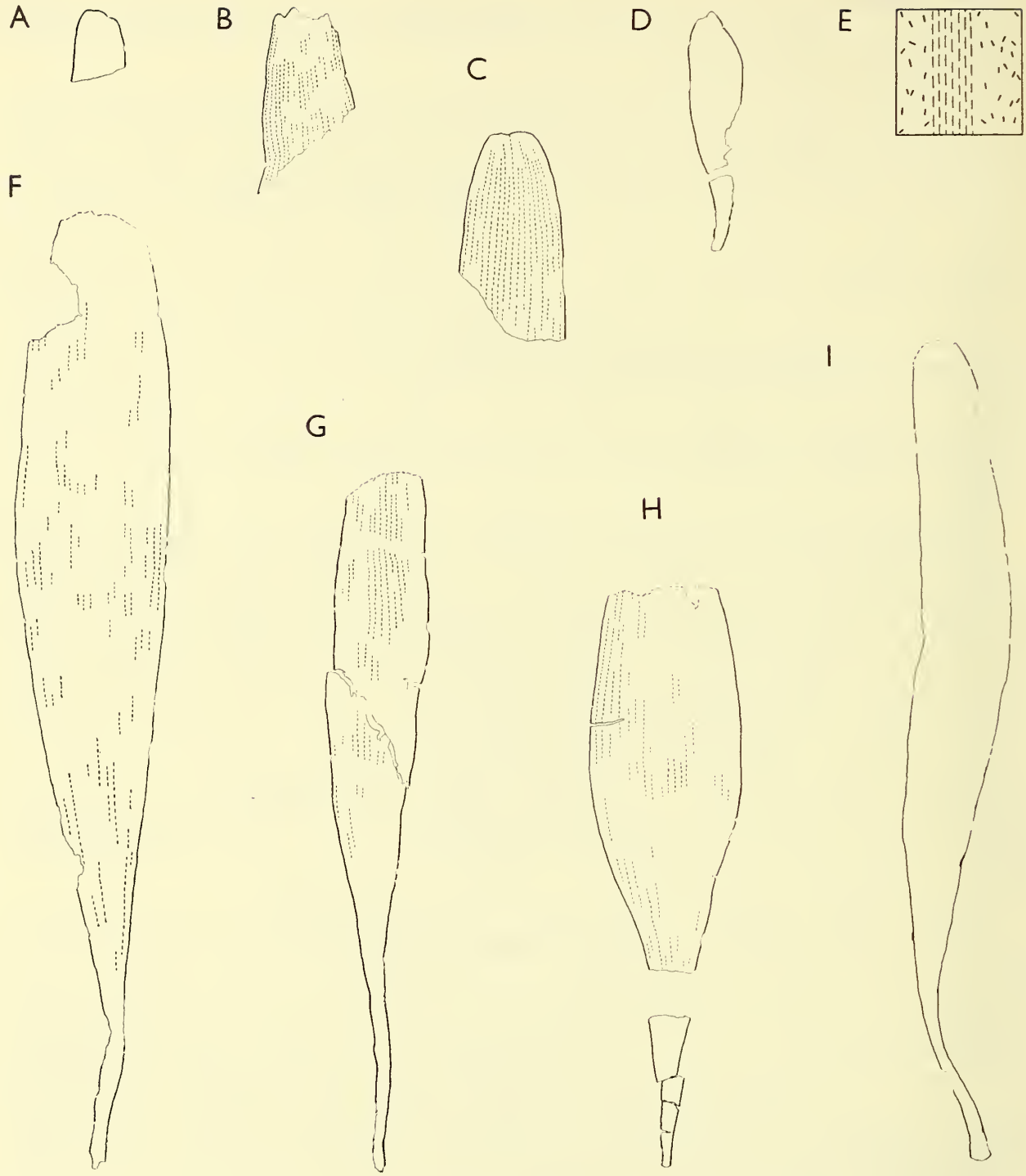


Fig. 20. **Eretmophyllum whitbiense** Thomas

A–C, leaf apices, actual size. D, F–I, leaves showing variation in size and shape, actual size. E, 1 mm² of lower cuticle showing distribution and orientation of stomata. A vein strip is shown in the centre. V.56469. All are from Whitby.

phyllum whitbiense in leaf shape, size and variation. The cuticles also match, but Thomas described the side showing distinctly marked vein strips with frequent stomata between them as the 'upper', but we call this side the lower because of the high stomatal density. Thomas's photographs of the 'lower' cuticle (1913*b*, pl. 7, figs. 6, 7) are like the side we call the upper. A diagnostic character that Thomas referred to was the presence of interstitial strands, sometimes anastomosing, visible on the 'upper' leaf surface. These may correspond to the interstitial rows of cells like the cells of the vein strips, sometimes seen on the lower cuticle of the present leaves, although they have not been observed to anastomose.

The leaf from Beast Cliff *Otozamites* Bed figured by Harris (1964) as *Pseudoctenis* sp. A we now identify as *E. whitbiense*, as it matches the present specimen (which shows a petiole) from that locality, in width, venation and cuticle structure.

Most of the present leaves are broken and their full range in size is not known. The largest whole leaf is 150 mm long (Text-fig. 20 F) and the shortest is 40 mm long. Leaf shape varies as shown in Text-fig. 20, D, F–I, one margin sometimes being straighter than the other, or occasionally the leaf is slightly falcate. The leaf apex can be rounded, retuse or wavy, and symmetrical or asymmetrical. The number of veins entering the petiole is not known; four is the lowest number of distinct vein strips seen on the lower cuticle near the lamina base. The shape and length of the resin bodies are very variable, but all shapes, and both short and very long ones, may be present in a single leaf.

The upper cuticle of a few specimens appears to be composed of two layers of cutin. The outer of these comes apart from the inner in places, to form tiny blisters seen in side view at a fold in the cuticle.

Thomas described both upper and lower cuticles as lacking papillae on the ordinary epidermal cells, though he called them 'convex', but only very few of the present leaves lack ordinary cell papillae on both sides, most having some papillate ordinary epidermal cells on the lower side. Isolated, short, conical trichomes were found on the vein strips of the lower cuticle of a single Whitby specimen.

The variation between leaves in stomatal density between the vein strips, and also that in the widths of the vein and intervenal strips are fairly normally distributed about the mean values. The vein strips of the lower cuticle are mostly well defined and devoid of stomata except in the lamina base, but occasionally a short row of stomata occurs within, though near the edge of, an otherwise well marked vein strip.

Some characters of the cuticle vary with distance from the leaf base. On the lower cuticle, the vein and intervenal strips become narrower (vein strips about 250μ (140μ–420μ) wide, intervenal strips about 625μ (295μ–870μ) wide) and stomata slightly more numerous in the apical region. Ordinary epidermal cells bearing a well developed surface papilla are usually more frequent distally, but become rare at the apical margin itself. Cells of the intervenal strips are often more elongated at the leaf margins and in the lamina base towards the petiole where the vein strips are usually indistinguishable. On the upper cuticle stomata are more frequent in the lamina base than in the central or apical regions.

The Whitby block collected in 1966 which had more of this leaf than anything else was ultimately broken into small pieces in the hope of finding shoots or reproductive organs but nothing of the sort was seen.

Comparison. *Eretmophyllum whitbiense* is similar to *E. pubescens* in the shape of the leaf apex and base, and in venation, but it less often possesses resin bodies.

The cuticle of *E. whitbiense* differs from that of *E. pubescens* in being thicker, in showing wider cell outlines on both sides, in the more frequent occurrence of stomata, and in the lack of conspicuous papillae on the upper side. It also differs in always showing distinct non-stomatal strips and often having less numerous papillae on the lower side. It lacks the distantly wavy cell outlines often seen on the cuticle of *E. pubescens*, and has slightly fewer stomata in the stomatal strips of the lower side.

For other species see under *E. pubescens*.

Occurrence

Lower Deltaic:	Whitby
	Beast Cliff, *Otozamites* Bed
	Hasty Bank

Material from Whitby was collected on two occasions by T. M. Harris from large fallen blocks which may well have come from the upper part of the plant bed. *Eretmophyllum whitbiense* has not been recorded in the part of the plant bed that is easily accessible.

Thomas's specimens are from 'one of the plant beds on the Scar at Whitby', and very likely come from our Whitby locality.

Cuticle fragments more similar to *E. whitbiense* than to any other Yorkshire species were obtained from the following localities, but they are not identified with confidence:

Upper Deltaic:	Fylingdales, Upper Kirk Moor
Middle Deltaic, Gristhorpe Series:	Leaholm, Hole i' th' Ellers Coalpit
Lower Deltaic:	Westerdale Stockdale Waterfall Sandstone
	Bilsdale, Todhill Beck B
	Sandsend Alum Pit B

Genus PSEUDOTORELLIA Florin 1936, p. 142

1957 *Pseudotorellia* Florin: Lundblad, p. 760.
1968 *Pseudotorellia* Florin: Lundblad, p. 189. (General review)

The following is Lundblad's translation of Florin's diagnosis (Lundblad, 1957):

'Leaves coriaceous, entire, almost linear to narrowly tongue-shaped, falcately curved, with their maximum width in the middle region or more apically, and with an apex, which is broadly rounded off; basally narrowing gradually, although hardly forming a petiole, at the basis itself not distinctly swollen, and traversed by a moderate number of veins, formed by dichotomies chiefly in the basal part. Leaves further hypostomatic. Lower side with indistinctly defined stomatal stripes between narrower, non-stomatic longitudinal zones. Stomatal apparatuses within these stripes in short longitudinal rows or quite irregularly

arranged, mostly sparse, and always longitudinally orientated, further of the haplocheilic type, monocyclic or incompletely amphicyclic (dicyclic). Guard cells sunken, next to the slit showing a strong, cutinized ridge ('Vorhofleiste'), and strongly cutinized, too, in the side wall facing the lateral subsidiary cells. Subsidiary cells 4–6, the lateral ones in particular being proximally (if at all) more strongly cutinized than the encircling epidermal cells. Epidermal cells with very faintly sinuous to straight outlines, often papillately cutinized and bulging'.

The 'encircling epidermal cells' mentioned above are not 'encircling cells' in the technical sense but are neighbouring ordinary epidermal cells.

Type Species. *Fieldenia nordenskioldi* Nathorst (1897, p. 56).

Discussion. In addition to the above diagnosis, an important character of *Pseudotorellia* is that the leaves are not usually found attached to caducous short shoots, but they are shed individually by abscission at the leaf base. (Krassilov (1970), however, figures an attached leaf and also denuded shoots.) Also, the veins end separately at, or just below, the apical margin. Resin bodies are absent. More or less elongated upper epidermal cells and median, longitudinal ridges on the surface of ordinary epidermal cells of one or both sides of the leaf are a common feature of the genus. Poor definition of stomatal and non-stomatal strips on the lower epidermis, and sparse distribution of stomata in the stomatal strips are characters of many species of *Pseudotorellia* but they do not apply to all the species (*Pseudotorellia grojecensis* Reymanovna (1963) and *P. heeri* Manum (1968) both have the stomata rather densely distributed in the stomatal strips, and in *P. heeri* the stomatal and non-stomatal strips are fairly well defined). *Pseudotorellia heterophylla* Watson (1969) is exceptional in that the lower cuticle does not show stomatal and non-stomatal strips and the stomata are fairly densely distributed throughout.

Pseudotorellia is similar to *Torellia* in leaf shape and in being hypostomatic, but is distinct from *Torellia* in not having leafy short shoots which are shed, in having longitudinally orientated stomata, and in epidermal cell outlines being much less sinuous.

Eretmophyllum differs from *Pseudotorellia* in usually being a larger leaf, with less crowded veins and in sometimes having resin bodies. It has shorter upper epidermal cells than those of *Pseudotorellia*, the stomata are irregularly orientated, and median longitudinal ridges are not present on the epidermal cell surface walls.

Krassilov (1970) attributed a female fructification called *Umaltolepis* to *Pseudotorellia*. It is incompletely known but differs from the fruit of *Ginkgo biloba* in many respects.

Like many Ginkgoales the genus *Pseudotorellia* is fairly widespread and each locality provides a set of specimens which appears to be a distinct species. If further work merely continues this the result will be unfortunate. Possibly some may be best regarded as local populations which though distinguishable are hardly distinct at specific level.

Pseudotorellia tibia sp. nov.

Text-fig. 21

Diagnosis. (Based on lower half of leaf only.) Leaf exceeds 20 mm in length, up to at least 4 mm wide, narrowing gradually below. Leaf asymmetrical, with one margin straight, the

other slightly curved. Veins inconspicuous, branching below, giving rise to at least eight more or less parallel veins above. Upper leaf surface with fine longitudinal striations throughout width. Leaf substance fairly thin, resin bodies absent.

Cuticle thick on both sides (upper about 8μ thick), hypostomatic, with stomata confined to intervenal strips of lower side. Upper cuticle not showing distinctly marked veins, but with mostly quadrate, more or less elongated cells, about 6 times as long as wide (up to 14 times as long as wide), rarely isodiametric. Cells arranged in longitudinal rows. Cell outlines conspicuous, distantly wavy or straight, occasionally interrupted. Anticlinal walls broad, sometimes single, but more often composed of two to four narrow bands of thickening separated by narrow thinner strips. Cell surface walls with one, or occasionally two, conspicuous median longitudinal ridges of thickening of similar width, or slightly narrower than anticlinal walls. Ridges of thickening more or less straight, usually single, but very occasionally divided by median thin strip. Ridges of thickening usually continuing unbroken over surface of several cells before terminating at one end of a cell, occasionally limited to one cell. Surface walls often showing faint sculpturing of longitudinal striations. Papillae and trichomes absent.

Lower cuticle with more or less ill-defined stomatal strips, between narrower non-stomatal strips marking veins. Cells of vein strips more or less elongated, up to 14 times as long as wide, mostly quadrate, arranged in longitudinal rows. Intervenal strips with outermost cells quadrate, slightly shorter than cells of vein strips, and arranged in longitudinal rows. Cell outlines straight or distantly wavy, occasionally interrupted. Anticlinal walls narrower than those on upper cuticle, single, or sometimes composed of two or more bands of thickening separated by narrow, thinner bands. Cells of vein strips often with broader cross walls than long walls. Surface walls with a median thickening occupying nearly whole of surface or sometimes with one, or rarely two, median longitudinal ridges of thickening of similar width or slightly wider than anticlinal walls but often expanded at cell ends. Surface thickenings usually continuous longitudinally over several cells. Ordinary epidermal cells between veins very occasionally with a low, solid papilla at one end of their surface. Surface walls with sculpture of faint mottling or occasionally longitudinal striations.

Stomata occurring at density of about 24 per mm^2, on lower side (35 per mm^2 between veins). Stomata orientated longitudinally, scattered between veins, occasionally some arranged in short longitudinal file. Guard cells slightly sunken and poles overhung, margins partly overhung by subsidiary cells but aperture exposed. Guard cell surface walls thin apart from narrow band of thickening alongside aperture. Boundary wall between guard cells and lateral subsidiary cells thick and broad. Subsidiary cells 4–7, not radially arranged but of similar shape (often elongated) to surrounding ordinary epidermal cells. Each subsidiary cell usually bearing a single solid surface papilla projecting towards stomatal pit in addition to surface thickening similar to those of ordinary epidermal cells. Papillae of polar subsidiary cells often less well developed than those of lateral subsidiary cells, but rarely absent. Encircling cells absent.

The specific name *tibia*, is from *tibia*, a shin bone and refers to a frequent shape of the median thickening of the epidermal cells.

HOLOTYPE. V.56464 (Text-fig. 21).

DISCUSSION AND COMPARISON. The present material consists of a single leaf fragment,

broken at both ends, on a small block from Hillhouse Nab, Farndale. The cuticle agrees with Florin's description of *Pseudotorellia* (1936, p. 142) in being hypostomatic, with sparsely distributed stomata confined to the intervenal strips of the lower side, and in having longitudinally orientated stomata. (However, a single oblique stoma was seen.)

Some additional specimens have been collected from Hillhouse Nab recently. The larger ones still lack both ends but agree with the holotype in being slightly curved. One (C. Hill collection) is 12 mm long and 1·6 mm wide below increasing to nearly 4 mm above. It has nine

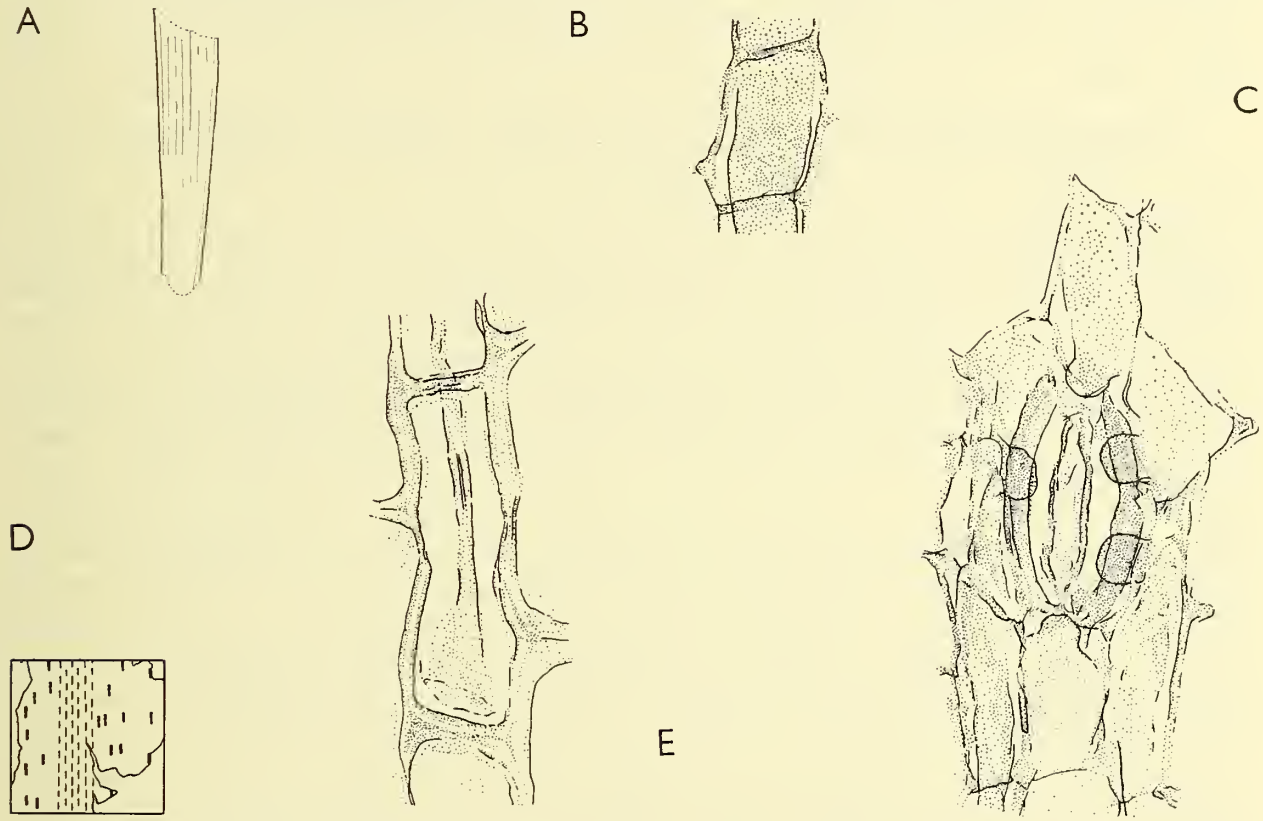


Fig. 21. **Pseudotorellia tibia** sp. nov.

A, Holotype specimen, magnification ×2, V.56464. B, cell from intervenal strip of lower surface showing broad band of surface thickening, magnification ×400. C, stoma from intervenal strip of lower surface, magnification ×400. D, lower cuticle showing vein strip and distribution and orientation of stomata, magnification ×20. E, cell of upper surface showing median longitudinal ridge of surface thickening, magnification ×400. All from the holotype, Hillhouse Nab Plant Bed.

veins. The other is almost 40 mm long, 1·6 mm wide below, increasing to 4 mm at 20 mm and diminishing to 3·5 mm at the top. It has ten stomatal strips, and presumably eleven veins except at the base where there are fewer. The margins are distinctly thickened and project downwards and are partly marked off by folds. Both specimens have thick cuticles which agree with that of the holotype. Two small differences are that the anticlinal longitudinal walls mostly appear single in the new specimens and their stomatal strips are relatively narrower, being narrower than the vein strips, but the sculpture of the cell surface and the very characteristic

subsidiary cell papillae are just the same. Under high magnification the longitudinal ridges on elongated cells often show many (up to 20) fine longitudinal striations and the pads on the short cells may show many minute pits but there is also corrosion pitting.

Although these new specimens do not fill the gaps in the description they provide evidence that the holotype is a normal leaf and thus that its characters are diagnostic of the species.

Pseudotorellia tibia, even if only occurring as a small isolated fragment, is easily distinguishable from other Yorkshire Ginkgoalean leaves by the longitudinal striations on the upper surface, by being hypostomatic, and by the elongated, quadrate cells with a surface, median, longitudinal ridge on the upper epidermis. The sparsely distributed stomata occurring scattered within ill-defined stomatal strips on the lower leaf surface distinguish it from conifer leaves.

Pseudotorellia augustifolia Doludenko, from the Upper Jurassic of East Siberia (Vachrameev & Doludenko 1961) and *Pseudotorellia minuta* Lundblad, from the Rhaetic of Sweden (Lundblad 1957) both differ from the Yorkshire leaf in being narrower (neither exceed 3 mm in width), with fewer veins (neither have more than four veins). The upper cuticle of *P. augustifolia* does not show prominent median longitudinal ridges on the surface of the epidermal cells, and *P. minuta* differs from the present leaf in the longitudinal arrangement of the stomata in files. *P. nordenskioldi* (Nathorst) from the Wealden of Spitzbergen (Florin 1936), *P. longifolia* from the Lower Cretaceous of East Siberia (Vachrameev & Doludenko 1961) and *P. grojecensis* from the Middle Lias of Poland (Reymanovna 1963) all differ from *P. tibia* in that the subsidiary cells do not usually bear a well developed papilla. *P. longifolia* and *P. grojecensis* also differ from the present leaf in lacking continuous, prominent, median longitudinal ridges on the surface of the upper epidermal cells, and the cell arrangement on the upper side of *P. grojecensis* is distinctive in the cells being arranged in small groups, the cells within a group being either all elongated transversely or all elongated longitudinally. The leaf from the Jurassic of Kazakhstan, figured by Orlovskaya (1962) as *P. nordenskioldi*, is narrower than *P. tibia* and the cuticle is also distinct in being thinner and in lacking prominent longitudinal ridges on the upper epidermal cell surfaces. *P. ensiformis* (Heer) from the Upper Jurassic of East Siberia (Vachrameev & Doludenko 1961) differs from the present leaf in the longitudinal ridges on the surface of the lower epidermal cells being much more conspicuous than those on the upper epidermal cells, in having less well developed subsidiary cell papillae, and in the cells of the intervenal strips of the lower side being more elongated. *P. vachrameevi* Gomolitzky, from R. Tyrna Dar'ja (Gomolitzky 1965), differs from *P. tibia* in having the stomata arranged in longitudinal rows, and *P. heeri* Manum, from the Upper Jurassic of Northern Norway (Manum 1968), is distinct in having much less elongated cells on the upper epidermis and more numerous stomata on the lower epidermis. *P. ephela* (Harris) from the Lower Lias of East Greenland (Harris 1935), differs from *P. tibia* in the cuticle being much thinner and in the subsidiary cells less often bearing a papilla. The leaf from the Jurassic of Kazakhstan, figured by Orlovskaya (1962), as *P. ephela* differs from the Yorkshire leaf in lacking prominent median, longitudinal ridges on the upper epidermal cell surfaces, and in the anticlinal cell walls often being sinuous.

There are numerous specimens determined as *Pseudotorellia*, *Torellia* and *Fieldenia* whose cuticles are not known, and our Yorkshire material is too fragmentary for comparison macroscopically, see Lundblad (1968).

Occurrence

Lower Deltaic: Farndale, Hillhouse Nab Plant Bed.
(Hand specimen.)

Cuticle fragments which match *Pseudotorellia tibia* were obtained by macerating shale from the following localities:

Upper Deltaic: Scalby
Lockwood Gill Head.

REPRODUCTIVE ORGANS OF THE GINKGOALES

Very few organs apart from leaves have been found in Yorkshire that could be attributed to the Ginkgoales. We do not know whether the older collectors looked for them but since 1900 they certainly did. Two were recognized as possible, but both as we now know wrongly. There was *Beania gracilis* which Seward (1900, 1919) thought might be Ginkgoalean but we now relate it firmly to the Cycad *Nilssonia compta*. There were also the groups of little pollen sacs which Seward (1900) called 'Pollen sacs of *Ginkgo*' and in 1919 called *Antholithus*, with a strong suggestion that they belonged to *Ginkgo digitata*. In 1920 Johnson described similar pollen sacs as *Ginkgoanthus phillipsi*. These organs are a species of *Caytonanthus*, probably *C. arberi*.

More recently M. Black collected fruits and seeds associated with *Baiera furcata* (*B. gracilis*) and similar seeds were collected by Thomas and Harris and are described here. Similar seeds were collected by Harris with *Ginkgo huttoni* and recently also a fruit and a male cone, both as we think reasonably attributable to it.

If the reproductive organs that have been identified as Ginkgoalean are correctly identified they make the Ginkgoales a varied class and raise doubts whether it can remain a coherent class at all.

We will not consider the rich series described by Heer (1876–80) from Siberia because he gave no reasons for identifying them, but some may prove rightly identified and significant. Elsewhere such organs are seldom met. There are a few Mesozoic seeds identified as Ginkgoalean, including *Allicospermum xysteum* Harris (1935) and those described here which seem closely similar to those of *Ginkgo biloba*. We are less certain about the 'Ginkgophyte seed I' of Florin (1936, pl. 25, figs. 6–9) since this looks like a *Leptostrobus* valve (with numerous stomata). His seed II, in longitudinal section, certainly is a seed but not certainly Ginkgoalean. Braun (according to Florin 1936) considered some small branched organs to be seed-bearing fructifications of *Baiera muensteriana* (like the more branched forms of *Ginkgo biloba*) and this view has been accepted but Schenk (1867) who examined their cuticles thought they were merely unusual leaves. They deserve fresh study.

Stachyopitys presli (Schenk 1867) is regarded as the male cone of *Baiera muensteriana* and it is not too different from that of *Ginkgo biloba* but it does merit further study, particularly because fossils of very different affinity have been included in *Stachyopitys*. A very striking male cone attributed to *Sphenobaiera furcata* (Heer) was described by Leuthardt (1903) from

the Upper Trias of Switzerland. Kräusel (1943, 1955, 1961) gives further details and mentions a similar cone *Antholithus wettsteini*.

There are also some fructifications which are so different from *Ginkgo* that they were attributed to the Ginkgoales (association with a leaf and sometimes agreement in structure) in spite of strikingly different morphology. The large male cone *Bernettia phialophora* (Lower Lias of East Greenland) was attributed to *Sphenobaiera spectabilis* by Harris (1935). The female organ *Umaltolepis* is attributed by Krassilov (1970) to *Pseudotorellia*. *Karkenia incurva* Archangelsky (1965) was attributed to *Ginkgoites tigrensis* and another species (unnamed) to a *Sphenobaiera* by Krassilov (1970). *Karkenia* is disturbing because *Ginkgoites tigrensis* seems a very normal leaf, rather like *Ginkgo huttoni*.

Seeds (with flesh) attributed to ***Ginkgo huttoni*** (Sternb.)

Pl. 7, fig. 9, Text-figs. 22 N–P, 23 I

In 1970 B. A. Thomas collected a block in the Scalby Ness *Ginkgo* Bed which showed two associated pairs of seeds. Both seem to be connected at one end by a scrap of cutinized tissue and we regard this as a relic of the top of a seed bearing axis, just like that of *Ginkgo biloba*. Preservation of this is so poor that it cannot be confirmed and nothing remains of any stalk.

The seeds are represented by a brown membrane which is the external cuticle of the integument. This is much cracked evidently by slumping during preservation, and inside a little blackish tissue can be seen which is taken to be a vestige of the seed stone and of inner cuticles. A layer of matrix has penetrated between the integument and stone. Small cuticle preparations were made from the integument, but the stone was not tried. The integument cuticle is thick and shows cells with prominent lateral walls with slight uneven thickenings. Many of the cells have a specially thickened surface, in the middle of which is a pale circular patch. In a few of these cells the surface is raised to form a cone, but in most it is only slightly raised or nearly flat. A few of these cells were seen in optical section along wrinkles caused by compression and in these the pale patch is seen to be much thinner than the rest of the surface.

This form of preservation is common in the Scalby Ness *Ginkgo* Bed. The matrix is the sandy shale of a river channel and we believe that the plant organs, after burial, suffered biological oxidation from time to time through a fall in the water level before they were finally buried deeply and sealed off. All the numerous fragments of *Ginkgo huttoni* leaves consist merely of their cuticles without inner tissues.

The specimens are identified as *Ginkgo huttoni* because they are strikingly associated with it. They are, in addition, of the right size to accommodate the seed stones also attributed to *G. huttoni*.

The present specimens are too poorly preserved to provide much botanical information but what they show is fully consistent with the idea that *Ginkgo huttoni* belongs to the genus *Ginkgo* in the strict sense. The only special feature of the cuticle is the peculiar cells with thin patches. These are very like integument cells of *Ginkgo biloba* but there almost every cell has one.

Prinada (1962, p. 170, pl. 11, figs. 6, 7; text-fig. 34) figures as belonging to *Ginkgo*, some small branched specimens similar to those figured by Heer (1876, pl. 4, fig. 14*b*, pl. 10, fig. 8*b*). The seeds are missing (but there are loose seeds). These fossils certainly suggest the seed bearing organs of *Ginkgo*, but their seeds must be smaller.

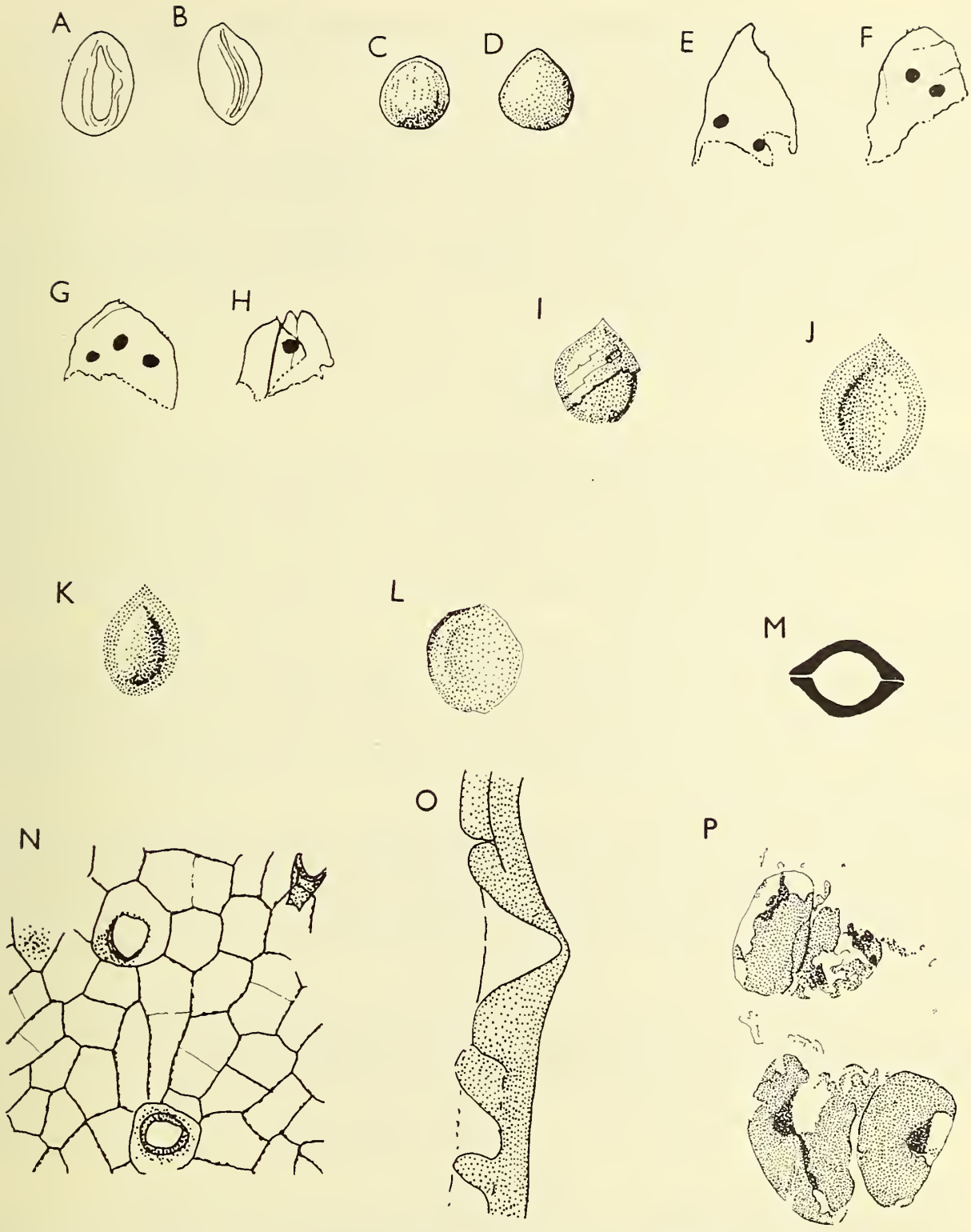


Fig. 22. Organs associated with **Ginkgo** and **Baiera**

A–H, organs associated with *Ginkgo huttoni*. A, B, pollen grains adhering to bud scales, magnification ×500, V.27499*a*. Stainsacre Beck. C, seed stone, magnification ×2, V. 27495. Langdale Plant Bed. D, seed stone, magnification ×2, V.27494. R. Derwent *Ginkgo* Bed. E–H, bud scales, magnification ×10. The black spots are resin bodies, E is an inner scale and H is two scales. V.27499*a*. Stainsacre Beck. I–M, seed stones associated with *Baiera furcata*, all magnification ×2. I, half stone still retaining some of its coaly layer; the compression border becomes abruptly narrow in one part, V.56380. J, imprint of external surface of half stone, V.56381. K, mould of internal surface of half stone, V.56382. I–K all from Scalby, Black Clay. L, whole stone, impression after removal of coal for maceration (note weaker definition of compression border than in half stones), May Beck Bed B, V.56383. M, diagram of imaginary section through stone before compression, showing crack along marginal rim. N–P, *Ginkgo huttoni* seed. N, integument showing cells with raised centres, magnification ×200, V.56501. O, fold in integument showing a cell in optical section with raised and thin centre, magnification ×500, V.56502. P, two pairs of seeds, shown also in Pl. 7, fig. 9. The integument cuticle and also traces of cuticle of connecting pad (brown membranes) is lightly stippled and where it has fallen off leaving a visible imprint, this is outlined. The stone tissue (black) is stippled dark, magnification × 2, V.56411. Scalby Ness.

Seeds (stones) attributed to ***Ginkgo huttoni*** (Sternb.)

Text-figs. 22 C, D

Harris (1948, p. 205) described some seed stones associated with *G. huttoni* in two Upper Deltaic localities on the River Derwent. The drawings reproduced here show all that is known. The stones, or half stones, have lost all the outer flesh and outer cuticles and no inner cuticles remain. Only the hard tissue of the stone is preserved and this forms a compression border at the sides which is narrower than the border of *Baiera furcata*, so we conclude that its stone is thinner walled. It is, however, thicker than in *Ginkgo biloba*. The seed stone of *G. huttoni* is intermediate in size between that of *Ginkgo biloba* and *B. furcata*.

Bud scales attributed to ***Ginkgo huttoni*** (Sternb.)

Text-figs. 22 A, B, E–H

A shale full of *G. huttoni* (Stainsacre Beck) when macerated yielded numerous bud scales which Harris (1948, p. 204) described and attributed to *G. huttoni*. The figures are repeated here. Most of the scales are semicircular and 1·5 mm–2·0 mm long and towards the apex their outer cuticle is very thick (up to 12μ), but diminishes to 1μ at the base and is then lost. The inner cuticle becomes delicate just below the apex. Occasional round resin bodies, 200μ–300μ wide, occur in the substance. A few more triangular and less thickly cutinized scales were found and regarded as inner ones.

The outer cuticle shows polygonal cells with strongly marked walls interrupted by pits. Most epidermal cells have strong papillae and in the middle region there are a few stomata. These are like one form met on the leaves, the guard cells are sunken and the subsidiary cells are strongly papillate, and the papillae may point upright or may overhang the guard cells. A few trichomes occur mainly on the margins. Towards the base, cells often show a transverse wall produced by late division.

Many of these bud scales have oval pollen grains sticking to them, sometimes in hundreds, and they are nearly all of one type. Perhaps they belong to *G. huttoni* (though pollen of this form occurs also in Cycads and Bennettitales). Harris suggested that if such association of pollen were repeated, it would be evidence that the pollen was produced early in the year before the bud scales were shed and the leaves expanded. Such pollen is not ordinarily seen on the leaves.

Very little search has been made for bud scales. One was noted with *Baiera furcata* but although its cuticle has some character and the scale appropriately contains resin, it does not seem worth description. It has *Ginkgo*-like stomata but no adherent pollen.

Seeds attributed to ***Baiera furcata*** (L. & H.)

Text-figs. 22 I–M

Black (1929, p. 42, text-figs. 10, 11) described and figured seeds and seed bearing axes he had collected at Scalby and attributed them to *B. gracilis* (*B. furcata* in this work) on the grounds of their association and also on the agreement of their stomata, particularly on their seed bearing 'petioles', with those of the leaf. He figured a stoma of the seed integument with

an isodiametric subsidiary cell group and another on the seed bearing axis where the cells are elongated. He mentioned that the axis bears 4 or 6 seeds but did not describe them in detail nor did he figure them. Unfortunately these specimens have not been traced, but more should be looked for.

We have examined a large number of seeds from Scalby collected by Black and by Thomas and others. These all look similar.

None of the present series is complete. They are isolated stones of seeds which have lost both flesh and integument cuticle and all but a few are mere half stones. These half stones are very characteristic, they show a central rock filled cavity and a sharply defined, broad compression border giving them a *Samaropsis*-like appearance. The substance is compressed to a thin coal which is crumbly so that nearly all the half stones are seen as internal or external moulds perhaps with a few crumbs of coal remaining. That in Text-fig. 22 1 is unusual in retaining half its coal. It is also unusual in showing a narrow compression border in part (bottom right), and a few other stones are like this.

The seed stones here accepted as *Baiera furcata* vary from 9·0 mm × 7·5 mm to 7·0 mm × 5·0 mm or 6·2 mm × 6·0 mm. Black's figures agree with these and as some (with a wrinkled surface) had the skin of the integument, the flesh must have been very thin. The compression border is usually about 1·5 mm, rarely 2 mm broad. The border becomes less distinctly marked towards the apex which is pointed, and it grows narrower towards the base which may be rounded or flat, or very slightly hollowed but then with a small median bulge.

A few stones are complete. Here the coaly substance scarcely shows the compression border though the inner part may have sunk. When the coal is removed a moderately clear border is seen around the central depression but the border is still not so definite as in the half stones. Where the border abruptly narrows, as in Text-fig. 22 1, we suppose that the stone has split above the rim and exposed the thickness of the stone apart from its rim.

Both surfaces of the stone show imprints of cells which are narrow but not very long. When normally macerated the stone substance dissolves, but when only half oxidized, crumbs are seen to consist of solid masses of stone cells. These are about 100μ × 25μ, and the walls are pitted and the lumen small. With a little more maceration the walls dissolve but sometimes an internal cast survives as a spindle armed with spikes, the filling of pits. There are also very fine threads which seem to be the filling of intercellular spaces. Both these dissolve with further maceration and they are difficult to mount, being soluble in glycerine. The seed of *Caytonia sewardi* yields similar but more resistant stone-cell casts.

Most half stones gave no internal cuticles at all but some yielded fragments of the megaspore and the rock mould filling the cavity is sometimes brown and this in transfers proved to be the megaspore. Compressed whole stones did give internal cuticles, but these are delicate, fragile and poorly preserved, partly we think because of degeneration before the seeds were preserved. They may well be abortive.

The seed in Text-fig. 22 D gave a collapsed megaspore much folded on itself and confined to the top. No other cuticle was seen. A similar seed from May Beck gave a similar megaspore but there was also a fragment of nucellus. Another whole seed yielded fair sized pieces of cellular cuticle, possibly all nucellar. Some of these merely show two similar layers of cells sticking together, slightly pitted walls and a mottled surface. Other fragments show similar but

longer cells and enclose brown matter, presumed to be the remains of the megaspore. The megaspore is 1μ–2μ thick, noncellular and very finely granular. The granules are crowded and probably less than 1μ wide. No cuticle lining the integument and no micropylar canal were recognized.

Discussion. These imperfectly known internal cuticles are merely those of a normal Gymnosperm seed with a megaspore membrane and a nucellus free in its upper part. *Ginkgo biloba* has such a seed, but so do Cycads and various other fossil Gymnosperms.

In the absence of the specimens we cannot usefully discuss the fruiting axes but clearly if they normally bear 4–6 seeds, this fact would be interesting in relation to specimens of *G. biloba* with more than the usual pair of seeds.

The present seeds are attributed to *Baiera furcata* on the evidence given by Black (1929) and on some further evidence of association. Similar seeds were found in another locality (May Beck Bed B) in a similar Upper Deltaic black clay. This clay also contains much *B. furcata*. The waste rock from both the Scalby and the May Beck material was macerated in bulk in the hope of finding seed integuments. None was found but the rock was full of *B. furcata* leaf fragments and nothing else was recognized apart from a lycopod megaspore.

The present seeds have stones only half the size of those of *Ginkgo biloba* but are similar in shape, and also have a prominent ridge or rim along the sides. The shell of the stone is, however, much thicker and normally splits along the rim but it does not so far as we know in *G. biloba*. The fibrous cells composing the stone appear to be similar, and what we know of the internal cuticles may also be comparable but it must be stressed that knowledge is incomplete and insecure and what we have, even if correctly interpreted, is not exclusively Ginkgoalean.

Male cone attributed to ***Ginkgo huttoni*** (Sternb.)

Text-fig. 23 A–H

1971 *Ginkgo huttoni* male fructification, van Konijnenburg-van Cittert, p. 45, pl. 9, figs. 3, 5; pl. 10, fig. 6; text-fig. 6.

Description (in diagnosis form). Male cone nearly 3 mm broad (length exceeding 6 mm), axis delicate, bearing loosely arranged appendages more or less at right angles. Appendages about 1·5 mm long, slender, at the end dividing into two short diverging branches (assumed to be microsporangia). Whole cone almost uncutinized. Pollen grains (adhering to cone) monocolpate, outline elongate-elliptical with acute ends; longest axis 35μ (extremes 29μ–42μ); colpus (in distal surface) extending about whole length of pollen grain, slit-like to broad; wall (exine) 1μ–1·5μ thick, consisting of two layers; nexine and sexine; nexine smooth, 0·5μ thick; sexine 0·5μ–1·0μ thick, not completely smooth, but structure rather vague.

The only specimen was collected by Dr van Konijnenburg–van Cittert from Scalby Ness, *Ginkgo huttoni* Bed, and deposited in the Botanical Museum and Herbarium, State University, Utrecht. No. 2967 (Yor-72).

The specimen is delicate and consists merely of coaly streaks in a fine-grained whitish sandstone. When dry it is only just visible but under oil (xylol or petroleum) it becomes more conspicuous. Certain parts were removed for maceration after it was drawn and thus the lower

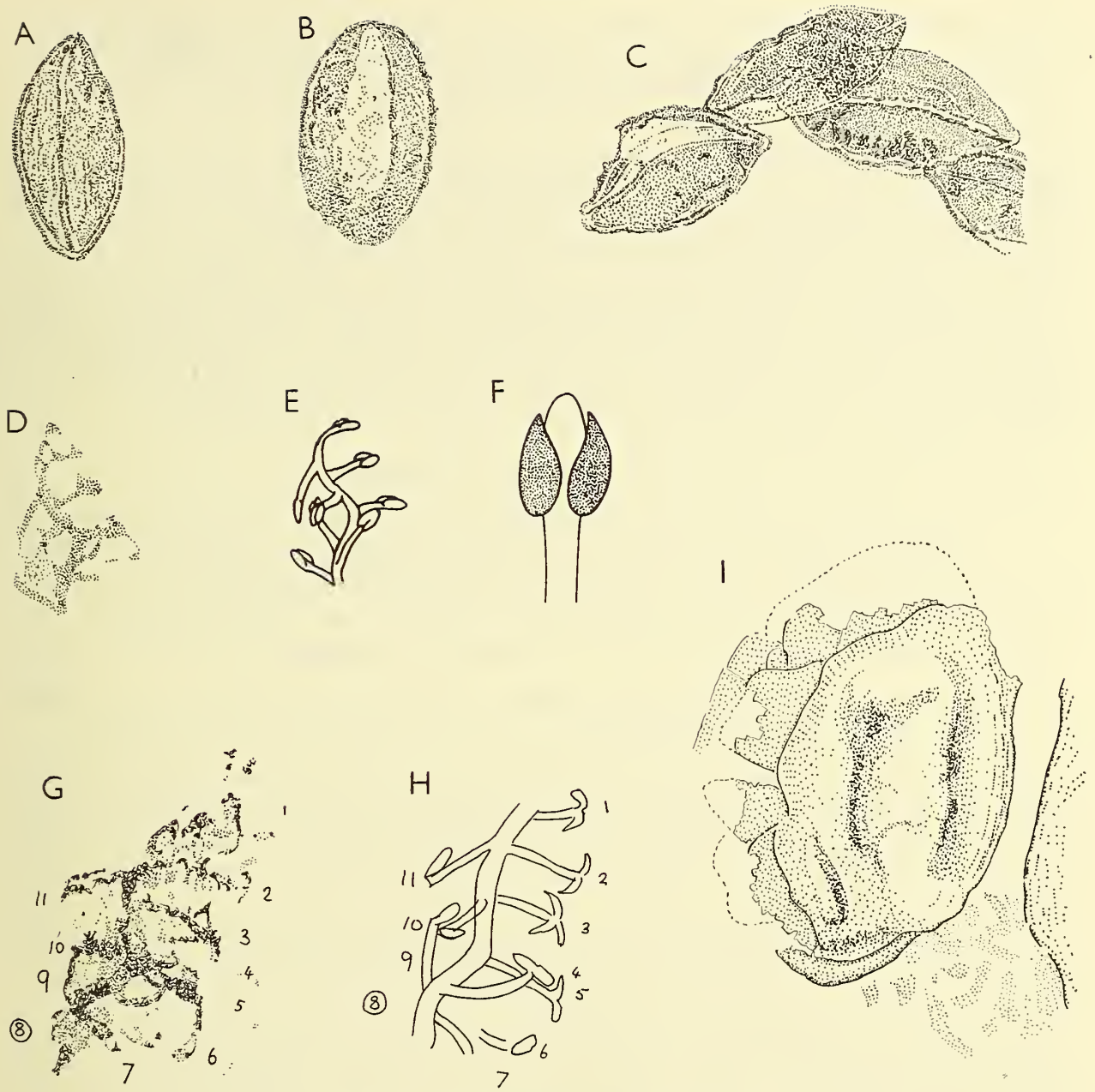


Fig. 23. **Ginkgo huttoni,** male cone and seed

A–G, drawings of the male cone in the Botany Dept of Utrecht University. A–C, pollen grains drawn from the photos of Van Konijnenburg-van Cittert (1971) × 1000. D, copies of original drawings and E, its restoration, magnification ×about 6. F, original restoration of microsporophyll (from text-fig. 6B–D). G, drawing of cone in its present state, as seen under petroleum (sporophyll 8 now missing). H, possible restoration with the pollen sacs shown divergent × 10. I, seed of *G. huttoni* with shreds of cuticle of seed-bearing head at the base and part of adjacent seed on the right (see also Text-fig. 22 P and Pl. 7, fig. 9) × 8. V.56411. Scalby Ness.

(Figs. A–G by permission of Van Konijnenburg-van Cittert, University of Utrecht.)

part now looks somewhat different from the original figure, the appendage (number 8 in Text-fig. 23 E) has vanished but some others are better exposed than in the original figure. The new drawing is based on re-examination of the specimen and on photographs taken under petroleum and provided by Dr van Konijnenburg–van Cittert. We give a slightly different restoration from hers as we think the pollen sacs (some of them) diverge from one another and from their stalk much as they do in an old and withered *Ginkgo* male catkin. There is no sign of any extension of the sporangiferous stalks (sporophylls) beyond the sporangia. It is a pity the specimen is not better preserved as all that can be said of its form is that it can be readily interpreted as just like a *Ginkgo* male cone, but we cannot be certain that it really is one. If it were not for the *Ginkgo*-like pollen grains found adhering to this small cone, it would barely seem worth describing. These grains were not obtained from intact pollen sacs, of which there are none, and indeed their precise position is unknown, but since they are fairly numerous and all look much alike we agree that it is reasonable to believe that they belong to it.

The specimen is attributed to *Ginkgo huttoni* on the following grounds:

(1) It is associated in the Scalby Ness *Ginkgo huttoni* Bed with great numbers of *G. huttoni* leaves. Other species do occur in the same bed but none is particularly common. On this block there is only *G. huttoni* and the conifer *Haiburnia blacki*.

(2) Its width and its form, as interpreted, agree well with the *G. biloba* male cone.

(3) The pollen adhering to it agrees closely with that of *G. biloba*.

(4) The pollen of this cone also agrees closely with grains adhering to certain bud scales of *G. huttoni* (from another locality).

If we accept it as the male cone of *G. huttoni* it gives strong support to the general conclusion that *G. huttoni* is a species of the genus *Ginkgo* in the strict sense. But it will be appreciated that we have already used its resemblance to the male cone of *G. huttoni* in form and in pollen for its identification with that plant. Further specimens need to be found and examined.

The original account emphasizes the acute ends of the colpus in the pollen of this cone and of *G. biloba* as against its more rounded ends in Cycadales. (In the Bennettitales the sulcus is often pointed also.) Apart from this Ginkgoalean and Cycadalean pollen are much alike.

Heer (1876, p. 59, pl. 10, fig. 8*c*) identified a very different fossil as the male amentum of *Ginkgo huttoni*. His figure closely resembles that of *Stenorhachis lepida* from the Amur and from Afghanistan figured by Seward (1912, 1912*a*) which we regard as an *Ixostrobus*. In this work and also in 1878 and 1880 Heer figured a whole series of amenta attributing them to particular species of *Ginkgo*, *Baiera* and *Czekanowskia*. A good many of these are *Ixostrobus* and almost certainly are not related to *Ginkgo* or *Baiera*, but others may belong to the Ginkgoales. These are the rather delicate amenta with slender microsporophylls apparently bearing terminal pollen sacs, i.e. there is no extension beyond the pollen sacs, if the figure is reliable. He identified them as *Baiera czekanowskiana* and others as *B. longifolia*. Other cones identified as *B. longifolia* do have such an extension, however. Prinada (1962) refers both sets of cones to *Sorosaccus sibiricus* but no extension is obvious in his figures. Presumably catkins with an extension are not organs of *Ginkgo* or *Baiera*.

2. Czekanowskiales

Pant (1957) named this order as an isolated Gymnosperm group. He did not define it, and even now we cannot define it satisfactorily. We cannot even characterize any member fully but what we know does set *Czekanowskia* apart from other Gymnosperms. Krassilov (1968, 1970) has given us a fuller picture but it is still incomplete. He includes narrow leaves (*Czekanowskia* and *Hartzia*) and broader ones of the *Phoenicopsis* group. The fruits he accepts are *Leptostrobus* and *Staphidiophora*, and the male cone *Ixostrobus* as probable but less certain.

Until the fruits were recognized, *Czekanowskia* was confidently placed in the Ginkgoales as an extreme member of the series. Its forking leaves form thin threads, but several species of *Baiera* (always included in the Ginkgoales) are very similar. Its cuticle is easy to accept as Ginkgoalean and some kinds of *Baiera* are similar, but it must be remembered that it is of the basic type most widespread in Gymnosperms (e.g. the Cycadales). However, Oishi (1930) pointed out some differences. The way the leaves are borne—on a caducous short shoot—is shared by other genera normally placed in the Ginkgoales, e.g. *Phoenicopsis*, and even by certain species hitherto included in *Sphenobaiera*, i.e. *Sphenarion*, and though this is different from *Ginkgo*, the difference has not been regarded as important. Previous authors have included *Czekanowskia* in the Ginkgoales unreservedly, or at least as a sensible treatment for isolated foliage.

It was the female fructification *Leptostrobus* which upset this. When Heer (1876, 1880) described *Leptostrobus* from Siberia he thought it a conifer female cone allied to *Voltzia*, and that its association with *Czekanowskia* was accidental. He did however attribute some associated reproductive organs to *Czekanowskia* though subsequent authors did not consider them seriously. Some of these organs do look like *Leptostrobus*, and it is interesting that foliage which Heer attributed to *Leptostrobus* looks like *Solenites* and may belong to that genus. Thus Heer came near to the present position without realizing it. Harris (1935) described some Greenland specimens of *Leptostrobus* which he attributed to *Czekanowskia*. The evidence was not impressive, and the nature of its fertile capsules was uncertain; he thought they might be cup-shaped and have produced pollen. Unfortunately a well-preserved immature specimen which did produce seeds was described under another name (*Microcheiris enigma*). In 1951 Harris described Yorkshire material, and showed that the capsules produced seeds and were composed of upper and lower valves, like an oyster. The nature of *Microcheiris* was recognized and reasons for attributing the fossils to *Czekanowskia* or *Solenites* were stated explicitly. The evidence published in 1935 apparently did not convince others but the 1951 statements were widely accepted. Since then, Russian authors have given supporting evidence. At first this evidence (from association) seemed confused by the presence of leaves of *Phoenicopsis* but Krassilov (1968, 1970) has reached the conclusion that these leaves are closely allied to *Czekanowskia* and also have *Leptostrobus* fruits. He has added considerably to our morphological understanding of *Leptostrobus* as well, though his findings are so far only published in a preliminary form.

We pick out a list of what seem to be salient points of these diagnoses, and of those of some other genera, and we offer it provisionally; not as a firm characterization, but as a list inviting correction.

Provisional list of characters

Foliage leaves persistent, but borne in limited numbers on caducous short shoots, short shoots surrounded with scale leaves. Foliage leaves elongated, simple or dichotomizing, vein single at base of leaf but normally forking several times, not anastomosing, and each vein ending in a separate leaf lobe or at least a separate point at the terminal margin. Leaf well cutinized, if narrow amphistomatic and with numerous stomatal files unrelated to veins; if broad, sometimes hypostomatic and with stomatal files avoiding veins. Subsidiary cell group normally elongated, forming pit round sunken guard cells. Ducts if present not containing resistant resin. Female cone an elongated axis bearing numerous scale leaves below and loosely arranged seed capsules above. Seed capsules wedge-shaped or rounded, almost sessile on cone axis, or shortly stalked and stalk sometimes with a few scale leaves (Krassilov 1968, 1970). Capsule composed of similar upper and lower valves. Valves with somewhat lobed terminal margin. Each valve bearing row of small elongated seeds on its inner face; seeds delicately cutinized but with distinct megaspore membrane. Chalaza situated just under each valve lobe, micropylar end facing cone axis. Seeds readily lost from ripe capsules. (Male cone possibly *Ixostrobus*.)

This list of characters is intended to cover *Czekanowskia*, and the two very similar monotypic foliage genera *Hartzia* and *Solenites*, together with some at least of those usually included in *Phoenicopsis*. These were described by Florin (1936) from Franz Joseph Land, *Stephanophyllum*, *Windwardia*, *Arctobaiera*, *Culgoweria*, and to these we add certain leaves of the *Sphenobaiera* shape, i.e. those borne on caducous short shoots such as *Baiera pauci-partita* Nathorst here included in *Sphenarion*.

Some of the above-mentioned characters deserve further discussion. The statement that the leaf of *Czekanowskia* has a single vein at its base is due to Florin (1936). He showed that *Czekanowskia* leaf bundles preserved as lignite, when sectioned, displayed a single well-defined vein at the leaf base, which later divides. This is equally true of the *Phoenicopsis*-like leaves *Arctobaiera*, *Stephanophyllum* and *Windwardia*. On the other hand, *Ginkgo* as is well known has two bundles in its petiole and these arise separately from different bundles in the stem. The taxonomic weight of this difference is doubtful; Florin himself considered it was small for he placed all these genera in the Ginkgoales. Apart from Florin's work we have little information; for most Ginkgoalean leaf bases are dense and show no veins; this is also true of *Czekanowskia* and *Solenites*. A few fossil *Ginkgo*-like leaves do show just two dark strands in the petiole (Lundblad, 1959).

There has been divergence of opinion about the number of veins in a leaf of *Czekanowskia*, and also of *Solenites*. Apart from sections, the veins of a fossil leaf are recognized on the following evidence. (a) The vein may form a visible ridge on the surface. (b) It may form a dark strand as seen by transmitted light and in the most favourable specimens tracheids may be recognized. (c) It may be marked by differences in the cuticle, for instance on the lower side

there may be stomata between the veins and none along them. (d) Each vein may end separately at the leaf apex in a little tooth. (e) The units considered to be veins may branch in the manner of veins near the leaf base.

Where these lines of evidence agree unequivocally there is no doubt. But in *Solenites* and *Czekanowskia* it is not so clear. No ridge is seen along the leaf to mark the vein and the distribution of stomata has no relation to veins. We may have dark strands (in favourable specimens which had to some extent rotted before preservation and had become partly macerated and cleared). Secondly we have the leaf apex and the behaviour of these dark strands in relation to the apex and to any leaf dichotomies.

The dark strands seen in naturally cleared leaves have been interpreted variously. In *Czekanowskia hartzi*, Harris (1935, p. 38) figured leaf fragments which showed a single robust dark strand ending in a pointed leaf apex or one which divides to give two below a dichotomy.

Florin (1936, p. 140) strongly affirmed that *Czekanowskia* segments have two veins and four below a dichotomy and based this on a naturally cleared fragment of *C. rigida* in the region of a dichotomy. This shows some dark lines which he dismisses as folds (doubtless with good reason) and two or four slender strands which he considers as vascular bundles. The specimen is not very satisfactorily preserved (see Florin's pl. 38, fig. 14). Possibly the veins are different in *C. hartzi* and *C. rigida* but probably not. We suggest that in this naturally cleared fragment the dark strands are not whole bundles but separate fragments of one or two bundles. We believe the bundle in *C. blacki* and in *Solenites* disintegrates in the same way after decay.

Fossil leaves in general which have suffered decay before preservation often show their fibro-vascular elements clearly by transmitted light and these may separate from one another and be laterally displaced. Further it may be noted that Florin's sections of the *Czekanowskia* bundles show groups of tracheids separated by softer cells and such bundles might well disintegrate after decay. Florin on the other hand regarded the dark strand (or two dark strands), shown in Harris's figures, not as veins at all, but as softer tissue between veins. He had no cleared leaf apex and did not consider the venation of that part of the leaf.

In *Solenites* the better preserved leaves are massive and show no internal details, but there are many naturally cleared specimens showing dark longitudinal strands in the interior. There may be a broad one, or two separated by a paler gap, or there may be three (a common number) or there may be four, and these three or four tend to wander somewhat and may merge but scarcely in a way that suggests either true branching or true anastomosis. Between the main dark strands there may be an isolated thick walled fibre.

Naturally cleared apices were specially looked for and a number were found in which there were two dark strands which converge and unite as a single strand at the apex. We have no naturally cleared leaf bases to show the origin of these dark strands. The simplest explanation of the various appearances in cleared leaves is that they have a single rather broad bundle which easily disintegrates on decay. These dark strands of *Solenites* seem very different from those of *Hartzia tenuis* figured as whole bundles by Harris (1926) under the name *Phoenicopsis tenuis* and again in 1935 as *Hartzia tenuis*. There, the dark strands are often very conspicuous and pursue a steady course from a point near the leaf base where their origin can sometimes

be seen as a forking of a single strong dark strand to the leaf apex where each one ends separately in a little tooth. This is equally true of the narrow leaves with two and the broad leaves with four veins.

Very few Yorkshire *Czekanowskia* fragments were found which were sufficiently transparent to give any evidence. But a block of *C. blacki* from Scalby Ness, collected by M. Muir, yielded leaves which varied from black and opaque to quite pale, and the pale ones showed internal strands. Many of these look convincingly single but others show two or more strands which we believe, as in *Solenites*, are not whole bundles but disintegrated fragments of one broad bundle. As in the naturally macerated *Solenites* leaves, they wander about.

Apart from the single basal vein, another feature that *Czekanowskia*, *Solenites* and the various genera of the *Phoenicopsis* group share is that the leaves are borne on a short shoot covered with small scale leaves and this short shoot holds its foliage leaves firmly and the whole shoot falls off intact. The short shoot is evidently of strictly limited growth forming its group of leaves, 5–18, often about a dozen, all at once.

In *Ginkgo biloba* leaves are borne on long or short shoots and in the end fall off the shoot. Short shoots continue to produce leaves in unlimited numbers. For most Ginkgoales (i.e. excluding Czekanowskiales) we only know separately preserved leaves but these show cleanly cut off bases, as do fallen leaves of *G. biloba*. It is most likely that in these fossils the leaves are borne much as in *G. biloba*.

This difference is one to which some taxonomic weight is given but not usually very much. For instance, *Pinus* is distinguished generically from all other Abietineae by its possessing such caducous short shoots of strictly limited growth, but it is in the same family as *Cedrus* and *Picea*. In the Ginkgoales Florin gives it less than generic weight, for example, he puts species without such short shoots and species with them both in *Sphenobaiera* (*S. spectabilis* and *S. paucipartita*) and he puts *Eretmophyllum* and *Stephanophyllum* next to one another in a generic key. Here he was following current practice.

Though we feel no great assurance in using this character to separate the *Ginkgo* assemblage from that of *Czekanowskia*, we do in fact use it. The groups, as a whole are appallingly ill-provided with taxonomic characters in their foliage which would indicate a major division. Here is one, the only one we know, and we prefer to use it rather than neglect it. It could well be that a single basal vein (in Czekanowskiales) as against two (in Ginkgoales) is another character separating the two classes generally. But we have too little evidence.

There may be some difference between the Ginkgoales and the Czekanowskiales in their resin contents. As is well known, Ginkgoalean leaves often contain spindle-shaped resin cavities and in fossils the resin, forming a kind of amber, resists maceration. *Czekanowskia* and some members of the *Phoenicopsis* group certainly possess small ducts between pairs of veins (Florin 1936) but so far as we know these never yield resin that is resistant to maceration —the duct just vanishes. Some leaves, however, which are confidently placed in the Ginkgoales (as species of *Ginkgo*) have no resin at all, and we have the leaf described by Harris (1935) as *Baiera leptophylla* which has bundles of leaves as well as resin bodies.

There are in Yorkshire only three genera and one of these is imperfectly known from a single specimen. There is nothing like *Phoenicopsis*. We have tried to distinguish these genera by easily visible characters, keeping the cuticles for the species, but we have been unable to

do this as consistently as we wished because we were unsure of certain facts. We would have separated *Czekanowskia* from *Sphenarion* on the number of veins in an ordinary segment, one we believe in *Czekanowskia*, though this is in dispute, and more than one in *Sphenarion*. Various species of *Sphenarion* certainly have several but the single specimen here described hardly shows its veins at all but we guess there are at least two. So we reinforce this by the fact that its cuticle is unlike that of *Czekanowskia*.

Generic key to the Czekanowskiales

(1) Leaves about 1 mm or less broad (believed to have a single vein)
  (a) Leaves entirely unbranched . . . . . *Solenites*
  (b) Leaves forked . . . . . *Czekanowskia*

(2) Leaves broader than 1 mm (believed to have more than one vein) . . . . . *Sphenarion*

The character of forking while obvious even in small pieces of some species (e.g. *C. microphylla*) requires large specimens of some others to demonstrate; e.g. *C. furcula* leaves, about 180 mm long, seem to fork but once and some leaves of a bundle possibly not at all. Harris (1951) considered that forking did occasionally happen in *Solenites* but we now believe that the forked specimens belong to one of the species of *Czekanowskia* not at that time recognized.

The species of the narrow-leaved *Czekanowskia–Solenites* group are difficult to distinguish, and this causes the long and wide range of the names *C. setacea* and *C. rigida*. In this work we recognize five species based on good specimens and these are given specific names. Less good specimens, which are very common, are named more doubtfully or not at all. Even the five best gave trouble, for specimens of each which we select as typical are not very different from those of the other species and there is also considerable variability among the specimens identified as belonging to each of these five species.

We considered the possibility that our material might, because of its nature, prove unsuitable for division into species. There might, for instance, be very many taxonomic units separated by morphological differences too small and too indefinite to recognize in the Yorkshire fossil leaves. There might even be continuous variation. However, we prefer to use the idea that there are just a few taxonomic units (species), and that these are really distinct, though requiring knowledge of good material to separate. The field evidence is in our view consistent with this. This conception we consider more likely to contribute to botanical and geological progress than description without specific boundaries. *Czekanowskia* leaves characteristically make bad fossils, for the dwarf shoots disintegrate when rotten, and the long leaves break into short pieces. The cuticles remain, but these look rather alike in the different species.

It is convenient also to save the well-known genus *Czekanowskia* from becoming a synonym. Harris (1951) was the first to revive *Solenites* as a fully valid genus. Previous authors (e.g. Seward 1900, Florin 1936) used the name *Czekanowskia murrayana* (L. & H.) and at the same time gave diagnoses of *Czekanowskia* which would have excluded this species (with its simple leaves).

Key to the Yorkshire Species of Czekanowskiales

All the species included in this key are known to have leaves in a persistent bundle of 5 or more on a caducous short shoot.

(1)	Leaves unbranched, linear	*Solenites vimineus*
	Some leaves at least forked	2
(2)	Leaves up to 2 mm broad and under 50 mm long	*Sphenarion muiriae*
	Leaves up to about 1 mm broad and over 50 mm long	3
(3)	Leaves forked once at most	4
	Leaves forked 2–3 times	5
(4)	Leaves mostly about 1 mm wide and over 120 mm long	*Czekanowskia furcula*
	Leaves well under 1 mm wide and under 120 mm long	*Czekanowskia thomasi*
(5)	Leaves forked twice	*Czekanowskia blacki*
	Leaves forked three times or more	*Czekanowskia microphylla*

Cuticle Characters

We are unable to key out these species on cuticle characters alone but the following characters separate most specimens of Yorkshire leaves.

Sphenarion muiriae	Broad cells, exposed stomata.
Solenites vimineus	Cells rather long, surface flat, stomatal pits mostly narrowed laterally.
Czekanowskia furcula	Stomatal pits mostly wide with a rim all the way round (suggesting frame of a picture or a window).
Czekanowskia thomasi	Cell surface usually with a thickened pad, stomatal pits often very long and narrow.
Czekanowskia blacki	Cells of stomatal files short, cells between stomatal files very long, cell surface with a thickened pad; stomatal pits mostly narrow.
Czekanowskia microphylla	Cell surface thickened, stomatal pits of very varied shape.

Relationships of the Czekanowskiales

While we only knew the leaves, *Czekanowskia* and *Phoenicopsis* seemed easy to place among the Ginkgoales. But *Leptostrobus* is quite unlike the seed-bearing organ of *Ginkgo*. Now we have Krassilov's idea that the *Leptostrobus* capsule is comparable with a *Czekanowskia* dwarf shoot, but with a shorter stem, more or less suppressed scales and just two leaves which bear ovules adaxially, the difference seems increased. The morphology of the *Ginkgo* female organ is debatable but since its origin is axillary, it is scarcely to be regarded as a true sporophyll though that idea has been supported. Nearly all see it as some sort of reduced axis, and Florin (1949) summarizes the various confused interpretations. We know so little about fossil *Ginkgo* or *Baiera* fruits that they give little help. The Permian *Trichopitys* which Florin regarded as a true primitive Ginkgoalean suggests that the ovule-bearing axis of *Ginkgo* has become much reduced, but is still a real branched axis. We cannot see a *Leptostrobus* valve as a branched axis.

We would rather compare *Leptostrobus* with the more leaf-like ovuliferous organ of a

Pteridosperm or a Cycad, but clearly it is different and any connection must be remote. We see no resemblance to the ovule-bearing organs of Bennettitales or Coniferales or Taxales; with the Caytoniales there are a few points of agreement but homology only unless *Caytonia* has been greatly misunderstood.

Krassilov (1970) also likened a *Leptostrobus* capsule to a bicarpellary ovary of an Angiosperm and further suggested that the papillose rim (in some species) was stigmatic. We agree there is resemblance to an ovary but regard it as the result of convergent evolution. In the Mesozoic and later we have several different ways in which ovules are protected—the compact cone of Conifers and modern Cycads, the *Caytonia* 'fruit', the Bennettitalean gynaecium and now *Leptostrobus*. We think that *Leptostrobus* was pollinated in a purely gymnospermous way (the capsules opening to admit pollen) but we recognize that facts are scanty. *Ixostrobus* is left out of this discussion because we are uncertain that it belongs to *Czekanowskia*. Even if included it would not help. It can be compared with *Ginkgo* but such comparison is ruled out by the female organs. It is very far from a Pteridosperm microsporophyll.

We thus reach the unwelcome conclusion that the Czekanowskiales at present are isolated. We do not imply that they have no relationships but merely that we see no way to link them convincingly. This has unfortunately become normal for the main classes of the Gymnosperms. It was said many years ago that the 'phylogenetic tree' had become less like a tree than a bundle of sticks! Now there are more separate sticks than when that was said. We need to find clear links among the fossils not less than we need to know our present fossils better. It is easy by using the imagination to build sticks into a coherent tree but the exercise is no longer held in esteem, for we know it can be done in many different ways.

However isolated as we must regard them we have no doubt that the practical place to put them is next the Ginkgoales because their commonest fossils—the leaves—are so much alike that they are difficult to separate. It is much the same for the Conifers and Taxales.

Range in space and time

Until the last few decades, information was scattered and one could only say that the Czekanowskiales are met in the Rhaetic and become widespread in the Jurassic and Lower Cretaceous of the Northern Hemisphere, but especially in Siberia. Recent work by Russian authors, summarized by Vachrameev, Dobruskina, Zalinskaya & Meyen (1970) has given us a remarkably interesting picture. The Czekanowskiales are consistently northern in distribution in the Northern Hemisphere; thus in the Jurassic of Western Europe they are seen in the floras of Yorkshire and of Scotland, but not of Central or Southern Europe. By Middle Jurassic times *Czekanowskia* was very widespread and at its maximum but *Phoenicopsis* was less widespread and did not occur so far west. In the Upper Jurassic both appear to have lost much of their more southern distribution (though this may be partly due to there being rather fewer floras available). By the Lower Cretaceous they have vanished from the West and South but persist in large numbers in North and East Siberia where they overlap the earliest Angiosperms; then they are seen no more. Some other genera behave similarly (e.g. *Coniopteris*) but there are many like several Bennettitalean genera which behave in a strongly contrasted way. Their data are summarized on pp. 277–278, text-figs. 33–35. They also give many references to the occurrence in the U.S.S.R. of Czekanowskiales not available to us.

Genus SOLENITES Lindley & Hutton 1834, p. 105

1951 *Solenites* L. & H.: Harris, p. 484.

Solenites vimineus (Phillips) is the oldest described species of the whole group. Phillips (1829) sketch of a Gristhorpe specimen under the name *Flabellaria* (?) *viminea* is a poor one but there is nothing else it is likely to apply to (see Seward 1900, p. 280). We consider the specific name valid but not the generic, for *Flabellaria* had been applied to very different fossils earlier. Phillips work was apparently overlooked by Lindley & Hutton (1834) who gave a good figure under the name *Solenites murrayana* (even including a crude figure of the cuticle) and discussed it at some length. They thought it an ally of *Isoetes* and Brongniart (1849) accepted this and renamed it *Isoetes murrayana*. This work was completely overshadowed by Heer's account of the Siberian fossils he called *Czekanowskia*, so much so that later authors (e.g. Seward 1900, Florin 1936) regarded *Solenites* as a synonym of *Czekanowskia* in spite of its earlier publication in a very well known work. In a way, they went further in its debasement for both Seward and Florin gave diagnoses of *Czekanowskia* which would have excluded '*C. murrayana*' with its simple leaves. Credit is due to Nathorst (1906) who pointed out that there was a case for using the name *Solenites* for short shoots bearing simple leaves and *Czekanowskia* for similar short shoots with branched ones. But he did not press this idea and Harris (1951) was the first to take it up and revive *Solenites*.

This distinction seems simple and obvious and we know no other difference of generic value. This course besides conforming to the rules has the merit that it saves the much used generic name *Czekanowskia* from becoming a synonym, as it would if *Solenites* were considered to be of the same genus as the forked leaves. Heer (1876) did indeed discuss *Solenites* in relation to his new genus *Czekanowskia* but decided that it was too poorly characterized and therefore rejected it.

No other species has been placed in *Solenites* but as Seward pointed out, Heer's (1880) Siberian specimens *Leptostrobus angustifolius* and *L. rigida* look like it. Prinada (1962) names these *Angariella* and relates them to *Isoetes* rather than to *Czekanowskia*. This recalls the view about *Solenites* held by most authors until 1900.

The specimen described by Seward (1911*a*) as *Czekanowskia murrayana* from the Upper Jurassic of Scotland should, as Seward's text indicates, be called *Czekanowskia* sp. indet.

We feel sure that *Czekanowskia murrayana* of Yokoyama (1906) is distinct as its leaves (or leaf segments) are stouter than in the Yorkshire specimens. *Czekanowskia murrayana* described by Krasser (1905) from Mongolia is indeterminable from the figure.

Diagnosis (slightly emended from Harris, 1951). Caducous short shoot covered with scale leaves and bearing persistent foliage leaves. Foliage leaves filiform, simple, not forked at all, ending in an acute apex; leaf substance thick, leaf probably oval in section. Venation consisting of broad central strand often divided into 2, 3 or 4 indefinite subordinate strands. Resin bodies absent.

Cuticle well-developed, similar on the two sides, amphistomatic; stomata occurring mainly in more or less short longitudinal files unrelated to vascular tissue. Epidermal cells with nearly straight walls, commonly forming longitudinal files. Stomatal files almost evenly distributed over whole epidermis (including leaf margins). Stomata longitudinally orientated, haplocheilic,

guard cells sunk in a pit formed by 4–8 subsidiary cells, 2 of which are terminal. Pit commonly reduced by rim or papillate pads of subsidiary cells. Encircling cells occasional.

Type Species. *Flabellaria viminea* Phillips 1829, pp. 148, 154, pl. 9, fig. 4.

Discussion. This emended diagnosis differs from Harris (1951*a*) in excluding forked leaves and in mentioning the occurrence of three dark strands (the commonest number) in certain naturally cleared leaves, and in describing the cuticle.

Thus this diagnosis is almost the same as that given for *Czekanowskia* except that the leaf is simple (always so far as we know), and the vascular strand also fails to dichotomize. It remains simple to the apex, but in *Czekanowskia* the vein forks well below a dichotomy. Thus the simple form of the leaf (and related simpler venation) is the sole distinction between the two genera. A *Solenites* leaf is only slightly narrower than a leaf of *Hartzia* Harris (1935). *Hartzia* differs in having two or occasionally four very distinct veins and these end separately in little lobes at the leaf apex. *Solenites* tapers to a single point and here all the vascular tissue converges.

Solenites vimineus (Phillips) Harris

Pl. 4, figs. 1, 2; Text-figs. 24, 25

1829 *Flabellaria* (?) *viminea* Phillips, pp. 148, 154, pl. 9, fig. 4. (Name and rough sketch)
1834 *Solenites murrayana* Lindley & Hutton, p. 105, pl. 121. (Good figure, description)
1848 *Isoetes murrayana* (L. & H.) Brongniart, p. 105. (Name)
1900 *Czekanowskia murrayana* (L. & H.) Seward, p. 279, text-figs. 48–50. (Discussion and references not all belonging to this species)
1906 *Czekanowskia murrayana* (L. & H.): Nathorst, p. 11. (Discussion of genus *Solenites*)
1919 *Czekanowskia murrayana* (L. & H.): Seward, p. 64, text-fig. 660. (As 1900)
1936 *Czekanowskia murrayana* (L. & H.): Florin, pp. 129, 131. (Brief discussion)
1951 *Solenites vimineus* (Phillips) Harris in part, p. 915, text-fig. 1 B-E, G, I, J, text-fig. 2. (Text-figs. 1 A, H refer to *C. furcula* and text-fig. 1 F may be *C. thomasi*)
1951*a* *Solenites vimineus* (Phillips): Harris, p. 502, text-fig. 3 H-K. (Stomata, relation to *Leptostrobus cancer*)

Emended Diagnosis. Short shoot small, about 5 mm × 5 mm, covered with bud scales, but these scales commonly lost. Outer scales rounded, about 1·5 mm wide, fairly robust; inner ones more delicate. Outer scales fibrous below, becoming delicate and scarious towards margin. Occasional inner scale leaves with irregularly toothed margin. Cuticle moderately thick, cells forming more or less elongated polygons; surface finely mottled, lateral walls distinct, sometimes appearing moniliform. Stomata occasional, like those of leaf, or less regular, but usually broader. Towards the delicate margin the two cuticles usually adherent and giving double set of cell outlines. Scales of elongated shape intermediate between bud scales and foliage leaves sometimes present, length up to 20 mm, apex pointed.

Foliage leaves in bundle of 11 to 16; length typically about 180 mm. Width increasing from 0·5 mm to 0·7 mm above base to about 0·8 mm, occasionally reaching 1 mm and then constant to near apex where it diminishes. Leaf probably about half as thick as broad, margins rounded. Leaf apex attenuated but minutely rounded at tip. Cuticle normally becoming more delicate towards apex, but cells not specialized, no stoma or trichome present at apex.

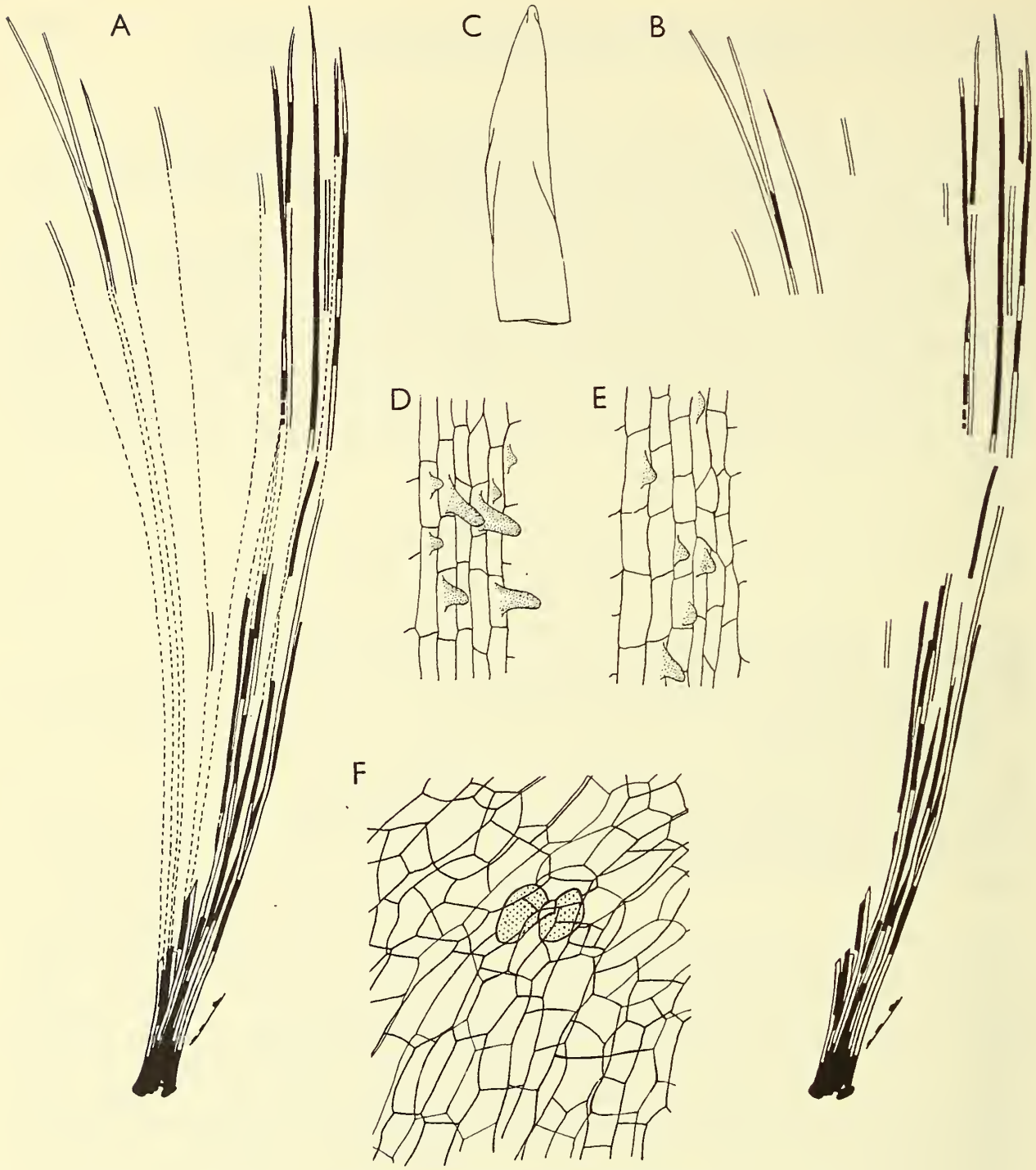


Fig. 24. **Solenites vimineus** (Phillips)

A, bundle of sixteen leaves, partly restored, actual size. Solid black indicates leaf material; empty black lines, an imprint; one dotted line, left side of a buried leaf, two dotted lines, a restored leaf not seen in the specimen. 13518. B, the same bundle of leaves, actual size. Actual leaves or clear leaf prints shown only. C, cuticle of leaf tip, magnification ×20; slight crushing shown.V.56478. D, cuticle with trichomes from extreme leaf base, magnification ×200, V.56479. E, cuticle with papillae from leaf base, magnification ×200, V.56479. F, portion of bud scale, the two cuticles adherent, one with a stoma, subsidiary cells stippled, magnification ×200, V.56480. A, B, Gristhorpe Bed. C–F, Cloughton Wyke *Solenites* Bed.

Substance of leaf very dense, often showing thicker central region occupying $\frac{3}{4}$–$\frac{7}{8}$ of the width with a thinner marginal region. Central region, after natural rotting, often showing 2, 3 or 4 dark strands and a few longitudinally orientated isolated fibres, 5μ–10μ in width and of variable length. Dark strands not at all represented in cuticle. Mesophyll sometimes represented as small blocks which may be placed in longitudinal files and sometimes by separate irregular blocks. Resin bodies absent. Cuticle thick, 5μ–9μ in folds, sometimes one side slightly thicker than the other, more often no discernible difference. Margins of leaf showing no difference from surfaces (apart from signs of crushing). Stomata placed in 5–10 longitudinal files on each surface, but some files ill-defined, and some stomata occurring out of any file. Files rather unevenly spaced, not forming compound stomatal bands. Epidermal cells between stomatal files elongated, several times as long as broad and forming short longitudinal files of cells with transverse or rather oblique ends; cells at ends of file with a pointed end. Cells between successive stomata of stomatal files shorter and sometimes square (also forming longitudinal files). Lateral and end walls of cells broad and prominent, usually straight and continuous, sometimes interrupted by small pits, never sinuous or flanked by teeth. Cell surface flat or slightly bulging, finely mottled, exceptionally showing faint longitudinal striae, under phase contrast often showing large thickened pad in middle of cell or few smaller pads. At leaf base, particularly on inward-facing side of leaf, cell surface often much thickened and bulging or forming conical trichome up to 30μ wide at its base. Trichomes otherwise absent and not always present even on leaf base, and unevenly developed on different leaves of a single bundle.

Stomata always longitudinal, and subsidiary cell-group nearly always elongated, most commonly with 2 terminal and 2–4 lateral subsidiary cells. Outer surface of subsidiary cells rather darker than rest of epidermis. Surface, especially of lateral subsidiary cells, often showing conspicuous thin strip. Stomatal pit narrow. Rim of cuticle of lateral subsidiary cells sometimes constricting mouth of stomatal pit to a slit, but pit sometimes wide and exposing part of the guard cells. Rims of lateral subsidiary cells usually continuous, but sometimes projecting over pit as separate broad papillae. Terminal subsidiary cells often with smaller undeveloped rim. Encircling cells occasional, where present unspecialized and unthickened.

Near leaf apex cuticle of reduced thickness, cells shorter and stomatal apparatus often isodiametric. Near leaf base stomata absent or very few.

LECTOTYPE. Specimen figured by Phillips (1829, pl. 9, fig. 4).

DISCUSSION. This account differs from that of Harris (1951) chiefly in rejecting some of the specimens there described. We think that all of the material in the Cloughton *Solenites* Bed (where it is very abundant in certain layers) belongs to this species and that many specimens in the Gristhorpe Bed (from which Phillips obtained his *Flabellaria viminea*) belong to it, but at Gristhorpe there are *Czekanowskia microphylla* and *C. thomasi* also. The forked leaves from Whitby (Harris 1951, text-fig. 1 A) and the galled ones (text-fig. 1 H) are *Czekanowskia furcula*.

The only specimen showing the full length of the leaves is one collected by Murray from the Gristhorpe Bed and figured here (Text-fig. 24 A, B). None of the leaves is forked, and we have seen no forking in any leaf we can identify with *Solenites vimineus*. Not one forked

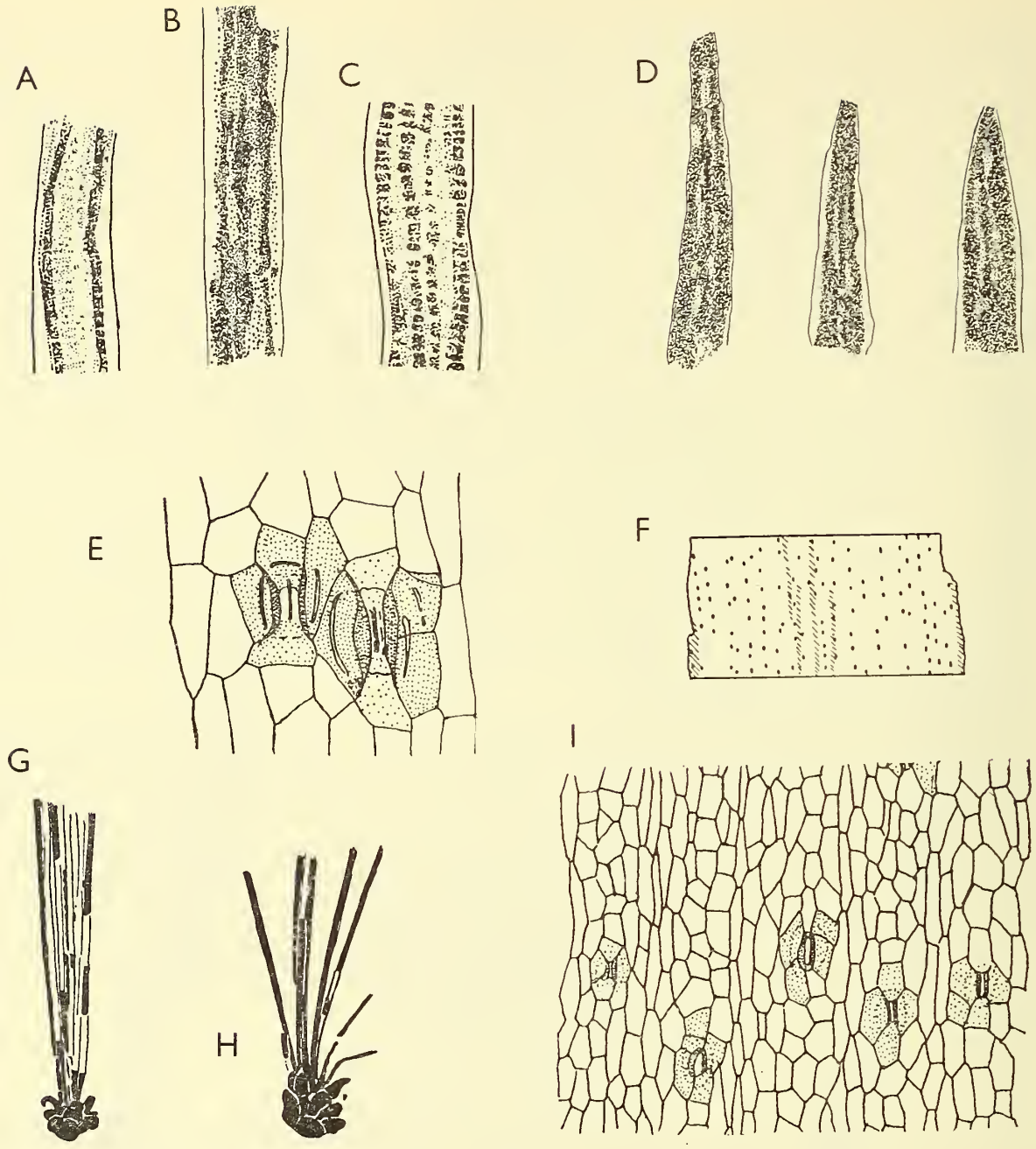


Fig. 25. **Solenites vimineus** (Phillips)

A–C, three naturally translucent leaves showing two, three and four dark strands respectively, all magnification ×20. A, C, are from Haiburn Wyke Plant Bed. V.28437, figured Harris (1951, text-fig. 1 B, C); B is from Cloughton Wyke *Solenites* Bed, V.56481. D, three naturally cleared leaf tips, magnification ×20, showing convergence of dark strands at apex. Cloughton Wyke. V.56482. E, two stomata (exceptional in being in contact), magnification ×400, V.24678*a*. F, cuticle showing distribution of stomata, a little cut away from outer edges in preparation; the right side is thicker, shaded areas represent crushed zones, magnification ×20, V.24678*a*. G, H, bases of shoots with leaves and bud scales, magnification ×2, V.28392 and V.24678. I, cuticle, magnification, ×200, V.24678*a*. Except Figs. B and D, all figures are from Harris (1951, text-figs. 1, 2) and specimens from Gristhorpe Bed.

leaf has been seen at Cloughton though many thousands of large fragments were examined. We reaffirm the early estimate of the original thickness of the leaf as being about one half or two-thirds of its width (this is based on specimens twisted before they were compressed), and also that the leaf margin is rounded in section and unspecialized.

Many naturally cleared leaves show internal dark strands; three being a very common number, but two and four also occur. A single dark strand is seldom seen. These were discussed earlier (Harris 1951, p. 923) and are regarded as separated fibro-vascular elements of a broad and more or less compound bundle (i.e. of a single vein as in the leaf of *Pinus*). The subordinate dark strands converge at the leaf apex. A new feature noted in these naturally cleared leaves is that of scattered thick-walled longitudinal fibres lying isolated.

Some of the specimens we identify as *Solenites vimineus* have cuticles which caused us misgivings, in particular the one shown in Text-fig. 24 A, B. This Gristhorpe Bed specimen is the best we have seen but its cuticle is not typical. Its cells are rather short and many of its stomatal pits are wide open and with a continuous rim (as in a typical stoma of *C. furcula*). Other stomata, however, have narrow pits more or less occluded by lateral ingrowths as is typical for *Solenites*. We regard it as true *Solenites* but with an extreme form of cuticle, and not many *Solenites* leaves (from Cloughton) are as aberrant as this.

Comparison. Although we consider that *Solenites vimineus* may be closely allied to *Czekanowskia rigida* (as is suggested by the form of the short shoot and leaf bundle, the leaf cuticle and particularly by the reproductive organ *Leptostrobus*) it is at once distinguished by its simple leaves.

Because of the similarity of the cuticles of various *Czekanowskia* species to that of *Solenites* and the variability of the cuticle of *Solenites* itself we feel doubtful about determining isolated cuticle fragments obtained from bulk macerations of rock. Some specimens indeed previously determined as *Solenites* we now regard as *C. furcula*, and a number of others though perhaps belonging to *Solenites* seem unconvincing. We now only determine a cuticle fragment as *Solenites* when its characters seem fully typical and so in spite of some new finds the present number of recorded localities is less than was given by Harris (1951). Even thus restricted, it occurs widely in the Lower and Middle Deltaics and if the doubtful specimens truly belong to it, then it is almost ubiquitous.

Occurrence. Good hand specimens are frequent in the Gristhorpe Bed (the Type locality) but there is some possibility of confusion with two *Czekanowskia* species. At Cloughton Wyke in the main plant bed (called the *Solenites* Bed) it is extremely abundant and in places its matted leaves form a paper coal. Here there are no *Czekanowskia* species that could cause confusion. A few other Middle Deltaic localities gave fairly good hand specimens. In the Lower Deltaic good and typical specimens are known from Blea Wyke and fallen blocks from the Hawsker Cliffs by the Red Spring. Less good ones were found at a few other places (Marske Quarry and Roseberry Topping) where again, however, some associated *Czekanowskia* leaves are a possible source of confusion.

Isolated cuticle fragments resembling *Solenites* to a greater or less extent are very widespread. Harris recorded them from every stage except the Upper Deltaic. The recognition of several new species of *Czekanowskia* with fairly similar cuticle has made a revision of the determinations necessary. About a third of the fragments (particularly those from the *Lower*

Deltaic) are more like *C. furcula*, and another third, though possibly *Solenites*, are somewhat unusual. The specimens remaining as more rigorously acceptable are distributed as follows:

Middle Deltaic Gristhorpe Series	12
Middle Deltaic Sycarham Series	5
Lower Deltaic	13

Some small coprolites 3 mm × 2 mm were isolated from the Cloughton Wyke *Solenites* Bed by bulk maceration of the rock with HF (see Harris 1951, p. 927). These coprolites consist largely of coaly matter, readily dissolved by oxidation followed by ammonia but they do contain very many small fragments of cuticle probably all of them *Solenites*. The fragments are mostly less than 0·5 mm on their longest axis and many were very small indeed.

The fruit, *Leptostrobus cancer*, which we attribute to *Solenites* is described and discussed on p. 114.

Genus CZEKANOWSKIA Heer 1876, p. 65

Emended Diagnosis. Caducous short shoot covered with persistent scale leaves and bearing bundle of foliage leaves. Foliage leaf, as a whole, wedge-shaped, dividing by dichotomies into number of filiform segments; segments ending in acute apex. Leaf substance thick, probably oval in section. Vein single at leaf base, forking well below lamina dichotomy; apex with single vein. Resin bodies absent.

Cuticle well developed, similar on the two sides, amphistomatic; stomata occurring mainly in more or less short longitudinal files. Epidermal cells with nearly straight walls, commonly forming longitudinal files. Stomatal files almost evenly distributed over whole epidermis (including veins and at leaf margins). Stomata longitudinally orientated, haplocheilic, guard cells sunk in pit formed by subsidiary cells, two of which are usually terminal. Pit commonly reduced by rim or papillate pads of subsidiary cells. Encircling cells occasional.

Type Species. *Czekanowskia setacea* Heer (1876, p. 68, pls. 5, 6), for cuticle see Florin (1936, p. 178).

A key to the Yorkshire species is given on p. 84. The number of veins in a leaf segment is discussed on p. 81.

Czekanowskia furcula sp. nov.

Pl. 5; Text-figs. 26–28

1951 *Solenites vimineus* (Phillips) Harris in part, p. 915, text-figs. 1 A, F, H only.

Diagnosis. Short shoot very small (scale leaves usually lost). Foliage leaves in bundle of about 8, length typically 180 mm but occasionally more, width over most of leaf about 1 mm, near apex tapering to point. Lamina rather flat and thickness estimated at barely half the width, margins rounded in section. Substance of leaf dense, no resistant resin bodies present. Many

Fig. 26. **Czekanowskia furcula** sp. nov.

About one quarter of a large slab showing some of the numerous leaves and leaf bundles, actual size. The holotype is the leaf group on the left, ending in pointed tips above. Leaf forkings are marked X; others, more doubtful, are unmarked. Galls are seen at the bottom left. V.28393. Whitby Long Bight.

leaves (possibly all) forked once in middle region, none known to fork more than once; halves of dichotomy diverging at small angle.

Cuticle up to 5μ or occasionally 10μ thick in folds, one side thicker than the other, but the two sides and margins otherwise similar. Stomata forming about 8 longitudinal files on each surface, but some files irregular and some stomata out of any file. Files rather regularly spaced, epidermal cells between files elongated, their length 2–6 times their width and their ends often pointed and cells themselves not forming very obvious files. Lateral and end anticlinal walls of cells conspicuous, interrupted by small pits, never sinuous or flanked by teeth. Cell surface normally bulging slightly or considerably, cell surface sometimes of even thickness, sometimes thickened in middle to form a pad.

Cell surface smooth or finely granular, occasionally faintly striate. At dichotomy cells on inner sides strongly bulging or forming short conical trichomes up to 45μ long. Trichomes otherwise absent except at extreme base of leaf. Stomata nearly all longitudinal (very occasionally transverse), subsidiary cell group varying from slightly elongated to isodiametric often with two terminal and one or two lateral on each side or whole set almost radially arranged with none particularly terminal. Outer surface of subsidiary cells often no thicker than that of ordinary cells but in some leaves surface distinctly thickened. Occasional subsidiary cells showing slight thin strip, stomatal pit normally wide, often round, square or oval but only slightly longer than broad; sometimes considerably longer than broad but then usually with transverse, unconstricted ends. Middle of aperture only very seldom narrowed by ingrowths from lateral subsidiary cells. Border of pit normally broad, conspicuous and uniform, hardly ever forming papilla-like ingrowths, border at terminal cells normally fully developed. Encircling cells absent or undistinguished. Near leaf apex cuticle remaining normal.

The name *furcula* is from *furcula*, a forked prop.

HOLOTYPE. V.28393 (Pl. 5, fig. 2; Text-figs. 26, 27 A, B, 28 A).

DISCUSSION. The holotype specimen is a large slab fallen from the Whitby cliffs above the classic plant bed. The rock, a hard fine-grained sandstone, is so full of leaves and leaf bundles of this species that they confuse the picture (Text-fig. 26 is a typical sample). The back of the slab is similar and there are several bedding planes full of such specimens. Apart from this species there are only fragments of *Todites williamsoni*. Unfortunately, although the leaves can be followed for long distances, the fine details are indifferently preserved and most of the cuticle preparations are poor.

There are in addition some small hand specimens from Saltwick and from Marske Quarry, which, although they do not show whole leaves, provide excellent details. There are also hand specimens from Haiburn Wyke and from Roseberry Topping which, although having the dichotomy of *C. furcula* leaves, do not have typical cuticles. The stomatal pits are very reduced and narrowed, particularly so in preparations from Roseberry Topping, where they are mostly reduced to mere slits. However, the pits are all bordered by a typically broad, conspicuous and continuous cuticular rim and the narrowing is not caused by overhanging ingrowths from lateral subsidiary cells. Apart from this, these specimens agree with normal ones and are determined as ? *C. furcula*.

One specimen from Saltwick still has some scale leaves. They are about 2·5 mm × 1·5 mm

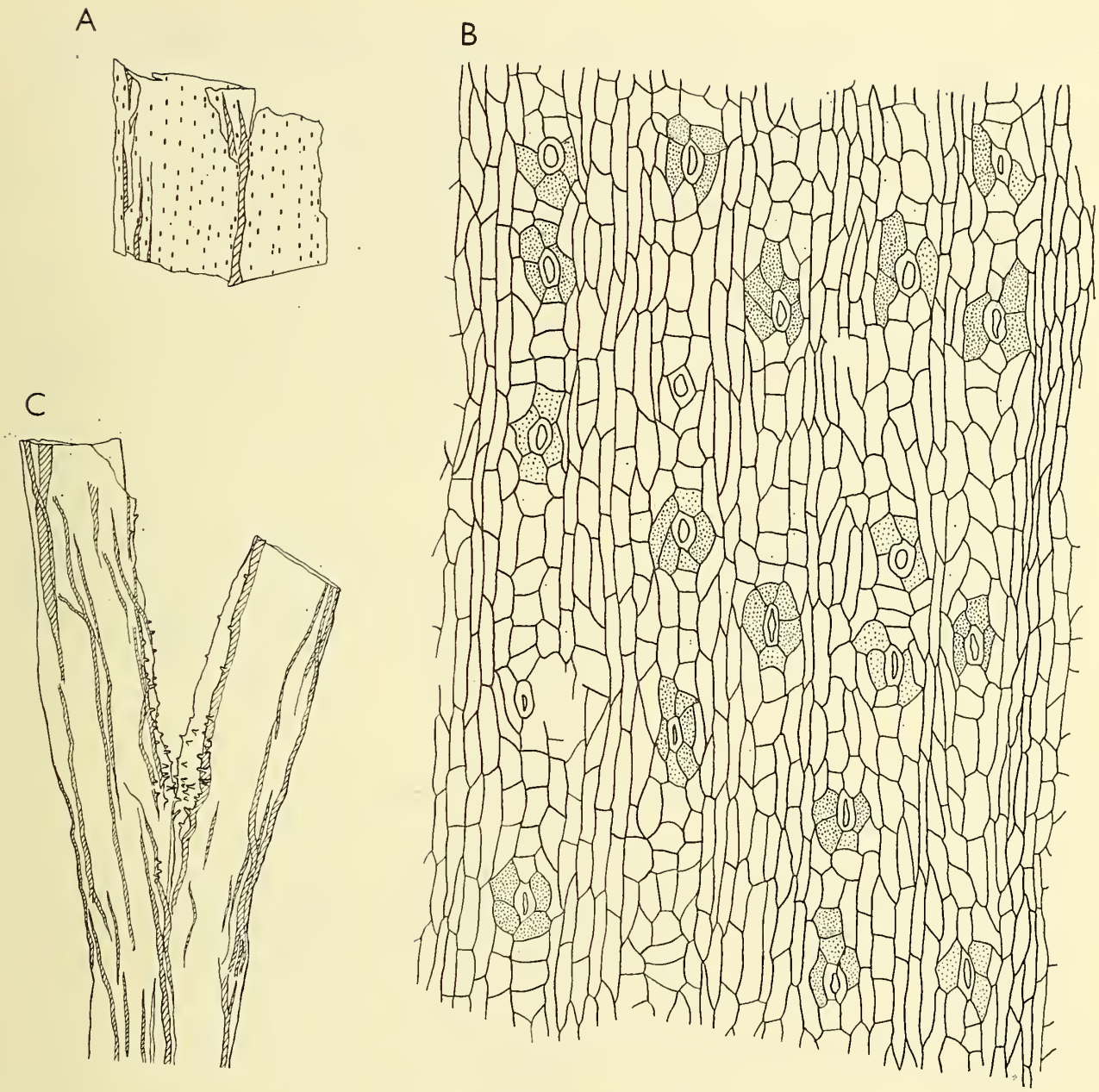


Fig. 27. **Czekanowskia furcula** sp. nov.

A, cuticle of holotype, Whitby Long Bight (fallen block). V.28393; cuticle split open and showing distribution of stomata, magnification ×20. B, portion of cuticle shown in A, magnification ×200. C, cuticle showing leaf dichotomy with associated papillae, magnification ×20, V.28418. Bilsdale 'Beacon'.

and pointed-triangular. In addition there seems to be a transitional leaf with a broad base and a slender filiform extension of 10 mm long.

The five localities referred to above are all Lower Deltaic.

Two points mentioned in the diagnosis need expansion. The lamina is described as flat. In fact no specimen is twisted (but in other species and in *Solenites* twisting before compression

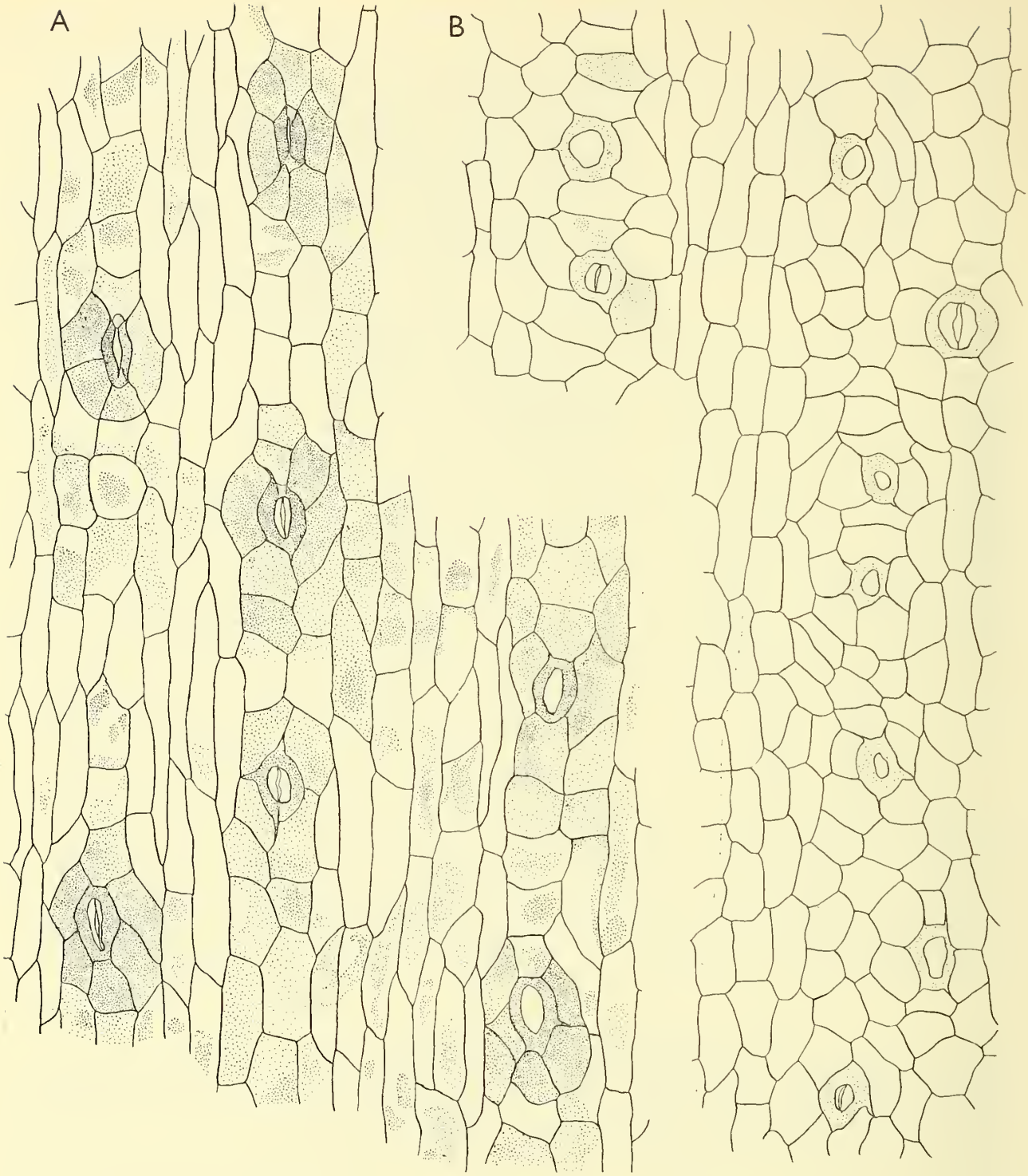


Fig. 28. **Czekanowskia furcula** sp. nov.

A, portion of cuticle of holotype, magnification ×400. V.28393*a*. Whitby Long Bight (fallen block). B, another cuticle from same specimen, magnification ×400.

is occasional and gives the basis for the estimate of thickness. Here we only have the absence of twisting which suggests flatness, and the rather slight amount of crushing seen near the leaf edges.

The leaves are said to be forked once and this is true of most of the nearly complete leaves and large fragments. But there are fragments up to 150 mm long, some in the same bundles as forked leaves, which are not branched and they may have been simple right to the apex.

The curious swellings figured by Harris (1951) as galls are present on several leaves of the Whitby block. They must have developed early in the growth of the leaf, for their epidermal cells extend transversely and are cutinized.

Comparison. Good specimens of *C. furcula* with typical cuticles are among the most easily recognized of the Yorkshire species. Apart from the macroscopic features—the long, once forked leaves—the cuticle is characteristic. No other species shows a high proportion of widely open stomatal pits with an even, narrow rim (giving them the appearance of a window or picture frame). The other species and particularly *Solenites* do however possess occasional stomata of this form.

Occurrence. *Czekanowskia furcula* is chiefly of Lower Deltaic age. In addition to the hand specimens already mentioned from five Lower Deltaic localities, there are isolated cuticle fragments from other Lower Deltaic beds which look typical *C. furcula*. In the Middle Deltaic cuticle fragments determined as *C. furcula* are known from two or three localities of the Sycarham Series and one or two of the Gristhorpe Series. There are none from the Upper Deltaic.

Czekanowskia microphylla (Phillips) Seward

Pl. 4, fig. 3; Text-figs. 29, 30

1875 *Baiera microphylla* Phillips, p. 200, Lign 9.
1900 *Baiera lindleyana* (Schimper): Seward in part, text-fig. 46 and description of that specimen only.
1919 *Czekanowskia microphylla* (Phillips) Seward, p. 65, text-fig. 661. (As Seward 1900, text-fig. 46)
1946*a* *Czekanowskia microphylla* (Phillips): Harris, p. 1, text-figs. 1, 2.

The above are all Yorkshire specimens.

Emended Diagnosis. Short shoot very small, bearing few rounded, delicate scale leaves of uneven size. Foliage leaves in bundles of about 5, often about 60 mm long, occasionally 120 mm. Leaf four or five times dichotomously branched, branching often unequal, one side being much shorter. Width of leaf segments typically 0·7 mm–0·8 mm only attaining 1·0 mm or 1·2 mm just below dichotomy. Leaf apices acute, angle of branching usually small. Substance of leaf originally thick, naturally rotted leaf segment usually showing single central thick strand, or two below point of dichotomy. Leaf margins rounded. No resin bodies present. Cuticle fairly thick, about 5μ in folds, tough; two sides often exactly similar but sometimes one side (perhaps the upper) slightly thicker. Stomata equally frequent on both sides, typically about 50 per mm^2, more numerous distally, fewer near leaf base. Stomata occurring in about 5–8 single, or occasionally double, longitudinal files on each side. Epidermal cells of stomatal files isodiametric or slightly elongated and forming rather short

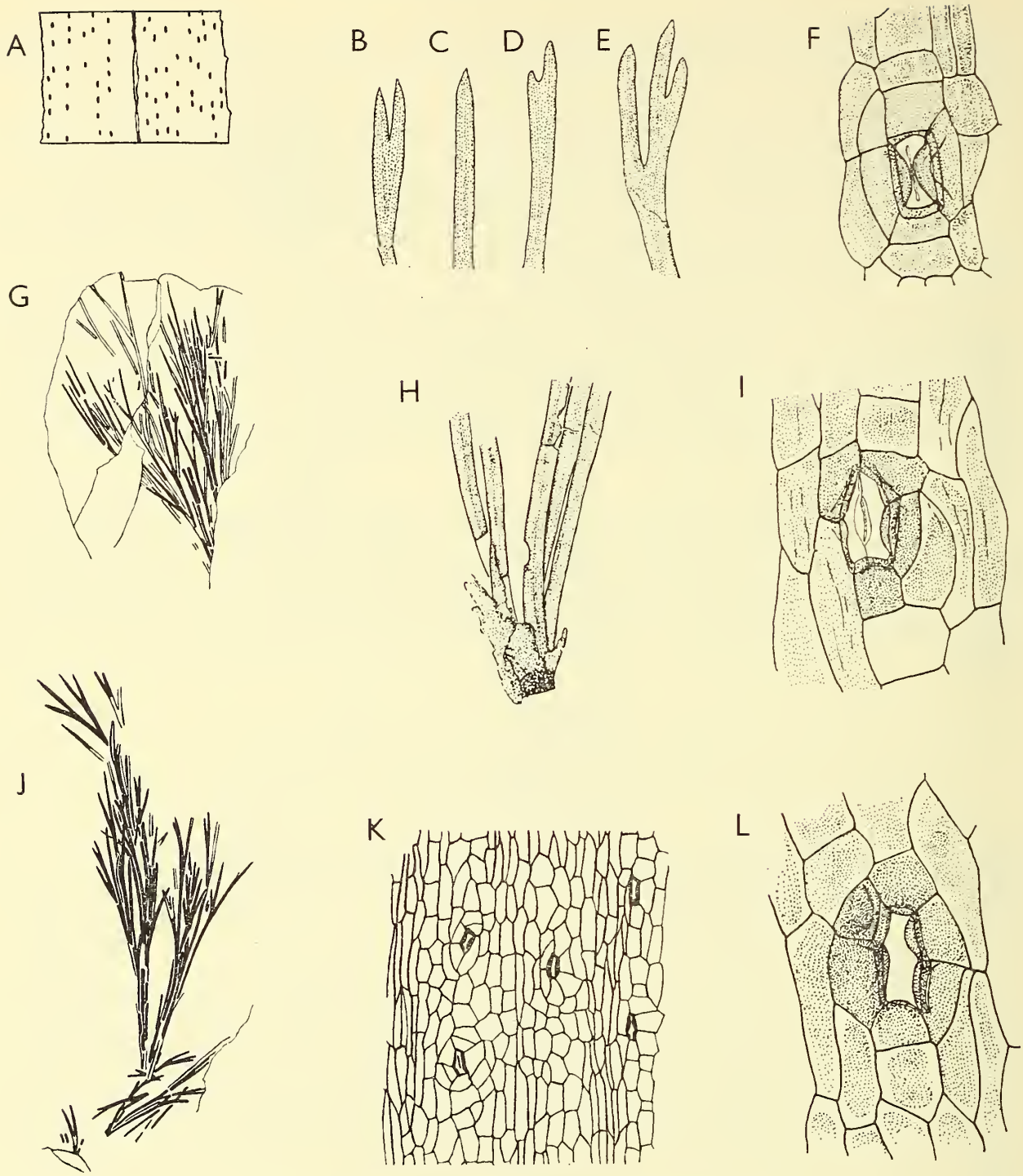


Fig. 29. **Czekanowskia microphylla** (Phillips)

A, cuticle (thick side on left) showing distribution of stomata, magnification ×20. Specimen in Yorkshire Museum. B–E, apices of leaf segments, all magnification ×4. B and D are from the holotype, C from leaf fragment at top and E from leaf at base of holotype. F, stoma from holotype (thick side), magnification ×500. G, specimen in Yorkshire Museum, actual size. H, leaf bundle and dwarf shoot (seen also in J) magnification ×6. I, stoma from leaf fragment above holotype; the unthickened cell below is unusual, magnification ×500. J, holotype (the group of leaves occupying the middle of the figure is regarded as actual type), actual size. Leckenby Collection 389. K, cuticle of holotype, magnification ×200. L, stoma from leaf fragment above holotype, magnification ×500. All are from Harris (1946).

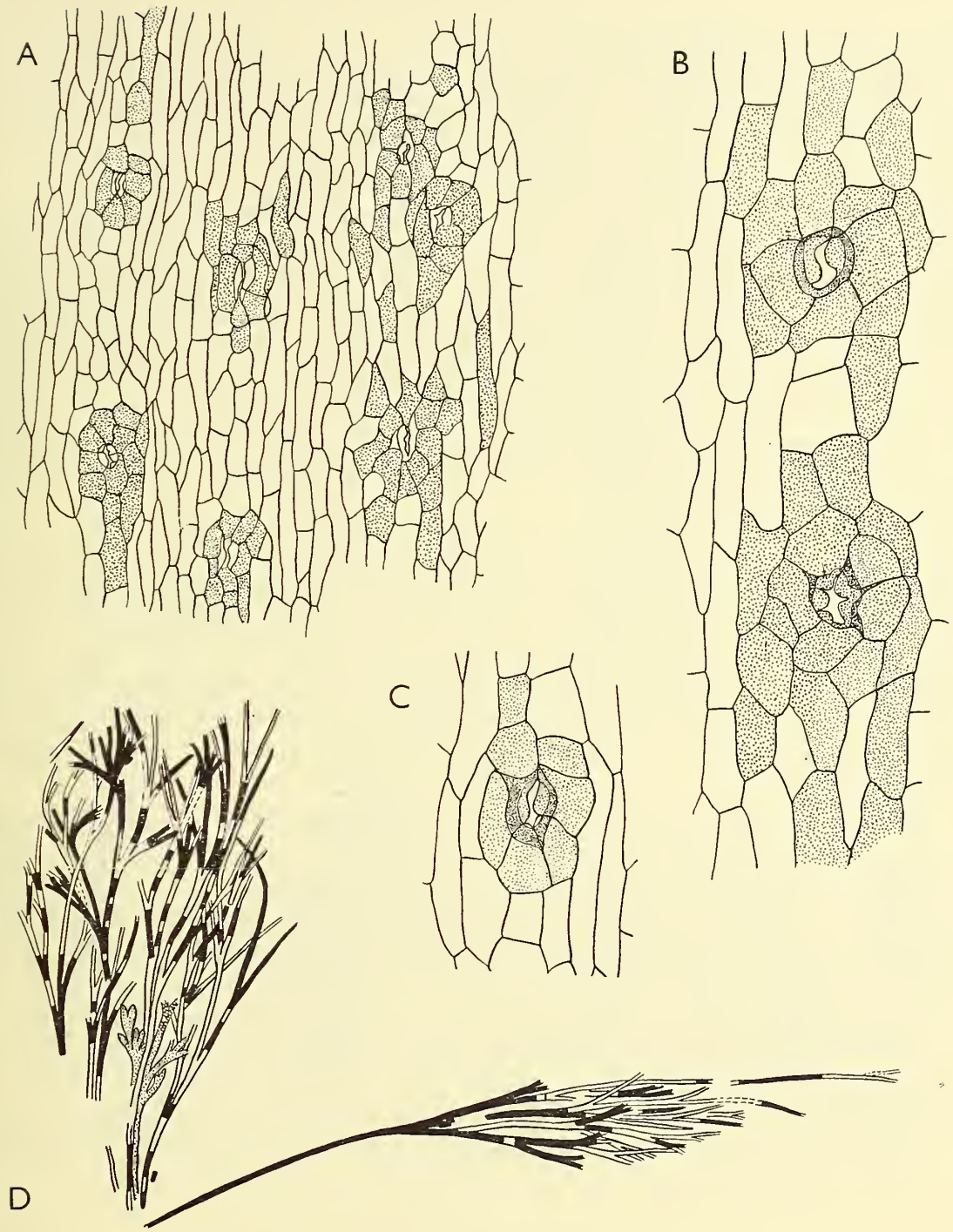


Fig. 30. **Czekanowskia microphylla** (Phillips)

A, portion of leaf cuticle, magnification ×200, V.56419*a*. B, C, stomata from same cuticle as A, to show extreme extent of subsidiary cells bulging over stomatal pit, magnification ×400. D, bunch of leaves, actual size, V.56419. The leaf on the right is unusual in having a long proximal section with no dichotomies; two other leaves in the main bunch also indicate the same feature but are incomplete. The dotted portion is *Stenopteris williamsoni*. All specimens are from the Gristhorpe Bed.

longitudinal files, resulting in presence of many curved and oblique end-walls, the total effect being of somewhat irregular arrangement of cells.

Cell outlines shown by distinct, moderately broad, straight ridges. Surface of almost every cell bulging slightly and thickened to form low pad. Thickened area indefinite, but usually separated from lateral walls by thin region. Cell surface (especially on 'upper' epidermis) sometimes sculptured with few more or less longitudinal striae.

Stomata unevenly spaced in their files, longitudinally orientated. Guard cells sunken, apertures moderately cutinized, rest of cutinized surface very thin. Subsidiary cells forming rather irregular group, but two terminal ones (often ill-defined) and 2–6 lateral ones usually distinguishable. Subsidiary cell surfaces usually more thickly cutinized than rest of epidermis. Margins around stoma characteristically varying considerably from one stoma to next; often forming elongated, rather narrow pit with well-developed cutinized rim, but other forms of pit include widely open and rounded, rectangular, hour-glass shaped, star-shaped, and pits of irregular form, the shape being caused largely by inward projection of large flat papillae of lateral subsidiary cells. Unspecialized encircling cells often present but irregular in distribution and not forming complete ring.

Discussion and Occurrence. So far as we know *C. microphylla* is confined to the Gristhorpe Bed (Middle Deltaic) where it seems to be rare. This description and diagnosis has been slightly altered from that of Harris (1946*a*). The earlier one was mainly based on two specimens, but a third specimen has now provided wider knowledge of its form and cuticle.

There are three species of the *Czekanowskia* group in the Gristhorpe Bed; *Solenites vimineus* (unbranched), *C. thomasi* even more slender and with leaves only once forked, and finally *C. microphylla* in which the leaves branch four or five times. The main distinguishing peculiarities of *C. microphylla* are:

(1) The leaf is more branched than in any other species yet described. The number of leaves on the short shoot is small.
(2) The two branches of a dichotomy are often very unequal.
(3) There is remarkable diversity in the shape of the stomatal pit even in a single small piece of epidermis. On the other hand different specimens have, so far as we know, fairly similar cuticles.
(4) The epidermal cells look less regularly arranged than is usual in *Czekanowskia* and *Solenites*. This is because longitudinal files of cells are quite short and often hardly recognizable and there are many very oblique or curved end-walls of cells.
(5) The cell surface is thickened to form a pad which is often conspicuous. *C. thomasi* is similar but other species described here and those described from elsewhere show this feature feebly or not at all.

Czekanowskia thomasi sp. nov.

Pl. 4, fig. 4; Text-figs. 31, 32

Diagnosis. Short shoot very small, less than 2 mm × 2 mm, bearing a few rounded, delicate, scale leaves of uneven size; scale leaf cuticle moderately thick, cells forming more or

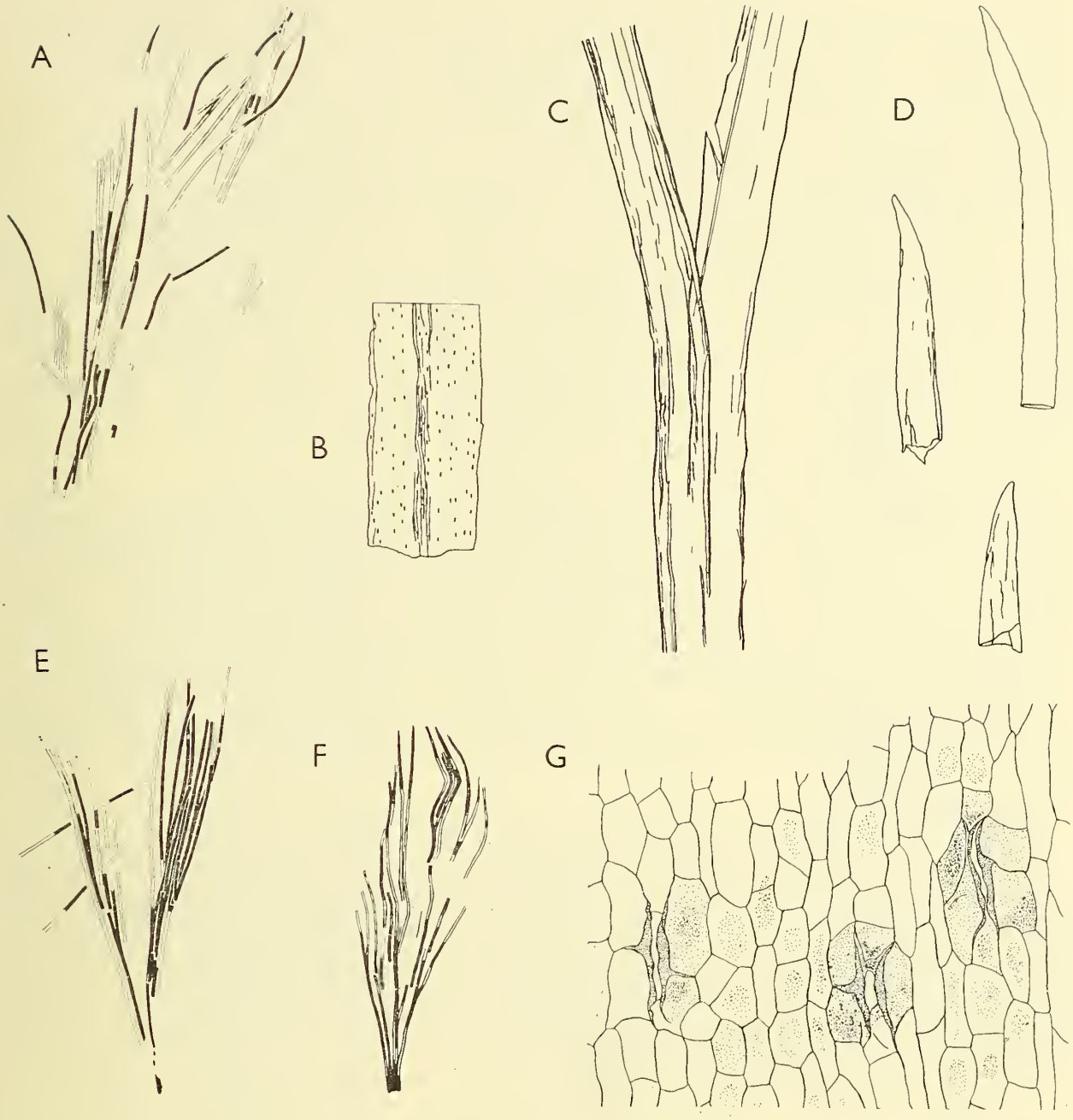


Fig. 31. **Czekanowskia thomasi** sp. nov.

A, two bundles of leaves, actual size; the main bundle on the left with leaf bases towards bottom left, the other bundle with leaf bases towards top right, V.56421. B, portion of cuticle split open and showing distribution of stomata, magnification ×20. Holotype V.56420. C, leaf dichotomy, magnification ×20, V.56491. D, leaf apices, magnification ×20, V.56492 and V.56493. E, bundle of leaves, actual size. Holotype V.56420. F, bundle of leaves, actual size, V.56422. G, portion of cuticle, magnification ×400, showing particularly elongated forms of stomata, V.56492. All specimens from the Gristhorpe Bed.

less elongated polygons; lateral walls distinct, nearly straight but sometimes with very small waves, or small uneven thickenings. Cell surface finely and evenly mottled. Foliage leaves in bundles of 7–8, up to 80 mm long. Most leaf segments forked once (no leaf known to have more than one dichotomy and none known to be simple). Leaf segments mostly about 0·5 mm wide, increasing up to 0·8 mm below dichotomy. Leaf apices acute, angle of dichotomy usually small. No resin bodies present. Cuticle fairly thick, about 4μ–5μ in folds, sometimes one side thicker than the other; leaf margins originally rounded. Stomata equally frequent on both sides, forming longitudinal files. Epidermal cells forming well marked longitudinal files; those among stomata isodiametric but those between stomatal files elongated and often narrow. Cell outlines distinct, forming moderately broad ridges with slight crinkles. Surface of many cells bulging slightly and thickened to form a low pad usually separated from lateral walls by thinner region. Many cell surfaces also with conspicuous thin strip. At leaf base, cell surfaces bulging strongly and extending as thick walled conical trichomes about 12μ wide at base and extending to 45μ long. Otherwise trichomes normally absent from whole of leaf, except for few about 10μ wide by up to 20μ long within angle of dichotomy.

Stomata longitudinally orientated, guard cells sunken, scarcely cutinized except along aperture. Subsidiary cells forming rather irregular group, two terminal and one to three lateral ones each side. Subsidiary cell surface usually more thickly cutinized than rest of epidermis. Margins next to stoma forming pit of variable shape but often very narrow and elongated; other pits more widely open and even rounded. At margin of pit a narrow cutinized rim often extending all round, or confined to sides but not recognizable in narrowest form of pit.

Surface of lateral subsidiary cells with tendency to bulge over stomatal pit, but never extending as a papilla. Encircling cells never specialized, normally absent.

The name commemorates Hamshaw Thomas who collected much of the material described here.

HOLOTYPE. V.56420. (Pl. 4, fig. 4; Text-figs. 31 B, E, 32 C–E.)

DISCUSSION AND OCCURRENCE. *Czekanowskia thomasi* is frequent in the Gristhorpe Bed, from which there are several hand specimens. There are additional specimens from Marske Quarry and from Roseberry Topping (Lower Deltaic). There are also cuticle fragments from a few Lower and Middle Deltaic localities which match the cuticles of the hand specimens. *C. thomasi* seems fairly well distinguished by its rather short and slender once forked leaves, and by a cuticle which shows many remarkably narrow stomatal pits. The mottled surface of its cells may also be characteristic.

Czekanowskia blacki sp. nov.

Pl. 6, figs. 2, 3, Pl. 7, figs. 3, 12, 13; Text-fig. 33

1929 *Czekanowskia rigida* Heer: Black, p. 428, text-fig. 16.

DIAGNOSIS. Short shoot about 3 mm × 3 mm, bearing delicate scale leaves of uneven size and about 7 foliage leaves. Foliage leaves exceeding 140 mm in length (perhaps about 200 mm), known to fork twice (but no evidence of further forking). Leaf and its segments

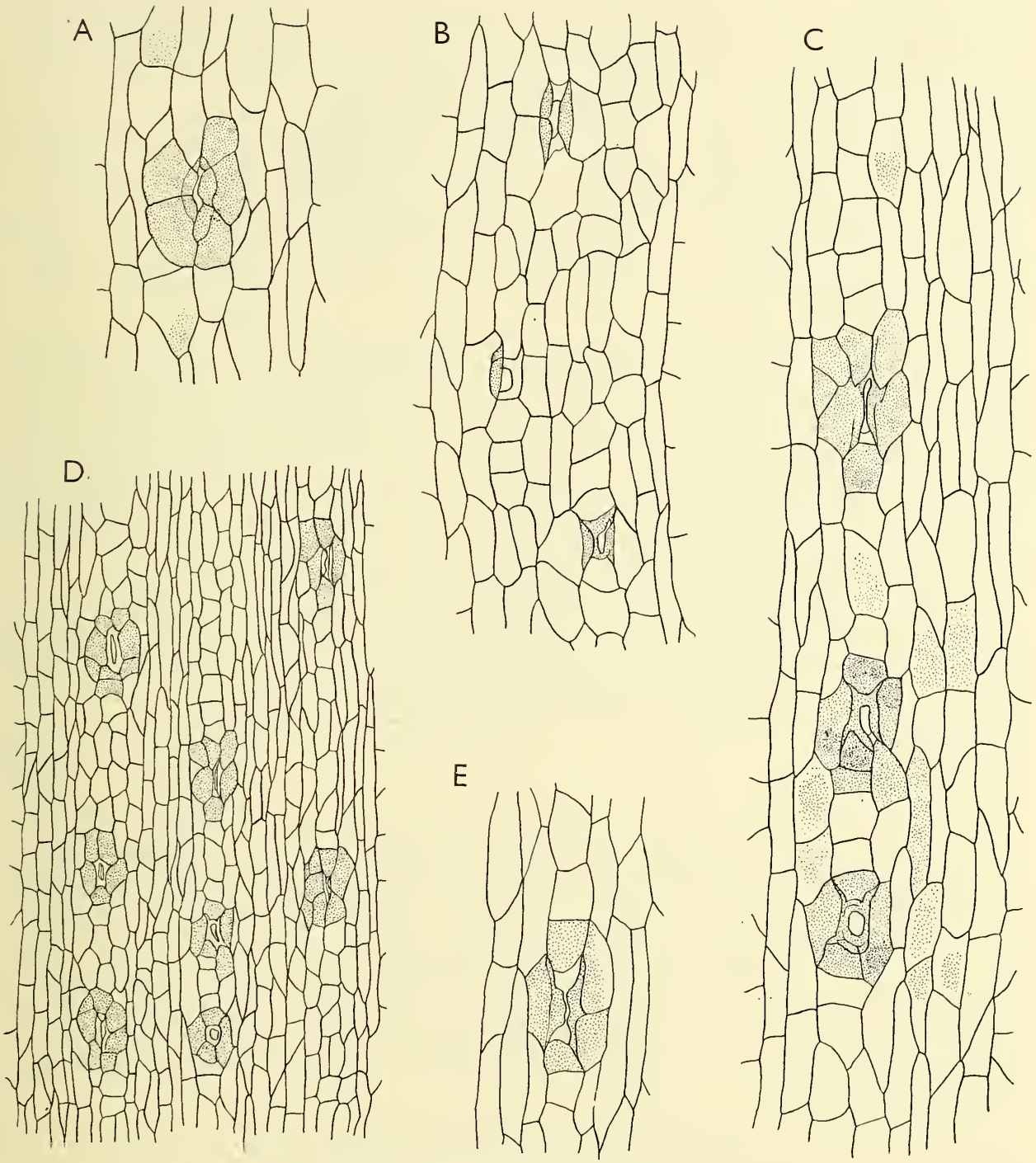


Fig. 32. **Czekanowskia thomasi** sp. nov.

Cuticles showing range of structure. A, V.56491, B, V.56492, C–E are from the holotype V.56420. B, is unusual in having unthickened subsidiary cells. A, B, C, E are magnification ×400; D magnification ×200. All specimens are from the Gristhorpe Bed.

mostly 0·7 mm–0·8 mm wide, only reaching up to 1·2 mm below dichotomy, upper part diminishing to 0·5 mm and then gradually tapering (the last cm being about 0·2 mm) to an acute apex. Angle of dichotomy small. Leaf originally slightly flattened but edges rounded. Vein single except below dichotomy, accompanied by fibres.

Cuticle of foliage leaves 2μ–5μ thick in folds, similar on two sides. Stomata in longitudinal files, ordinary epidermal cells also in distinct longitudinal files. Cells among stomata sometimes isodiametric but often somewhat elongated; cells between files very elongated, length sometimes twelve times their width. Epidermal cell surface quite flat, not thickened to form a pad but surface often mottled and sometimes marked with distinct longitudinal striae. Cell outlines distinct and moderately broad, straight or with small crinkles and sometimes interrupted by small pits.

No trichomes present, not even at leaf bases, nor in angle of dichotomy. Stomata longitudinally orientated, guard cells sunken, scarcely cutinized except along aperture. Subsidiary cells of varied arrangement, usually one at each end and one to two lateral ones on each side. Subsidiary cell surface sometimes slightly more thickly cutinized than rest of epidermis, but often no thicker. Stomatal pit varying considerably; usually more or less narrow and sometimes almost completely occluded, but sometimes rounded and wide. Some pits oval with no cutinized rim but more or less occluded laterally by overhanging bulges from lateral subsidiary cells; others with complete cutinized rim to pit formed from terminal as well as lateral subsidiary cells, in these pit usually extremely narrow and often almost closed.

Encircling cells sometimes present, when present unspecialized. No resistant bodies of resin present. Cuticle of scale leaves moderately thick, about 5μ thick in folds, cells forming elongated polygons; lateral walls distinct, nearly straight but often with very small waves, or small uneven thickenings. Cell surface finely and evenly mottled.

This species is named after Maurice Black who found and briefly described specimens from Scalby Ness.

Holotype. V.56428. (Text-figs. 33 c–e.)

Discussion and Occurrence. *Czekanowskia blacki* is found in some abundance at one point in the Scalby Ness plant bed, where it is the commonest leaf, but over most of this bed it is unknown. There is no doubt that Black's original specimens from this locality (from which he figured a fragment of cuticle) are the same as those we describe here. Apart from the Scalby Ness specimens we have only very small hand specimens and isolated cuticle fragments which though they agree so far as they go with the Scalby Ness material are not determined with full confidence. These come from another Upper Deltaic locality (Harwood Mill, Jugger Howe) and three Lower Deltaic localities, Marske Quarry, Sandsend Alum Pit and Hasty Bank.

Some of the Scalby Ness specimens had suffered some decay before final preservation and much of the internal substance had vanished leaving the leaf partly cleared. These leaves show something of the fibro-vascular tissue by transmitted light. Many have a single rather massive dark strand occupying the middle third or half of the width; this may be accompanied by about six very slender fibres. In some the dark strand shows subordinate dark strands and these shift somewhat along the length of a fragment. As in *Solenites* we interpret these subordinate strands not as whole bundles but as parts of a single bundle

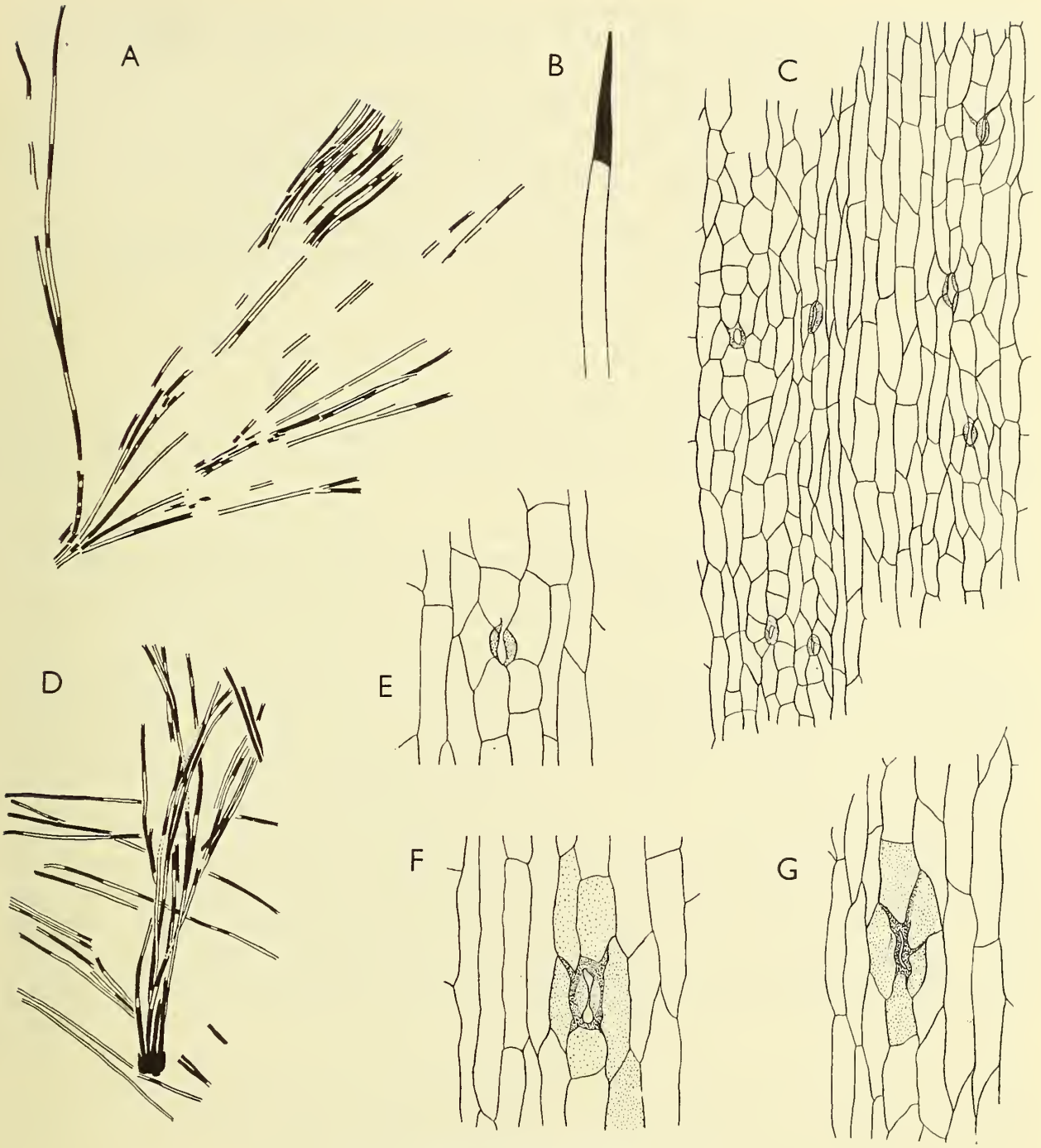


Fig. 33. **Czekanowskia blacki** sp. nov.

A, bundle of foliage leaves, actual size. V.56429, Scalby Ness. B, leaf apex, magnification ×20, V.56430. C, cuticle from holotype, magnification ×200, V.56428*a*. D, bundle of foliage leaves, with the distal part of another bundle of leaves underneath it; no apices present. Erect bundle is holotype, actual size, V.56428. E, stoma with feeble rim and unthickened subsidiary cells, magnification ×400, V.56428*a*. F, stoma with slightly thickened subsidiary cells, magnification ×400, V.56496. G, stoma with slightly thickened subsidiary cells, magnification ×400, V.56497. All specimens are from Scalby Ness.

isolated by decay. A few fragments with two broad dark strands are possibly from just below a dichotomy but others with two, three or four more slender strands are more likely to be the disintegrated fragments of one bundle.

The main distinguishing characters of this species, at least from other Yorkshire species, are the considerable length of the leaves, the slenderness of their ultimate several centimetres, the cuticle which is thinner than usual, the narrow and elongated epidermal cells with unthickened surface but sometimes showing parallel striae, the stomatal pit of varied shape but most often narrow, and the unthickened or only slightly thickened subsidiary cells. Trichomes are absent even at the leaf base or in a dichotomy. Where subsidiary cells are unthickened the stomata are very inconspicuous.

General comparison of the Yorkshire species of *Czekanowskia*

The four named species from Yorkshire have already been compared with one another and we are satisfied that they do differ though their differences are small and require good material for determination. We admit also that there are specimens from particular localities about which we feel unsure.

Their distinction from all other species is a very different problem. *Czekanowskia* is widespread in the Jurassic and Lower Cretaceous of the Northern Hemisphere and there are many records but most of these refer to the two species, *C. rigida* and *C. setacea*, which are separated only by the width of the leaf segments. The microscopic details of these two species, or of specimens identified with them, have only been furnished comparatively recently. The cuticle of a specimen of *C. setacea* from the Type locality in Siberia (Lower Cretaceous) has been figured by Florin (1936, text-fig. 12) and of *C. rigida* also from Siberia (Florin 1936, text-fig. 14 A, B and Vachrameev & Doludenko 1961, pl. 54, figs. 2–5; pl. 60, figs. 2, 3). Cuticles of other specimens determined as *C. rigida* have been figured by Nathorst (1906) and Johannson (1922) from the basal Liassic of Sweden; Florin (1936) from the Lower Cretaceous of Franz Joseph Land; Vladimirovich (1959) from the Jurassic of the Urals (together with *C. setacea*). The Lower Cretaceous Siberian specimens seem to agree with one another closely but we suspect that many of those from other localities are different. There is also *C. hartzi* Harris (1926, 1935) and *C. nathorsti* Harris (1935) from the basal Liassic of East Greenland both of which look macroscopically similar to *C. rigida*. Finally *C. latifolia* Turutanova-Ketova from the Khirgiz is very different and is here transferred to *Sphenarion* (p. 110). There are in addition numerous records of *C. rigida* and *C. setacea* without any microscopic details. The specimens (of which Oishi 1931 gives a useful list) may, when further studied, prove of value but at present they can add nothing to our comparison. In this they are like some of the Yorkshire material from which we failed to make satisfactory cuticle preparations and subsequently rejected as valueless.

Of the four Yorkshire species, three seem sufficiently distinguished by their form alone. *C. microphylla* in which forking occurs four or even five times and in which some branches are much smaller than others is like nothing else that has been described. The once forked *C. thomasi* and *C. furcula* are also unusual but it must be emphasized that since the leaves may be nearly 200 mm long, very good specimens may be needed to demonstrate the full number of forkings. There is just *C. blacki* which is forked twice and which resembles *C.*

rigida and *C. setacea* in form; it was indeed first determined as *C. rigida*. There seems to be a slight macroscopic difference. In *C. rigida* from East Siberia the ultimate leaf branches are only slightly thinner than the lower part of the leaf but in *C. blacki* the ultimate branches are only half as thick; in fact they are more like *C. setacea* though their lower parts are too thick for *C. setacea*. In the cuticle there is general agreement in the shape and positions of the various kinds of epidermal cells but there is a notable difference in appearance. In the photographs of *C. rigida* the stomata stand out as conspicuously dark because the subsidiary cell surface is strongly and evenly thickened or occasionally unevenly thickened to form a broad papilla. In *C. blacki* the stomata do not stand out in this way because the subsidiary cells are often not specially thickened or are only slightly thickened. The whole cuticle looks thinner. The more highly magnified photographs of *C. rigida* show a mottled pattern on the cell surface but none of the figures shows parallel striae. These differences are small but do suggest a specific distinction. Florin (1936) figured two sets of specimens from Franz Joseph Land which may not be the same as one another. Those from Windy Gully (p. 146, cuticle in pl. 38, fig. 15) look like the Siberian specimens. But those from Kap Flora (cuticle in pl. 33, figs. 1, 2; text-fig. 14 c) differ in their short subsidiary cells with an unthickened surface unlike either the Siberian cuticles or those of *C. blacki*. The specimens figured by Vladimirovich (1959) from the Lower Jurassic of the Urals appear so different in gross form as well as in cuticle from the other specimens that it may be doubted if it is a *Czekanowskia* species. The Swedish specimens described as *C. rigida* were renamed *C. nathorsti* by Harris (1935) and this was accepted by Florin (1936).

C. nathorsti (Harris 1935, Florin 1936, text-fig. 13) from the basal Lias of Sweden and East Greenland has slightly broader leaves which fork three times and are in bundles of 12–15 instead of about 7. The epidermal cells and whole stomatal apparatus is usually a little broader, the subsidiary cells agree with those of *C. blacki* in being not specially thickened and the epidermal cells may also be longitudinally striated.

C. hartzi Harris (1926, 1935) from the Lower Lias of East Greenland is very similar. Its leaves agree in their number in a bundle and in forking twice but they probably become less attenuated at the apex. The cuticle may be just as thin and its stomata often look similar for their subsidiary cells are unthickened. The stomatal pits are very narrow but almost all are rectangular while *C. blacki* has pits of varied shape and such of its stomata as have thickened subsidiary cells do look different. The proved differences may hardly justify specific separation but since the agreement is not perfect and their ages differ considerably it seems best to separate them.

Less can be said in comparing *C. blacki* with *C. setacea*. For this we have drawings of the stomata of specimens from the Type locality by Florin (1936) which while showing the shapes of the cells clearly do not deal with other features. The stomatal pit appears quite unconstricted by ingrowths from subsidiary cells. In the figures given by Vladimirovich (1959) the leaves look stouter than in the Siberian material and may belong to some other species.

In conclusion, it is clear that while *C. blacki* is not yet so sharply distinguished from all other species with known cuticles as we would wish, it certainly does not agree convincingly with any. As mentioned earlier, comparison with specimens of unknown microscopic structure is pointless.

Species of *Czekanowskia* or *Solenites* mentioned without specific names

During the course of bulk maceration of rocks from about 1,500 localities a great many cuticle fragments were obtained which agreed in their general characters with *Czekanowskia* and *Solenites*. Though only a centimetre long they are identified confidently as of this group (rather than as Conifers or Ginkgoales). The form of the whole leaf is unknown and for most of them we do not even know whether they fork; it therefore seems best to leave them unnamed. Their main value is that since they differ convincingly from every one of the species described above, they show that we are far from having exhausted the Yorkshire Czekanowskiales. These unnamed species are designated by the letters A–E, the species called 'A' being the best known.

Czekanowskia sp. A

Pl. 6, figs. 1, 4, 7; Text-fig. 34

Description (in diagnosis form). Width of leaf or leaf segments about 0·9–1·2 mm. No resin bodies present. Cuticle fairly thick, 5μ–8μ in folds. Leaf margins originally rounded. Stomata in equal frequency, in 5–8 longitudinal files, on each side. Ordinary epidermal cells also in longitudinal files; those of non-stomatal files elongated, up to nine times their width long; those of stomatal files isodiametric or somewhat elongated. Cell outlines forming distinct, broad ridges. Surface of epidermal cells sometimes bulging slightly and thickened to form a low pad usually separated from lateral walls by a thinner region; surface usually marked with longitudinally orientated striae. No trichomes seen in the fragments of cuticle available.

Stomata longitudinally orientated, guard cells sunken, but often visible, scarcely cutinized except along aperture. Subsidiary cells usually more thickly cutinized and darker than other epidermal cells, forming a conspicuous group, usually with one terminal, and 1–4 lateral on each side. Subsidiary cells with a marked tendency to project laterally under neighbouring epidermal cells. Margin of stomatal pit usually with a cutinized rim extending all round, following the outline of the subsidiary cells. Pit usually wide open, more or less rectangular or square and exposing the guard cells, but lateral subsidiary cells may project as flat papillae across the pit. Encircling cells never specialized, possibly absent.

Discussion. A number of leaf fragments from several Upper Deltaic localities agree closely with one another and form the basis of the foregoing description. They are very readily distinguished from all the named species by the large size of all the epidermal cells and by the wide, square-ended stomatal pits and by the subsidiary cell cuticles extending under neighbouring cells.

A curious feature seen in some preparations obtained by M. Black from Scalby is that almost every cell contains a dark globule looking just like a nucleus, but whatever its original nature it has plainly acquired similar chemical resistance to fossil cutin.

Czekanowskia sp. A is recorded from seven Upper Deltaic localities. So far as we know it is not abundant in any of them.

Czekanowskia sp. B

Rather like *C. furcula*, but the stomatal pits are larger, both longer and relatively more narrow, their ends are rounded. The pit has a fairly pronounced cutin rim.

2 Lower Deltaic localities (including a small and uninformative hand specimen from Hasty Bank).

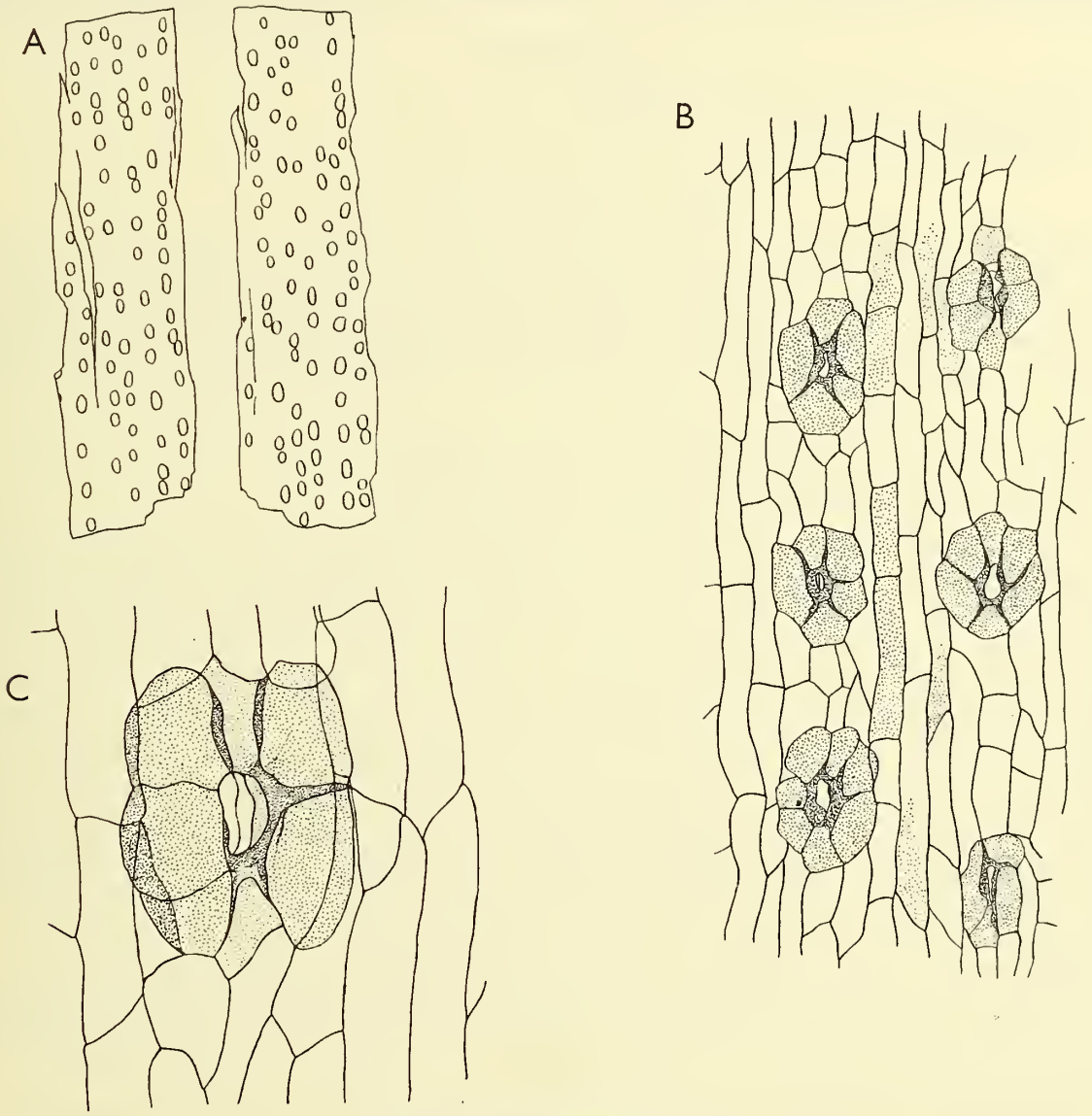


Fig. 34. **Czekanowskia** sp. A

A, cuticles of the two sides of leaf from Scalby Ness showing stomata, magnification ×20, V.56592. B, cuticle from Burniston Long Nab, magnification ×200, V.56593. C, stoma, viewed from inner surface of epidermis, showing subsidiary cells overlapping adjacent cells, magnification ×400, V.56592.

Czekanowskia sp. C

Stomatal pits oval, large and wide with rounded ends. The cutin rim is particularly developed laterally.

2 Lower Deltaic localities (including a small hand specimen from Haiburn Wyke).

Czekanowskia sp. D

Stomatal pit a narrow slit with a broad rim all round.

2 Lower Deltaic localities (including a small hand specimen from Hawsker Cliffs at Maw Wyke).

Czekanowskia sp. E

Epidermal cells conspicuously papillate.

1 Upper Deltaic locality.

Genus SPHENARION nov.

DIAGNOSIS. Leaves persistent on caducous dwarf shoot which also bears small scale leaves. Individual leaves narrowly wedge-shaped with no distinction between petiole and lamina; leaves mostly forking one or more times, segments traversed by more than one vein. Cuticles developed, stomata haplocheilic with ring of more or less equal subsidiary cells.

TYPE SPECIES. *Baiera paucipartita* Nathorst 1886.

The name *Sphenarion* is from σφηναριον – little wedge.

The Type species from the Rhaetic of Sweden is much the best known. Its form was described by Nathorst (1886) and its form and cuticle by Lundblad (1959). Lundblad included *Baiera amalloidea* Harris (1935) from the Rhaetic of East Greenland and we accept the identification so that there are independent accounts of both form and cuticle, and these agree closely. The other species presently included are *Sphenarion leptophylla* (Harris) comb. nov., Rhaetic of East Greenland (for *Baiera leptophylla* Harris 1935). *Sphenarion latifolia* (Turutanova-Ketova) comb. nov. (for *Czekanowskia latifolia* Turutanova-Ketova 1930, Sixtel 1960 (for form), Gomolitzky 1963, and Orlovskaya 1968 (form and cuticle). Lower Jurassic and Upper Triassic of Central Asia. The fossil named *Ginkgo sibirica* by Vasilevskaya (1960, pl. 5, fig. 5) looks very similar also. *Sphenobaiera flabellata* Vasilevskaya & Pavlov (1963) and Vasilevskaya & Abramova (1966) may be yet another species of *Sphenarion*.

Two species we considered but exclude at present for different reasons are:

Sphenobaiera horniana Florin (1936a). Lower Cretaceous; Franz Joseph Land. Leaf rather like *S. paucipartita* but fragmentary. There is no evidence whether it was shed separately or borne on a caducous shoot but the single vein at the leaf base recalls *Czekanowskia*. See also Krassilov (1970, p. 14).

Sphenobaiera boeggildiana (Harris) Lundblad (1959). The leaves are crowded on a shoot but this may not be of strictly limited growth. They are not in a bundle enclosed by scale leaves.

While several species of *Sphenobaiera* are based on abundant and good specimens, for instance *S. spectabilis* the Type, and these show an abscissed leaf base, others are based on a few fragments which had broken before preservation and do not show the leaf base. We merely assume that they are correctly placed in *Sphenobaiera* and leave them there. Apart from the way the leaves are borne, we have no evidence that *Sphenarion* belongs to the

Czekanowskiales rather than to the Ginkgoales: cuticles can give little help. Unfortunately we do not know whether there is a single vein at the leaf base, but if there was, it would afford supporting evidence.

Sphenarion muiriae is near to *Arctobaiera* Florin in its simple or once forked leaves but they are much narrower and probably with fewer veins. *S. paucipartita* (Nathorst) has leaves which divide more than do those of *Arctobaiera* and so do the other species mentioned above as possibly belonging to *Sphenarion*.

Sphenarion muiriae sp. nov.

Pl. 6, fig. 6, Pl. 7, fig. 1; Text-fig. 35

Diagnosis (based on holotype only). Leaves about five, persistent on small caducous dwarf shoot. Leaves 30–40 mm long, mostly forked once and with branches diverging at about 30°, occasionally simple. Leaf 1·0 mm–1·5 mm wide in its lower and middle parts, not contracted near base, widening slightly just below a fork, the two branches about 0·6 mm–0·7 mm wide and tapering to acute apex; undivided leaf also with acute apex. Lamina surfaces flat, margins rounded and unspecialized. Substance of lamina rather dense. Veins not apparent on surface nor obvious by transmitted light (possibly two below the fork and also in undivided leaf but one in each branch). Dwarf shoot about 2·5 mm long and 3·0 mm broad. Shoot perhaps bearing minute scales (details not clear). Cuticle of leaf about 2·5μ thick (in folds) on 'upper' side and along compressed margins 1·5μ on lower side, but two sides otherwise similar. Stomata equally numerous on two sides; widely distributed over surfaces. Most stomata occurring scattered in tracts about two stomata wide separated by narrow tracts with none, only seldom forming short files formed by longitudinal sequence of cells, about 8 of these tracts present on fragment 1 mm wide; but stomatal tracts often indefinite. Margin of leaf little specialized, probably rounded, cuticle slightly thicker but stomata occurring on both surfaces near margin. Veins (probably) represented by broader tracts without stomata on lower side but with more strongly cutinized cells which are also more elongated and with rather more trichome bases. Near margins, bulging cells frequent (? trichome bases). Veins less apparent on upper side. Epidermal cells between stomatal tracts forming short longitudinal files of cells with mostly transverse ends and cells two to three times as long as broad. End cell of file pointed. Cells among stomata mostly short, often nearly isodiametric or elongated obliquely, scarcely forming files but often in more or less longitudinal packets of about three cells. Anticlinal walls straight, clearly marked, rather thin but distinct, transverse walls slightly striated or pitted. Periclinal walls bulging slightly or almost flat, often sculptured with small round pale areas or occasionally with few longitudinal striations. Where anticlinal wall of a cell bulges it forms a low unthickened dome (its height about one quarter of its width) and on vertical compression may produce distinct crease in middle of cell. Stomata nearly all orientated longitudinally. Guard cell surface almost flat, almost on general level. Width of pair of guard cells often similar to ordinary cell. Subsidiary cells quite unspecialized but occasionally encroaching somewhat on a stoma and reducing exposed part of guard cells; guard cell cuticle not traceable beneath epidermal cells. Guard cell surface slightly thinner than rest of cuticle, but thickened around aperture and at margins.

Trichome bases rare over most of epidermis but more frequent along presumed veins. Those among stomata bearing small ring surrounded by faint larger ring which commonly overlaps two ordinary epidermal cells. Those on veins similar but more strongly cutinized and situated on rather strongly cutinized cells.

HOLOTYPE. V.56410. (Pl. 6, fig. 6, Pl. 7, fig. 1; Text-fig. 35.)

DISCUSSION. The holotype was collected by Dr M. Muir with one of us (T.M.H.) in 1964. The block showed several leaves of *Czekanowskia blacki* but the *Sphenarion* leaf bundle was largely buried and when collected was only considered as a rather stout leaved *Czekanowskia*. However when rock burying the specimen was removed by one of us (J.M.) its unusual form was realized and its cuticle showed that it was something entirely different from *Czekanowskia*. What gives the specimen a strange appearance is that while four of its leaves fork once, the leaf in the middle is broader and unbranched. Some damage was caused when the specimen was collected and further damage occurred when the overlying matrix was being chipped away but we believe that all the leaves were attached and perfect when the specimen was preserved. The four forked leaves are clearly attached but the simple one is separated from the dwarf shoot by a gap of about 0·2 mm. We think this gap was caused in cleaning. The undivided leaf might be quite separate and merely have drifted into a position suggesting attachment. Its cuticle, however, is like that of the forked leaves. No other fragment of *Sphenarion* is seen on the rock nor was any cuticle found when considerable pieces of the rock were disintegrated by bulk maceration. Evidently *Sphenarion* is a rare species even here and it is most unlikely that an originally separate leaf should come to lie in this deceptive position.

The specimen is moderately well preserved but the fossil substance was difficult to detach from the fine sandstone rock; and even with celloidin pulls only small pieces were separated. These were adequate for cuticle preparations, but not for counting veins that might have been visible in the leaf substance after partial maceration.

COMPARISON. *Sphenarion muiriae* resembles *Sphenarion paucipartita* (Nathorst) from the Rhaetic of Sweden and Greenland (see Lundblad 1959 and Harris 1935). It is, however, distinguished by its shorter and narrower leaves which fork only once instead of twice. Their cuticles are more different. *S. paucipartita* has scarcely any stomata on the upper side. Its stomata are rather more protected and the subsidiary cells may bear moderately developed papillae. Neither has resin. With *S. leptophylla* (Harris) it agrees in having only about five leaves on a dwarf shoot and in the narrowness of the leaves, but those of *S. leptophylla* are longer and usually branch twice and have resistant resin bodies. Its cuticle which agrees in having stomata on both sides differs in its narrower epidermal cells and subsidiary cell groups and it recalls a *Czekanowskia* cuticle.

S. muiriae resembles *Sphenarion latifolia* (Turutanova-Ketova) in several respects. *S. latifolia* leaves are, however, rather broader and have several veins, they are also longer (at least 90 mm). It is hypostomatic and the veins are more clearly indicated but the appearance of the cells and stomata of the stomatal strips is remarkably like that of *S. muiriae*.

OCCURRENCE. *Sphenarion muiriae* is represented by a single specimen from the Scalby Ness *Ginkgo* Bed of the Upper Deltaic. No cuticle fragments have been identified with it but its cuticle is not very robust, nor has it very striking features, so it might be missed.

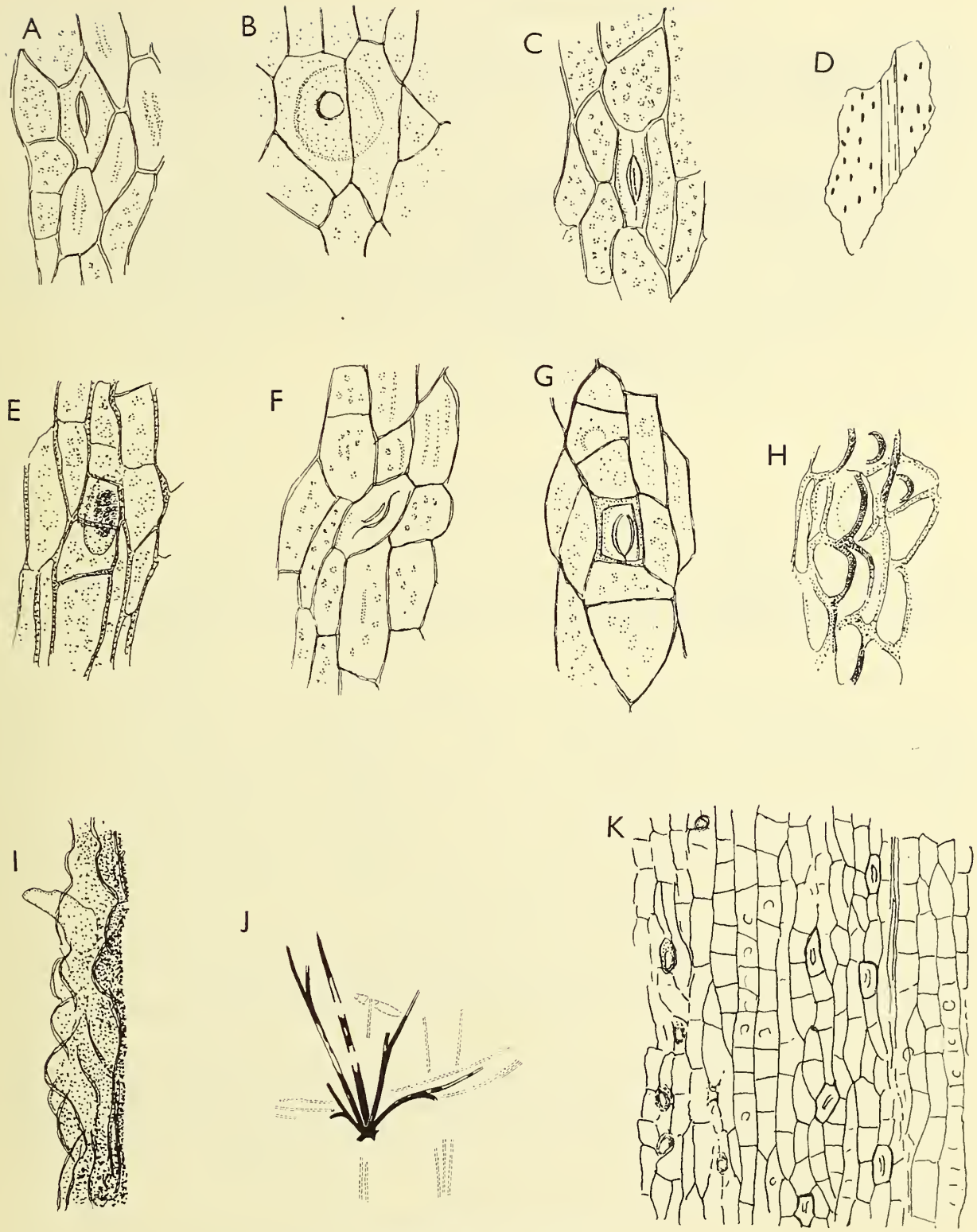


Fig. 35. **Sphenarion muiriae** sp. nov.

All the figures represent the holotype, V.56410, from Scalby Ness. A, commonest form of stoma. B, trichome base among stomata. C, slightly contracted stoma. D, orientation and distribution of stomata on lower surface; ruled lines represent a vein, magnification ×20. E, trichome base on a vein. F, unusual oblique stoma. G, most protected stoma seen. H, obliquely crushed, bulging cells along leaf margin. I, leaf margin. J, holotype specimen; actual size; black represents coaly substance present when drawn; firm outline the distinctly visible imprint; gaps probably due to damage in preparation. Broken lines are fragments of other species. K, lower cuticle with vein on left, magnification ×200. Further stomata occurred just to right of drawing. All magnification ×400 unless otherwise stated.

Genus LEPTOSTROBUS Heer 1876, p. 72

Diagnosis (slightly emended from Harris 1951). Cone axis elongated, lower part covered with small scale leaves, upper part bearing seed capsules in loose spiral. Capsules almost sessile, not abscissed but readily torn off, composed of similar upper and lower valves, valves with thickened and more or less lobed terminal margin. Outer surface of valves convex, interior concave, margins of valves in contact but not joined. Each valve with single row of 3–8 small seeds, one to each lobe, micropyle facing cone axis. Megaspore membrane cutinized. Cone axis and capsules well cutinized externally. Cell outlines nearly straight. Stomata frequent but scattered on outer surface of capsule, surrounded by ring or somewhat elongated group of subsidiary cells, surface of subsidiary cells somewhat thickened, forming elongated or rounded pit over guard cells. Encircling cells often present but variable.

Type Species. *Leptostrobus laxiflora* Heer 1876.

Discussion. See under *Leptostrobus cancer* Harris.

Leptostrobus cancer Harris

Pl. 7, figs. 4–8, 10, 11, 14, 15; Text-figs. 36–39

1951*a* *Leptostrobus cancer* Harris, p. 487, pl. 18, figs. 1–19, pl. 19, figs. 20, 22–26; text-figs. 2, 3 A-C, E-G, 4 A, B.
1962 *Leptostrobus cancer* Harris: Potonié, p. 162, pl. 17, figs. 479, 480. (Adherent pollen grains)
1971 *Leptostrobus cancer* Harris: Van Konijnenburg – van Cittert, p. 49, pl. 10, figs. 1, 3. (Adherent pollen grains)

Diagnosis (from Harris 1951*a* with very slight modification). Cone axis very slender, bearing capsules at intervals of about 5 mm. (Cone base imperfectly known.) Fruiting capsules typically flattened-globose, length 5 mm, width 5 mm, thickness possibly 3 mm, smaller capsules frequent. Valves of capsules rounded, sessile, distal end usually with up to 5 very obtuse lobes or else almost smooth, margin thickened, outer edge of margin sharply incurved. Surface of valves typically showing slight ribs from base to marginal lobes. At edge of valve inner surface exposed for nearly 1 mm; but then abutting on opposite valve. Two valves similar or one (? upper) with slightly thicker cuticle and more distinct cell outlines. Cuticle normally uniform over ribs and between them but ribs occasionally distinguished by more elongated and narrow cells. Seeds up to 5 in each valve, megaspore membrane about 2·0 mm × 0·75 mm (other cuticles scarcely known). Ripe isolated seeds not known.

Cuticle of cone axis showing straight-walled cells, stomata occasional, agreeing with more elongated ones of capsule.

Cuticle of capsule wall fairly thick (2μ–4μ measured in folds increasing to 6μ–12μ at marginal rim), of tough consistency. Stomata fairly frequent (20 per mm^2), evenly scattered, not forming files or arranged in bands. Epidermal cells isodiametric polygons, or slightly elongated in direction of capsule margin, mostly arranged in rather ill-marked files running from base to margin of capsule. Inner rim of capsule smooth.

Anticlinal walls of cells very strongly marked by broad prominent ridge of cuticle; straight but sometimes with very small jagged thickenings. Surface wall of cell typically flat, without a papilla, almost smooth but showing obscurely mottled surface. Occasional specimens showing

either a large very ill-defined thickening which forms a vestigial papilla, or with very ill-defined surface sculpture of longitudinal striations.

Stomata well developed, but of rather varied structure. Orientation varied, but often longitudinal. Guard cells sunken in pit formed by about five to seven subsidiary cells; pit

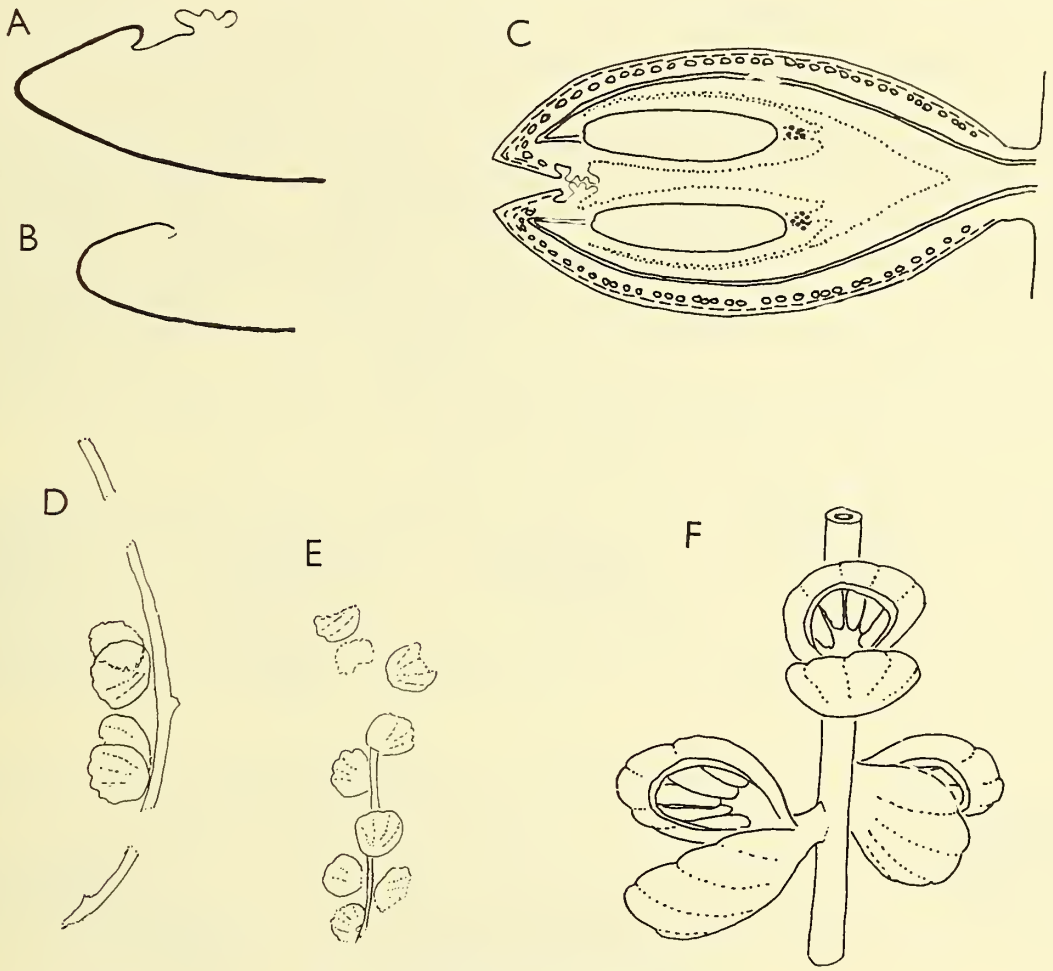


Fig. 36. **Leptostrobus cancer** Harris

A, restored section of cuticle of valve, distal margin showing the smooth outer flange, the groove and the pimply band, compare with lower valve in C, magnification × about 30. B, restored section of lateral margin. In A and B thicker lines represent thicker cuticles, 4μ over most of surface, 1μ in pimply band. C, restored section of whole capsule. From above downwards are: exterior cuticle, angular thick walled cells, rounded ones, fibro-vascular strand (2 lines), inner epidermis of valve and outer epidermis of seed (shown by dotted lines because not seen), megaspore (firm line) with pollen in micropyle on its right, magnification × about 15. D, drawing of capsules shown in both part and counterpart of V.56379 (see Pl. 7, figs. 10, 11), magnification ×2. E, similar drawing of V.56378 (Pl. 7, figs. 14, 15), magnification ×2. F, restoration of part of the cone, showing as pendulous and with gaping valves, magnification × about 5. D, E are from Cloughton Wyke *Solenites* Bed.

varying from round to longitudinally elongated. Subsidiary cells often with slightly thicker surface than other epidermal cells; usually forming rim constricting stomatal pit; pit either round and evenly constricted or elongated and rim better developed at sides than ends of pit. Encircling cells inconstant, but majority of stomata with some encircling cells, or even

with complete set. Encircling cells usually resembling other epidermal cells in thickness. Trichomes absent.

The specific name is from *cancer*, a crab, suggested by the resemblance in shape of the isolated valve to an empty shell of a crab.

HOLOTYPE. V.28568. Figured by Harris (1951*a*, pl. 18, figs. 6, 23, 24; text-fig. 2 E, F).

DESCRIPTION. The old collectors knew of *Leptostrobus cancer*. In the Yorkshire Museum there are three old blocks bearing it. One, probably from the Gristhorpe Bed, has the manuscript name '*Beania* (*Spaereda*) *parvula* Bean', the others are probably from the Cloughton *Solenites* Bed and one of these may be the original of Phillips (1829, pl. 7, fig. 25) 'small vegetable bodies in groups'. It is also labelled '*Sphaereda parva*' (the manuscript name '*Sphaereda parvula*' or '*parva*' was also applied to little coprolites). These old specimens yielded typical *L. cancer* cuticles. *L. cancer* is locally common in the Cloughton *Solenites* Bed and a single hand specimen may show a dozen capsules and others can be extracted by maceration. Probably they were concentrated by floating. Other layers of this bed though rich in *Solenites* have but few *Leptostrobus* capsules. Since 1951 *L. cancer* has been found in four additional Yorkshire localities, making six in all.

The material under study is similar to that described by Harris (1951*a*) but certain additional points have been made out. The new material provided cone fragments (Pl. 7, figs. 10, 11, 14, 15) and a few bits of cone axis stripped of appendages. The loose lying capsules, nearly 200, are very like those seen before.

Cone axis. The cone axis is slightly under 1 mm wide in the figured specimen but just over 1 mm in another. Clearly the cone was slender if as long as in *L. laxiflora* (110 mm) or *L. longus* (at least 150 mm).

The axis, when seen by transmitted light in a transfer, has a dark core occupying the middle two thirds. Even this core is not very substantial and decay had removed almost everything at its sides except the cuticle enclosing a few fibres. We picture the cone as a flexible and pendulous catkin. This axis fragment has shreds of cuticle from the bases of capsules and the numerous isolated capsules have torn bases. They were not neatly abscissed at maturity, but must have parted easily from the fallen and rotted cone. Both the cones and most of the enormous numbers of *Solenites* leaves in the *Solenites* Bed appear to have rotted and broken up before being deposited where they were preserved.

Cone base. There are no good specimens of cone bases but there are a few small fossils thought to be fragments of this region. They are little collections of broadly lanceolate scales, very like scales of the short shoot of *Solenites*, but the group differs in being elongated, the scales are arranged spirally. All these groups of scales were made into transfers (on balsam or on celloidin) in the hope that they might prove to be male cones but they did not. Even the axis was missing. The best group is shown in Pl. 7, fig. 4, and the scales in this and other groups are all about 4 mm $\times$ 2·5 mm in the part exposed. The substance of the scale is very thin but it is fairly coherent and the margins, which are scarious, are composed of a single layer of elongated cell cuticles. Towards the middle of the scale the cells have dark contents, so that the cell outlines are relatively pale and the scale has a misleading appearance of a sheet of fibres. Then towards the base there is more than one layer of these dark cells and the whole scale is dark. After maceration (in $HNO_3 + KCLO_3$, then NH_4OH) the dark cell contents

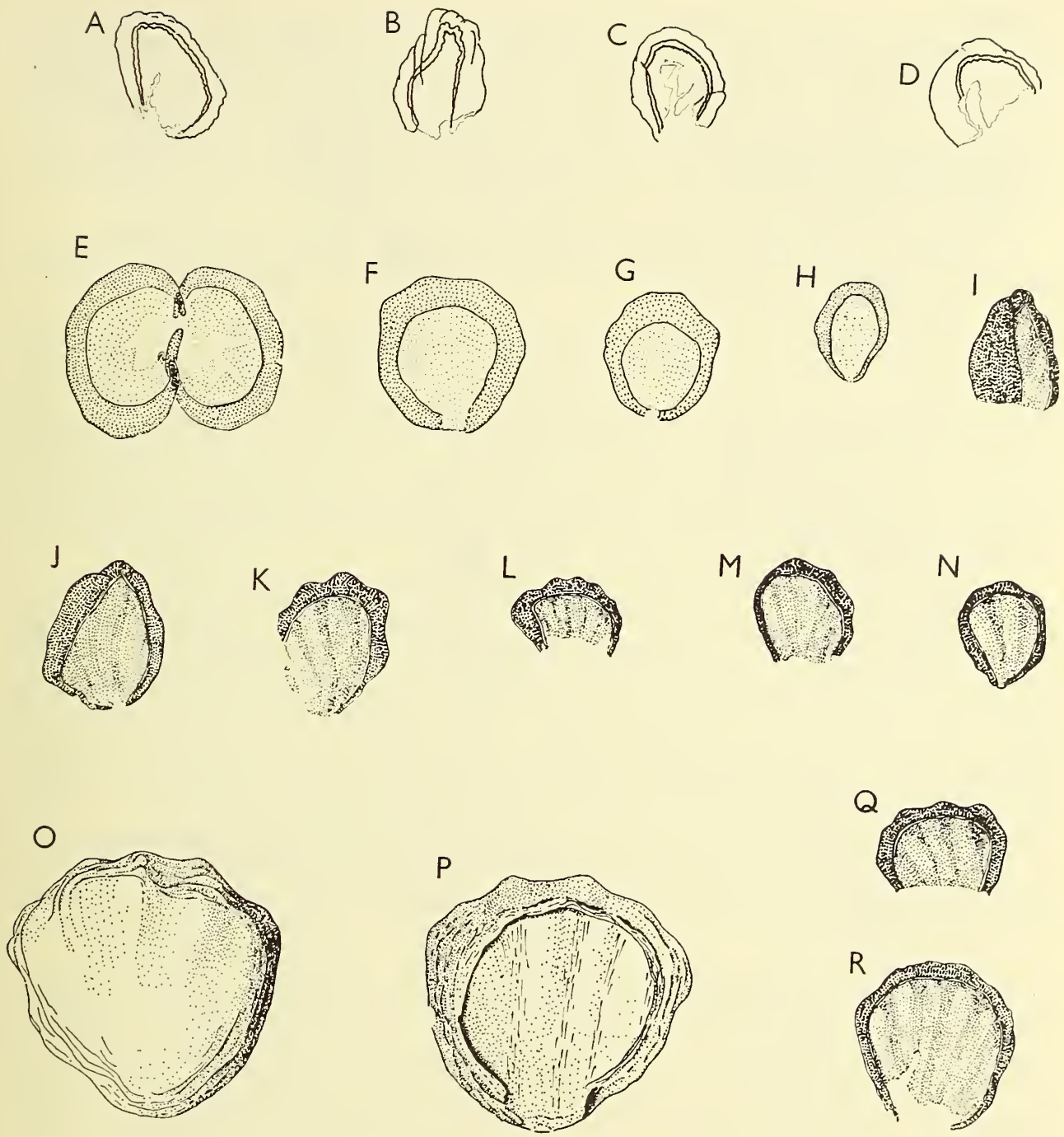


Fig. 37. **Leptostrobus cancer,** capsule valves

A–C, three valves from Beast Cliff Bed G., V.56508. D, valve from 30 ft above Haiburn Wyke, Iron Scar, V.56509. E–R, valves from Cloughton Wyke *Solenites* Bed; translucent specimens are all shown from the inner side, the inturned margin being darker. E is a valve pair, the left valve is the thicker, V.28564. O, P, Holotype, V.28508. O, as originally exposed, P, as seen in a balsam transfer.

All valves are magnification ×5 except O, P which are magnification ×10. F is V.28565, G is V.28566, H–N, Q, R all V.28567. A–C are new drawings; E–R are from Harris (1951) by permission of Royal Society.

vanish and nothing remains but an ordinary cuticle which is then only just coherent. The cells have finely marked outlines and their surface is smooth. The preparations were poor and no stomata were recognized. Apart from their association, these groups of scales are linked with *Solenites* and therefore *Leptostrobus* by the form and texture of individual scales which are much like certain inner scales of a *Solenites* dwarf shoot. They suggest a more elongated scaly cone base than in *L. laxiflora*, in fact more like that of *L. crassipes* Heer, though much less robust. Clearly we need better material for study.

Capsules. The capsules are robust little fossils, but they are not very conspicuous and were seldom found except when searched for. The valves are strong enough to survive intact when the rock is macerated in bulk.

The valves forming the capsules are normally compressed from above downwards and are then round or slightly broader than long and the distal margin is either smooth or with 3–5 weak bulges. A very few have a conspicuously crenate edge but these are shrivelled and perhaps died when immature. A considerable proportion of valves are below the normal size of 5 mm × 5 mm, the smallest seen is only 2 mm long × 1·5 mm broad, but it is obliquely compressed and may have originally been round. A fair number of capsules are compressed obliquely and although these make unsatisfactory specimens they give the basis for the estimate of original thickness from valve to valve of 2 mm–3 mm.

The valves are described as upper and lower rather than 'right' and 'left'. There is no direct evidence of this in *L. cancer* and in most of the intact cones of other species the valves lie in the plane of the cone, presumably through rotating when the cone was compressed. In some of Heer's cones the capsules are still in position in their phyllotactic spiral and here it is clear that one valve is above the other. In *L. cancer* though the two valves commonly look alike, one sometimes has a perceptibly thicker cuticle and stronger cell outlines. Krassilov (1968*a*) noted a similar difference of thickness between the valve cuticles of *L. laxiflora* but attributed it to an effect of preservation. We call the thicker the upper valve. The two valves of a capsule are separate almost to the base and are often slightly displaced in compression but though firmly in contact in the few capsules still with seeds they are separate in the empty ones and often slightly displaced in compression. The empty capsules have filled with fine mud (rock matrix).

The wall of each valve bends inwards to form a rather broad flange and the inner edge of this flange is specialized. The flange is 0·6–1·0 mm broad at the distal end of the capsule but diminishes in width towards the base. It is divisible into parts which were recognized repeatedly. The outer part is like the rest of the valve and has a few stomata. It is almost smooth, that is the cell surface is flat or only bulges slightly. It is thus different from this region of the capsules of *L. laxiflora* Krassilov (1968*a*, pl. 1, figs. 1–8, pl. 2, figs. 1–7; text-figs. A–G). Then the cuticle dips to form a deep trench with overhanging sides, it also becomes more delicate and has no stomata. It then rises again to form a curious band covered with pimple-like mounds, but these are flattened by compression. At its inner edge the cuticle, now still more delicate, bends back under the pimply band and is then lost. These specialized parts, the groove and the pimply band, are not restricted to the end of the valve but begin as a gradually broadening zone at the sides 1–2 mm from the base. Krassilov (1968*a*, p. 38) appears to have recognized a corresponding tissue in *L. laxiflora* (the internal cuticle of the

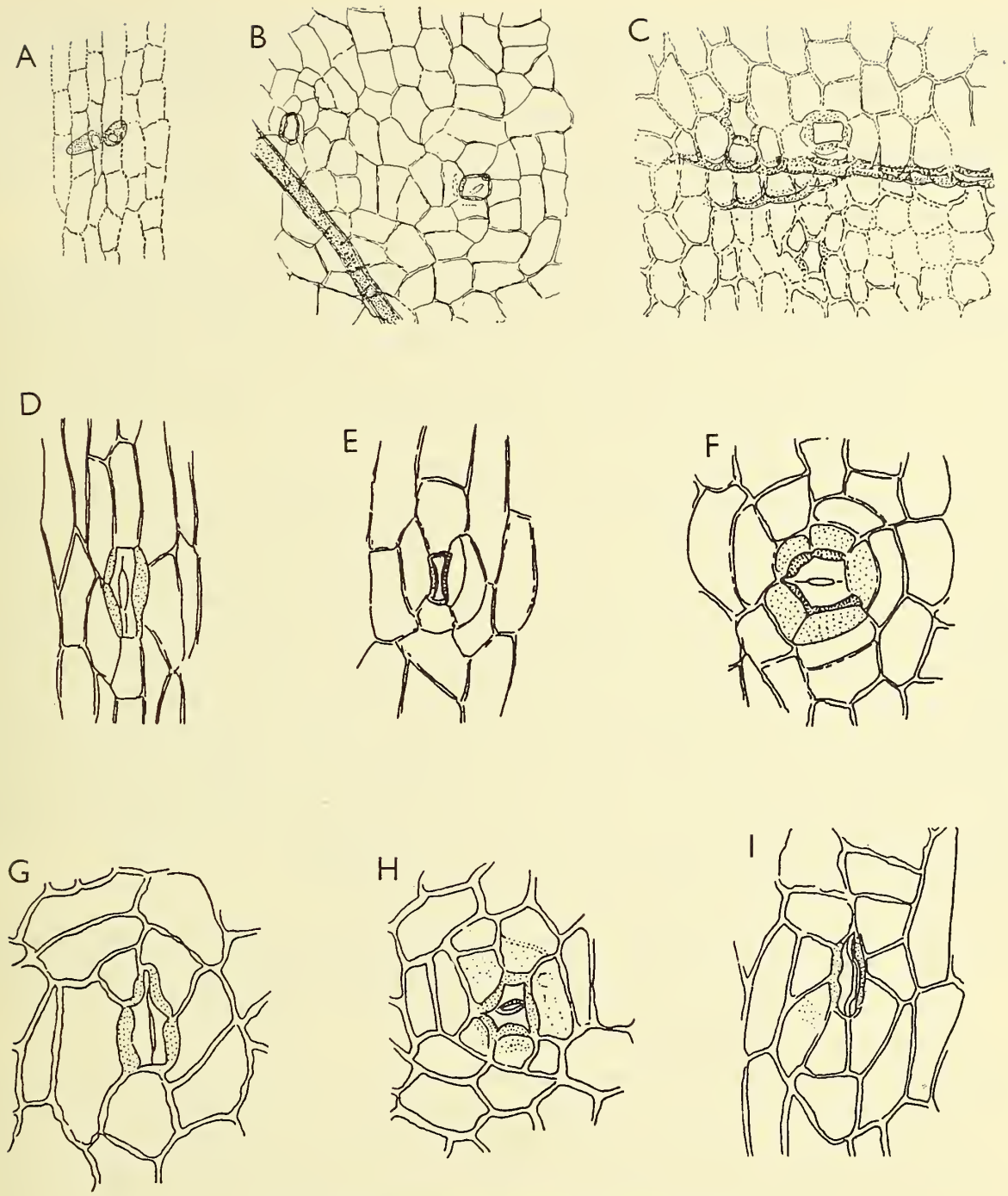


Fig. 38. **Leptostrobus cancer,** epidermal cuticle

A, axis showing two small trichomes, magnification ×200. V.56510. B, cuticle from middle of the valve. A compressed fold proves that the cell surface is flat, magnification ×200. V. 56511. C, cuticle from the inward facing margin of the same valve as B. The cuticle is slightly thicker and a fold here indicates that the cell surfaces bulge slightly, magnification ×200. D, E, stomata on axis, magnification ×400. V.28570. F, stoma on valve face with unusually numerous encircling cells and distinctly thickened subsidiary cells, magnification ×400. V.28565. G–I, three of the variously shaped stomata on a single valve, magnification ×400. V.28569.

All the specimens are from Cloughton Wyke *Solenites* Bed. Figs. D–I are from Harris (1951) by permission of Royal Society.

marginal edge figured in his pl. 1, fig. 7 and pl. 2, fig. 3). Its cuticle is more robust however and its cells have well defined cutinized papillae but collapsed bulges 'pimples' are present. The form of the cuticle along the distal end of the valve is represented diagrammatically in Text-fig. 36 c. (This form was inferred from the way the layers overlap in the flattened but folded cutin membrane.) The peculiar 'pimply band', 250μ wide, is covered with little bulges or pimples, about 100μ across, of originally hemispherical form. The overlapped edge of the trench forms a dark line under the pimply band.

More than half the specimens are isolated valves, always without seeds, and these are in varying states of preservation varying from pale straw coloured and consisting of the cuticle only to substantial and nearly black. A good deal of this loss of substance probably results from decay before the specimens were buried, but some probably from loss by oxidative decay after burial for the pale capsules are often found in layers in which *Solenites* and other leaves are also pale and consist merely of cuticle enclosing some of the most resistant inner tissues. These decayed specimens give some information about the uncutinized part of the valve wall when they are mounted without maceration as transparent objects. The layers are on top of one another and their order was only decided by their appearance under careful focussing and then was not always certain (in this account the order of layers 3 and 4 is the reverse of that given by Harris 1951*a*). Moreover it is likely that delicate tissues, as well as recognizable tracheids, have been missed. The wall of the capsule becomes much darker and stronger towards the margin and this may be partly due to compression but is probably caused mainly by the originally greater development of layer 2 here. The edge of the valve appears sharp in certain oblique compressed valves but the folds in normal compression suggest that it was not truly angular and keeled but just a curve of small radius. The ribs of the capsule wall end in a band of thick tissue running round the margin and do not extend into the inward pointing flange which seems less supported by strong tissue. This thick band of the margin is sometimes preserved prominently and specimens were found in which this tissue and the adjacent cuticles are the only part remaining.

The following tissues are recognizable in the valve wall:

(1) The outer cuticle which is easily prepared. Favourable specimens show something of the epidermis but its cells are hard to recognize (apart from the cell outlines in the cuticle). The cell walls are rather thin and the guard cells of the stomata have only weakly developed thickenings.

(2) Under the epidermis there is a layer of rather thick walled isodiametric cells about 40μ wide and of about the same size as the epidermal cells. (The possibility was considered that they might be epidermal but they seem not to correspond to the outlines in the cuticle.) These cells extend equally over the ribs and between them but there is a small gap opposite each stoma. At the valve margin these cells become thicker walled but smaller and there may be more than one layer. It is not known whether these cells were lignified but they seem rather resistant to decay. Maceration dissolves them. This seems to be the main mechanical tissue.

(3) A layer of separate thick walled cells. This again covers the whole valve including ribs and margin. These cells are mostly separate, but occasionally overlap slightly. They are typically 50μ–65μ × 40μ–50μ. The wall is about 15μ thick and the interior

is empty. They may be sclerids but against this is the fact that they seem to lose their wall substance on decay (much sooner than layer 2). Many valves have lost this layer, probably before being buried.

(4) The bundles of the ribs. These bundles of narrow, elongated cells form the ribs and when they have vanished through decay the wall scarcely shows ribs at all. The cells are in several layers and some are fibres about 15μ wide and their walls are fairly thick. Tracheids were expected but no tracheary thickening was recognized with certainty here (or anywhere else in *Leptostrobus*).

(5) Scattered fibres. Certain valves show a few (1–3) thick walled fibres near the rib bundles, and they may be part of the rib bundles. These fibres are broader (20μ) than most of the cells of the ribs and being separate can be seen distinctly, one was 500μ long. Similar fibres have been seen in *Solenites* leaves. It is not clear whether the fibres observed by Krassilov (1968*a*, p. 38) correspond to these in *L. cancer*.

These five layers are all that were recognized in the wall but it is likely that other more delicate cells occur. For instance the well developed stomata suggest the presence of some photosynthetic tissue and there should be an internal epidermis and perhaps an internal cuticle but nothing was recognized.

Seeds. A considerable number of capsules, and some of what may have been isolated valves have some relics of the seeds but these last are broken and often diminutive (probably abortive as in Pl. 7, fig. 8) and gave no fresh information. A very few capsules which were unusual in containing no rock matrix (mud) showed a full set of ripe seeds but the picture is obscure because we are looking through two layers of capsule cuticle and at two lots of seeds superimposed. When such capsules were further macerated and then opened the seed membranes always broke up. Thus we cannot add to the account given by Harris (1951*a*). Each seed is attached to a dark lump of tissue, itself attached just inside the valve margin and below a marginal bulge (Harris 1951*a*, pl. 18, figs. 7, 8). The only part of the seed clearly seen is the megaspore membrane, an oval sac 1·0 mm to nearly 2 mm long, and the various megaspores point towards the valve base. Here, but just separated from the megaspore a small dark spot has been seen in several specimens and this is largely composed of pollen grains. At this apical end of the megaspore small gaps have been seen in *L. longus* (Harris 1951*a*, pl. 19, fig. 28) which have been supposed to be the openings of archegonia.

The megaspore, a collapsed sac, is a dark coloured cuticle apparently over 1μ thick but its substance is fragile. It may show cell-like ridges which are probably only folds and it is thickly covered with irregular granules about 2μ wide; these are ordinary features of a Gymnosperm megaspore. Around the megaspore (but of unknown extent) there is a tissue composed of very narrow fibres in several layers and this may compose the seed coat. This tissue has a slight power of resisting maceration, but less than the megaspore and much less than an ordinary epidermal cuticle or a spore wall. It was not seen at all in valves from which the seeds had disappeared.

No isolated seeds have been seen but no adequate search has yet been made for them. They are much too delicate to survive the rough treatment of bulk maceration of rock and then sieving, but they might be expected in layers where plant fragments of this size are concentrated. They deserve a special search, for they might be useful.

Pollen producing organs. Apart from *Ixostrobus* there is no pollen producing organ reasonably attributable to *Leptostrobus.* Unassigned male cones happen to be rare in the *Solenites* Bed. All that can be considered is the pollen in or on the capsules, and this proves disappointing.

The seeds show little masses of pollen at their presumed micropyles but these are so

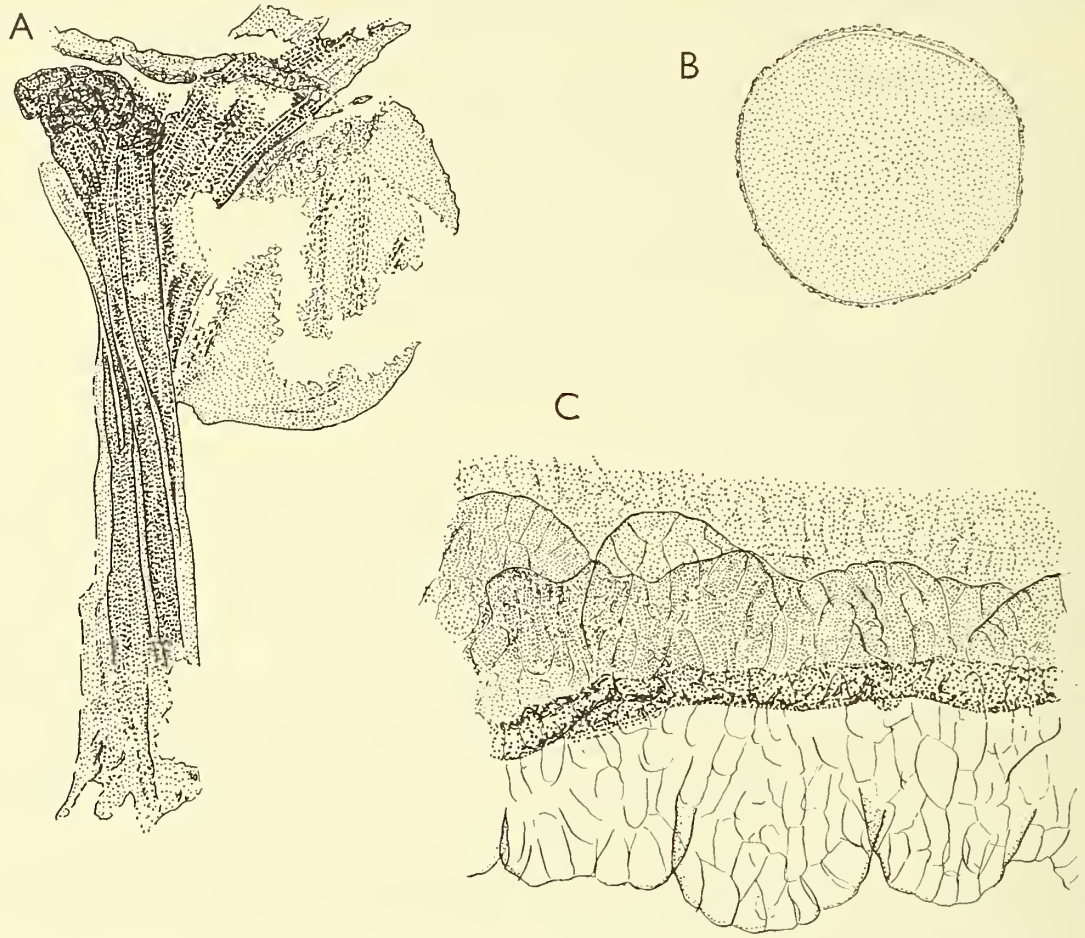


Fig. 39. **Leptostrobus cancer** Harris

A, fragment of rotted cone axis in transfer. Near top is a broken capsule and possibly fragments of others. The axis shows three vascular strands on this surface (and two at the back); the cortical zone is nearly empty, magnification ×20. V.56512. B, inaperturate pollen grain adhering to inside of the capsule in C, magnification ×600. C, part of the margin of a capsule. At the top is the trough cuticle (with obscure cells), this passes under the pimply zone making a darker band, 15–20 mm wide, and then turns upwards giving a still darker band of 5 mm. The lower half of the pimply zone has nothing behind it and so is pale, magnification ×200. V.56513. All from Cloughton Wyke *Solenites* Bed.

compact that individual grains have not been seen satisfactorily by us. Their size varies so there may be several kinds, but see below. Isolated spores and pollen grains are present in fair numbers on the outer and especially the inner walls and margin of capsules. Evidently the capsules were ready (at certain times) to pick up and retain pollen. Although capsules show a strong preponderance of a single type which would seem suggestive, this is countered

by the fact that the grains on capsules of different localities are different. The Greenland *L. longus* capsules show at least four species of pollen in large numbers, the most distinguished being a big oval two-winged grain, but from one locality only. No such grain occurs on *L. cancer* at Cloughton. By far the commonest grain, observed on at least half the Cloughton capsules, is a round featureless one, 50μ–70μ wide, which Dr Muir informs us would normally be called *Inaperturopollenites*. Couper (1958) described dispersed grains like these as *Araucariacites australis* and they are also like the pollen from the male cone of *Brachyphyllum mamillare* and of Recent Araucarians. He recorded such dispersed pollen in nearly all his Yorkshire localities including the *Solenites* Bed but it is not specially common there. *B. mamillare* shoots are known from this bed but are infrequent. It seems best to suppose that the pollen belongs to *B. mamillare* and not to the *Solenites* plant and that it is strongly associated because the capsules were retentive when this particular pollen was blowing.

Van Konijnenburg-van Cittert (1971) re-examined the pollen masses next the seeds in Harris's specimens. She recognized some rounded grains, 55μ–60μ wide, in which the inner layer (nexine) is separate from the outer layer (sexine). She considered the outer layer to be a single saccus and compared these grains with the 1-saccate dispersed grain *Tsugipollinites lucidus*. The grains could also be compared with many of those of *Brachyphyllum mamillare* in which again there is separation of the two layers, but the outer is not there regarded as a saccus. The grain figured here (Text-fig. 39 B) which was not near a seed micropyle, shows no separation.

Comparison. *Leptostrobus cancer* is very like *L. laxiflora* and *L. longus*. From *L. longus* (Lias of East Greenland and attributed to *Czekanowskia hartzi*) it is distinguished by its rounder and less lobed capsule. So far as is known trichomes are absent from the cone axis of *L. longus* (as well as from the leaf *C. hartzi*). Its cuticle is in general very similar but the subsidiary cell groups are mostly elongated in *L. longus* but often rounded in *L. cancer*. In *L. longus* encircling cells are absent on the axis and not mentioned for the cuticle of the cup but in *L. cancer* most stomata have some and a good many have a complete ring and occasionally even a few outer ones.

L. laxiflora is sometimes very similar indeed. The specimens described by Vachrameev & Doludenko (1961), however, have capsules up to 10 mm × 10 mm which is outside the range of *L. cancer*. The epidermis is similar but the stomata have more strongly thickened subsidiary cells and encircling cells are not usually present. The ribs on the capsule wall are more prominent but this might result from different preservation. The age is younger (uppermost Jurassic or Lower Cretaceous). *L.* ex gr. *laxiflora* Krassilov (1968, pl. 1, fig. 6 or *L. laxiflora* 1968*a*, pl. 1, figs. 1–8, pl. 2, figs. 1–7) differs in its strongly papillate border.

Leptostrobus marginatus Samylina (1967) from the Upper Jurassic of R. Silyap, Yakutia is like *L. cancer* in its slender axis (1 mm) and in the size and oval outline of the capsules and in their flat ribs. The margin, 1 mm wide, is more obvious and one of the valves is described as being more convex; there is no evidence of this in *L. cancer* or other species. Samylina figures a remarkable rock surface covered with detached capsules which recall little empty mollusc shells floated together after a flood. *L. cancer* also is locally concentrated but never in such numbers. The specimens are in a bed full of *Czekanowskia* cf. *rigida* and *Phoenicopsis* cf. *angustifolia*. *Leptostrobus limbatus* Vasylevskaya & Pavlov (1963) has a similar broad margin.

L. laxiflora looks more strongly lobed than *L. cancer* in Heer's figures but this may be due to preservation. *L. crassipes* Heer differs in its much stouter axis and larger capsules. We imagine that *L. microlepis* Heer merely represents small capsules of *L. laxiflora* produced at the end of the cone (as in *L. longus*). There are some small capsules with the normal ones of *L. cancer* which are presumably ill-formed, and occasional small specimens are to be expected. Strongly lobed forms of *L. cancer* are most exceptional and the few that occur look poorly preserved with shrivelled cuticles, and perhaps the lobing was produced by the collapse of softer tissues between the fibrous ribs of the capsule wall.

Krassilov (1968, 1970) recognized the following four kinds of fruit in the East Siberian flora but has only given descriptive notes and has not yet named them specifically, apart from *L. laxiflora*.

(1) *Leptostrobus* ex gr. *laxiflora* or *L. laxiflora*, attributed to *Czekanowskia* ex gr. *rigida*, with a strongly convex capsule. Its rim is rough with cellular outgrowths.

(2) *Leptostrobus* ex gr. *crassipes* (1) attributed to *Stephanophyllum* (in the Bureja flora). The capsule is larger, flatter and has up to eight seeds per valve. The capsule rim is less rough than in *L. laxiflora*. The axis epidermis is pilose.

(3) *Leptostrobus* ex gr. *crassipes* (2) attributed to *Windwardia* (in the Chemchulca flora); fruits similar but with specific differences in character of epidermal cells.

(4) *Staphidiophora* close to *S. secunda* and likewise attributed to *Hartzia*. The small capsules contain seeds with thickly cutinized megaspores.

Attribution of *Leptostrobus* to *Czekanowskia* and *Solenites*

The evidence consists of agreement in certain features of cuticle structure and repeated association in different localities and in floras of different ages.

The structural agreement is between the cuticle of the leaf and of the cone axis, and to a less extent of the valve wall. The leaf and cone axis, perhaps being of similar shape, have similar narrow cells and elongated subsidiary cell groups. The stomata on the axis, however, are few and scattered not crowded in files. The valves are broad and have broad cells and broad subsidiary cell groups but they have many features in common with those of the leaves. The evidence for *Czekanowskia hartzi* and *L. longus* and for *Solenites* and *L. cancer* has been set out by Harris (1951*a*) and is not repeated here, but we now have agreement for a third pair, *C. rigida* and *L. laxiflora* Vachrameev & Doludenko (1961). The various species are so much alike that most of this evidence merely repeats. However there are some specific peculiarities. *C. hartzi* and *L. longus* have only feebly thickened subsidiary cells and no encircling cells; *C. rigida* and *L. laxiflora* more strongly thickened subsidiary cells and again few encircling cells; *Solenites* and *L. cancer* have again distinctly thickened subsidiary cells and encircling cells are frequent. In both a few simple trichomes occur—in *Solenites* at the leaf bases, in *L. cancer* on the axis at the base of the capsules.

The little scale leaves at the base of *Leptostrobus* cones have much in common with those of the foliage dwarf shoots and may prove strikingly similar but are not yet sufficiently well known. We cannot properly use the scales, which we suspect belong to *L. cancer*, as evidence because we have tentatively identified them by such agreement. Krassilov (1970) with better material does use the scale leaf cuticles as evidence.

Association. *L. longus* is known in association with *C. hartzi* in three localities in the Lower Liassic of Greenland. It is, however, relatively rare and *C. hartzi* is abundant and has numerous localities in which *Leptostrobus* is unknown. No other leaf in these three localities has a cuticle which resembles *Leptostrobus*.

L. cancer was known (Harris 1951*a*) from three Yorkshire localities in all of which *Solenites* was common, now there are three more.

Lower Deltaic:

(1) At Blea Wyke, Ravenscar, there is a thin bed full of *Solenites* and in certain planes there are fairly numerous *L. cancer* capsules. No other fossils were recognized.

(2) A fallen block from the cliffs near the Red Spring in the Hawsker Cliffs (at 54° 28′ 2″ N) provides *Solenites*, *Leptostrobus* and nothing else.

Middle Deltaic Sycarham Series:

(1) At Haiburn Wyke, 30 ft above the Iron Scar (Eller Beck Bed) a clay yielded on maceration *Solenites* fragments and *Leptostrobus* capsules. Nothing else was recorded.

(2) At Beast Cliff Bed B (54° 21′ 50″ N) a shale yielded on maceration *Solenites* and *Leptostrobus*. We have no record of what other species may have occurred.

Middle Deltaic Gristhorpe Series:

(1) Cloughton Wyke *Solenites* Bed, which is full of *Solenites*, yielded some hundreds of capsules of *L. cancer*. (Specimens of capsules were collected from here and from the Gristhorpe Bed over a century ago and are preserved in the Yorkshire Museum.)

(2) In the Gristhorpe Bed, the locality of the Type of *Solenites* (where *S. vimineus* is common) *Leptostrobus* was collected long ago. It has not, so far as we know, been found again.

It must be noted that while *Solenites* (or *Czekanowskia*) fragments are widespread and sometimes abundant, *Leptostrobus* is rare. It is inconspicuous and was seldom noticed except when being specifically looked for. It is also true that the numbers of *Solenites* leaves and capsules do not run parallel, for instance in the *Solenites* Bed certain layers form a coal of *Solenites* leaves but with few capsules, although in other layers the capsules are common, we imagine through water sorting, and here *Solenites* is only moderately abundant.

Leptostrobus is known from several localities in Russia and Siberia but while *Czekanowskia* certainly does occur in the same flora, the significance of its association was not realized until recently so no details of association were recorded by Harris (1951*a*).

In the floras described by Heer (1876, 1877, 1880) from East Siberia *Czekanowskia* and *Leptostrobus* are certainly associated closely since specimens are seen on the same fragments of rock from Ust-Balei. They also occur at another locality, Kajamundunz, but there it is not clear how closely they are associated. More details would be welcome. Kryshtofovich (1933) also figures both from Ust-Balei. Samylina (1967) describes *L. marginatus* from the Upper Jurassic of R. Silyap, Yakutia, where it occurs in a bed full of both *Czekanowskia* cf. *rigida* and *Phoenicopsis* cf. *angustifolia*. She suggests that *Phoenicopsis* belongs to the *Czekanowskia* group.

Krassilov (1970) gives notes about the association of various *Leptostrobus* species with Czekanowskialean leaves in the Bureja Basin of East Siberia. The association was noted in several localities and must be impressive.

The following seem less significant because we have no details, but they indicate that both *Leptostrobus* and *Czekanowskia* occur in the same region.

1930 Turutanova-Ketova in a flora from Issik-Kall, S.W. Siberia.

1936 Brick records *L. crassipes*, *C. rigida* and *Phoenicopsis angustifolia* in the Middle Jurassic of Tanu Tuva.

Leptostrobus cf. *laxiflora* is known from the Rhaeto-Liassic rocks of Yamanoie, Japan (Oishi & Takahasi 1936, Oishi 1940) but apparently not the same precise locality as the bed from which *Czekanowskia* is recorded. There are no full species lists.

Thus, even if the records in which the association was not considered are discounted, the evidence of repeated association is impressive.

Genus IXOSTROBUS Raciborski 1892, p. 356

Emended Diagnosis. Male cone, detached when ripe. When ripe 50 mm–100 mm long and 5 mm–15 mm broad, lower part of axis bare and forming peduncle, upper part bearing microsporophylls but no other appendages. Substance of axis and microsporophylls thick and originally stiff, microsporophylls widely spaced, borne in irregular whorls or spirally, making wide angle with axis. Microsporophyll consisting of stalk more or less broadened distally to a head, continued by a small pointed scale below and four pollen sacs above, sacs united laterally to form cup-shaped synangium. After maturity pollen sacs and apical scale readily lost leaving a stump.

Cuticles present but very thin. Epidermal cells of axis and sporophyll stalks straight walled, elongated, uniform. Towards sporophyll head, cells shorter and isodiametric. Pollen sacs lined with granular membrane, adherent pollen grains oval, about 40μ–50μ wide; wall probably with a colpus, wall finely granular.

Type Species. *Taxites siemiradzkii* Raciborski 1891, p. 24, pl. 5, fig. 7.

Discussion. We note a discrepancy between the accounts of Krassilov (1968) and of Harris (1935). Harris reported two sporangia only whose walls form two widely gaping halves but Krassilov reported a ring of four united in a cup. Since Harris's material was unsatisfactorily preserved it may have been misinterpreted, or there may be real differences. The main locality, the Neill Cliff Liverwort Bed, though originally excellent was heated by a neighbouring Tertiary basalt sill and cuticles have been impaired, delicate ones like those of *Ixostrobus* becoming impossible to prepare.

We base our discussion of the association of *Ixostrobus* in various floras on the view that all the significant specimens are of the same kind, all belonging to one true genus or to closely allied genera of a single family. But of this we cannot be sure. Even Krassilov's Siberian specimens are not fully known and from most accounts we have just the naked-eye aspect, often of a rather denuded little catkin. Thus we cannot be certain that where authors differ in their accounts of morphology, that the differences described are real. Suppose for example that *Ixostrobus groenlandicus* Harris and the present *I. whitbiensis* were entirely different from

Krassilov's *I.* ex gr. *heeri* from East Siberia and were produced by different plant families, then there need be no conflict in morphology and none in the interpretation of associations. But all difficulty would not be removed, on the contrary a new one would be made. These three species look so much alike that to separate them generically would be almost impossible with present knowledge. It would also leave all the less closely studied specimens unplaced. But since we have no reason to link any Yorkshire Czekanowskialean leaf with a particular male cone, it would at least not make them seem any more lacking than they are now. The whole position is unsatisfactory and we greatly hope that new work will soon settle something.

We follow Krassilov (1968, 1970) who regards *Ixostrobus* as the male cone of *Czekanowskia* and *Stephanophyllum* (part of *Phoenicopsis*) and for this reason include it in the present volume.

Krassilov based this view on its association in the Amurland flora, and others who have collected there, notably Prinada (1962), were strongly impressed also, as indeed was Heer. We hope that this is right for its does much to make the Czekanowskiales a satisfying family. It is therefore with divided feelings that we present an alternative case, based on the Yorkshire material, for linking *Ixostrobus* with an entirely different leaf, *Desmiophyllum*.

Earlier, Yabe & Endo (1934) suggested that *Schizolepis jeholensis* which they found associated with *Czekanowskia* in the Lower Cretaceous of Manchuria might be its male cone. However no later support for this idea has been published.

Apart from this essential question we still have much to learn about *Ixostrobus*, for instance how it was borne. It might have sprung from a basal cup of little bud scales like that round the dwarf shoot of *Czekanowskia*. What we have been able to contribute to its morphology, particularly its cuticle, is far from complete and we certainly need to know more about its synangial cup. We assume that the lateral appendages are microsporophylls, the simple interpretation, making them therefore comparable with *Ginkgo* microsporophylls though more complex.

Although most of the cones called *Ixostrobus* are only known in their obvious, naked eye features, they look as though they may be a homogeneous group or genus and are so treated here, but with reservations. The lax insertion of the appendages (commonly just denuded stumps) and their striking, stiff appearance separates them from nearly all fossils and there is nothing very like them in living Gymnosperms. The main fossils which have been confused with them are the cones called *Stenorhachis*. Seward (1912, 1912*a*, 1919) indeed included the whole genus *Ixostrobus* in *Stenorhachis*, but this was at a time when we knew less about *Ixostrobus*. *Stenorhachis* is still a very unsatisfactory assemblage, perhaps of female as well as male cones but most of the kinds, though little known, have appendages with relatively slender stalks and which arise at a smaller angle.

The evidence for linking *Ixostrobus* with the Czekanowskiales has been summarized by Krassilov (1970) and we agree with him that none of the other associates he names is in the least likely to be concerned. Clearly the association in the Amurland flora is impressive. It was from there that the first specimens of *Ixostrobus* were described, and it is probably still true that more specimens from that region have been figured than from all other floras together. *Ixostrobus* has also been found in floras, all of them with members of the Czekanowskiales, in a good many other districts and we give a list of all those known to us on p. 130. There is, however, some uncertainty whether there is a close association in a precise locality,

that is a single plant bed. Sometimes such association clearly exists, but sometimes the two are recorded from different localities. It would be wrong, however, to take this as a real failure of association because several authors had no such link in mind and Czekanowskialean leaf fragments are easy to miss, even when common.

Raciborski (1891, 1892), however, did have this link in mind when he instituted *Ixostrobus* for Polish 'Rhaetic' (perhaps Middle Liassic) specimens and the association of the two at Gromadzic is important. (We note however that a *Desmiophyllum*, '*Podozamites*' *stobieckii* Raciborski also occurs.) Apparently also in Afghanistan, Seward's (1912) *Stenorhachis lepida*, a typical *Ixostrobus*, is associated with a leaf regarded as a *Phoenicopsis* but he did not discuss it. In the Lower Liassic of East Greenland *Ixostrobus* was reported by Harris (1935) from two localities only, one of which had a *Czekanowskia* but the other not. In spite of our knowledge of that flora the indications are in conflict. Associations in this Greenland flora were looked for, though not always with attention to the leaf now under discussion. Both localities belong to the basal Liassic. *Ixostrobus* was recorded as 'rare' in the Vardekloeft Liverwort Bed but 'very common' in the Neill Cliff Liverwort Bed. The first bed was only collected a little because it was awkwardly placed but the second was convenient and with a rich flora was vigorously worked, so that far more is known about its flora. Harris noted in both association with 'narrow leaved species of *Podozamites*', though he considered this association 'not at all striking'. These *Podozamites* leaves occur widely, in fact in about 40 of the 80 known beds. Harris thought there were several species, but they proved frustrating taxonomically, partly because their cuticles are delicate and could seldom be prepared. We dismiss them (as did Krassilov), for nothing like them occurs with *Ixostrobus* in Yorkshire.

Czekanowskia nathorsti occurred in the Vardekloeft Liverwort Bed only, but *C. hartzi* which occurred in neither was found a few metres above both of the beds with *Ixostrobus*. Harris briefly discussed its association but dismissed it, for the wrong reason; he then thought *Leptostrobus* was the male cone of *Czekanowskia*. He also dismissed *Ginkgoites hermelini* (now *G. marginatus*) which was associated with *Ixostrobus* in both beds because he expected something much more like a *Ginkgo biloba* male cone. A leaf which occurred with *Ixostrobus* in Neill Cliff (but not Vardekloeft) was '*Desmiophyllum* Type 2' but was not discussed. It looks almost exactly like *Desmiophyllum gramineum*. There is no record of its frequency.

These facts, though fuller than can be obtained from some old descriptions, settle nothing. In Japan, Oishi & Huzioka (1938) recorded both *Ixostrobus* and *Czekanowskia*, as well as some other leaves which might belong to the Czekanowskiales, from the Rhaetic flora of Nariwa. They are, however, recorded from different beds, the cone, *Stenorhachis* (*Ixostrobus*) *konianus*, being from 'Loc. 50' while *Czekanowskia* leaves and also *Phoenicopsis* leaves are from several numbered localities, but not 'Loc. 50'.

We deal more fully with the association in Yorkshire. Here *Ixostrobus* comes from only three localities (i.e. single plant beds) but in each of these it is represented by a number of specimens so that it clearly must be counted a characteristic member of its bed and not just a rare stray. It is under such circumstances that association seems significant. Only one of these localities (Saltwick) was visited repeatedly and even there the collecting was difficult. This and one other locality, also near Whitby, are at the base of the Lower Deltaic, fairly low in the Bajocian, but the third is in the Upper Deltaic, Bathonian. No special search was

made during the field work for *Czekanowskia* but every determinable leaf of any kind from each locality was kept.

The holotype of *Ixostrobus whitbiensis* and two other specimens are from the *Zamites* Bed of Whitby, Jump Down Bight. This bed is high in a vertical cliff and inaccessible, but was well represented in a cliff fall in 1946. The most noteworthy fossils besides *Ixostrobus* were leaves, stems and 'flowers' of *Zamites gigas* but in addition there were many leaves of *Desmiophyllum gramineum* (discussed below). No *Czekanowskia* at all was noticed, but when all the spare rock was trimmed off the *Ixostrobus* specimens and this rock was macerated in bulk, one fragment of *Czekanowskia* was found. It is poorly preserved and not specifically determinable, but might be *C. furcula*. This is association with *Czekanowskia* but at a minimum.

The six specimens of *Ixostrobus* from Saltwick were collected from a steep bank by a waterfall. Here there is a fairly large flora, mostly of ferns and Bennettitales and by far the commonest leaves are *Desmiophyllum gramineum* which are so numerous on many bedding planes that each leaf is crossed by perhaps ten others. Here also *Czekanowskia furcula* is represented by a fair number of good specimens, so that at this locality there is real association between them.

The Upper Deltaic locality R. Derwent 'Grass' or 'B' Bed (54° 21′ 10″ N, 0° 34′ 3″ W) is a sandy shale in which all fossils are poorly preserved. *Desmiophyllum gramineum* is overwhelmingly abundant and several blocks show it and nothing else. Three specimens of *Ixostrobus* were found. There was in addition a leaf of *Ginkgo huttoni* and indeterminable scraps of two conifer shoots. No *Czekanowskia* was recorded at the time of collecting, but when all spare rock was broken up a few leaf fragments, about 1 mm wide, were detected. Their determination could not be checked by their cuticles because these have perished (including even the tough cuticle of *G. huttoni*). No doubt for this reason the bulk maceration of spare rock from this locality yielded nothing.

Thus we have satisfactory association of *Ixostrobus* with *Czekanowskia* in one locality, slight association in a second and uncertain association in a third. With *Desmiophyllum*, on the other hand, we have in each locality association with that leaf in large numbers. *D. gramineum* is known from nowhere else (though a few fragments of that unimpressive leaf might well have been missed) but *Czekanowskia furcula* and other species as well as *Solenites* have many localities. A few of these gave also *Leptostrobus* (with *Solenites*) but none gave any male cone we considered attributing to them.

This distribution of *Ixostrobus* should be considered with a background of the distribution of plants in general in Yorkshire. There are but few really good localities—not more than twelve, to which for example one would take a visitor, but there are 50–100 useful second-rate localities. The three *Ixostrobus* localities are of this second rate sort. Then we have a much larger number, nearly 600, which gave pieces of leaves, already broken when deposited but still with good enough cuticle for specific or generic determination. Finally there must be an enormous number of localities yielding dispersed miospores.

Czekanowskia and *Solenites* are common and widespread, the total number of localities of determined specimens of the various species is about 70, but this number is incomplete. Where we had a fragment of *Czekanowskia* which we felt unable to determine specifically we omitted it from lists, and in the case of ill-preserved fragments not even determinable

generically as at R. Derwent Grass Bed, we kept no record. Even so Czekanowskialean leaves do not occur everywhere and some worked beds have yielded none.

The rival cases for linking *Ixostrobus* with *Czekanowskia* or with *Desmiophyllum*

Both cases depend on association but in different regions. We had hoped that structure might give some help, but it does not at present. Though the leaves of *Czekanowskia* and of *Desmiophyllum* differ greatly in cuticle as well as in form, there is some resemblance in the elements of their structure, for both have elongated straight walled epidermal cells and elongated haplocheilic stomata with narrow pits. They seem very different because the *Czekanowskia* cuticle is thick and the *Desmiophyllum* thin but we must not use this in identifying a different kind of organ like a male cone since this may often be much less thickly cutinized than the leaf of the same plant.

The only part of *Ixostrobus* which has so far given a cuticle that seems likely to be of use is the cone axis and peduncle and this delicate cuticle shows elongated cells with slightly moniliform walls and a coarsely mottled surface. Similar cells, indistinguishable both in the drawings (Text-fig. 40) and in the preparations, are to be seen on the upper epidermis of *Desmiophyllum*. The cuticle of a leaf of *Czekanowskia* looks different being so much thicker, but the plant did produce delicate cuticles (for instance on some of the scale leaves at the base of the leaf bundles) where cells can be found which match those of *Ixostrobus* just as well in shape, walls and surface sculpture. Such cells indeed occur widely in Jurassic plants though not in all.

The evidence for association has been mentioned. For Yorkshire the association of *Ixostrobus* and *Czekanowskia* is weak, but that with *Desmiophyllum* is strong. For the Amurland the association with *Czekanowskia* is striking while *Desmiophyllum* is not mentioned except by Prinada (1962), see p. 138 below.

Elsewhere the association almost certainly needs to be reexamined. The main reason for the inclusion of *Desmiophyllum* in the present work is the hope that it may stimulate further search for similar leaves, in Amurland for example. If they really are absent, that fact would impress us, but it is insufficient that they are not mentioned. The *Desmiophyllum* leaves are unsatisfactory to determine and would be easy to dismiss without name. The present material was in fact designated 'grass' till a late stage in this study.

List of foreign specimens which may belong to *Ixostrobus*:

1876	*Baiera longifolia* (Pomel): Heer, p. 53, pl. 9, figs. 8, 9; possibly 10, 11.	Jurassic; E. Siberia and Amurland
1876	*Baiera czekanowskiana* Heer, p. 56, pl. 10, fig. 5.	
1876	*Ginkgo huttoni* (Sternberg): Heer, p. 57, pl. 10, figs. 8, 9.	
1876	*Ginkgo sibirica* Heer, p. 61, pl. 11, figs. 1 B, 9–12.	
1878	*Ginkgo sibirica* Heer: Heer, p. 25, pl. 6, figs. 8, 9.	
1880	*Baiera czekanowskiana* Heer: Heer, p. 13, pl. 2, fig. 4 B.	
1880	*Baiera longifolia* (Pomel): Heer, p. 12, pl. 4, fig. 1 B.	
1880	*Ginkgo lepida* Heer: Heer, p. 17, pl. 4, figs. 9–12.	
1880	*Czekanowskia grandiflora* Heer, p. 19, pl. 6, fig. 7.	
1880	*Antholithus schmidtianus* Heer, p. 21, pl. 9, figs. 3–5.	
1880	*Antholithus paniculatus* Heer, p. 22, pl. 9, figs. 1 A, 2.	
1880	*Ginkgo grandiflora* Heer, p. 26, pl. 6, figs. 1–6.	
1891	*Txaites siemiradzkii* Raciborski, p. 315, pl. 5, fig. 7.	('Rhaetic' ?Middle Liassic; Poland)

1892 *Ixostrobus siemiradzkii* (Raciborski): Raciborski, pp. 12–15, pl. 2, figs. 5–8, 20 B. (?Middle Liassic; Poland)
1910 *Ginkgo* (fructification): Kryshtofovich, p. 13, pl. 3, fig. 5. (Jurassic; Ussuriland)
1912 *Stenorhachis lepida* (Heer): Seward, p. 23, pl. 4, figs. 52, 52 A. (Afghanistan, associated with *Phoenicopsis*)
1912*a* *Stenorhachis lepida* (Heer): Seward, pp. 13, 28, pl. 1, fig. 8. (Jurassic; Amurland)
1917 *Stenorhachis lepida* (Heer): Kryshtofovich,
1919 *Stenorhachis lepida* (Heer): Seward, p. 56, text-fig. 657. (Same as Seward 1912, 1912*a*. *Ixostrobus* included in *Stenorhachis*)
1931 *Stenorhachis lepida* (Heer): Turutanova-Ketova, p. 331, pl. 4, fig. 5.
1931 *Stenorhachis lepida* (Heer): Prinada, pl. 2, fig. 18; text-fig. 4 E. (Central Asia)
1933 *Antholithus kraschenninikovii* Kryshtofovich & Prinada, p. 21, pl. 2, figs. 6, 10. (Urals)
1933 *Stenorhachis paradoxa* Kryshtofovich & Prinada, p. 23, pl. 3, fig. 11. (Urals)
1933 *Stenorhachis* sp. cf. *Ixostrobus siemiradzkii* Raciborski: Kryshtofovich & Prinada, pl. 5, fig. 7. (Urals)
1935 *Ixostrobus groenlandicus* Harris, pp. 147, 150, pl. 12, figs. 12, 13; pl. 38, figs. 1–4, 7–10, 12; text-figs. 50 B. (Liassic; Greenland)
1938 *Stenorhachis* (*Ixostrobus*) *konianus* Oishi & Huzioka, p. 97, pl. 11, fig. 7. (Jurassic; Japan)
1957 *Ixostrobus* sp., Stanislavsky, p. 84, text-fig. 37 (see also figs. 35, 36). (Callovian; Donetz)
1962 *Ixostrobus heeri* Prinada, p. 279, pl. 16, figs. 7–13; text-fig. 75. (Good Siberian material, discussion in relation to *Czekanowskia* and *Phoenicopsis*)
1962 *Antholithus schmidtianus* Heer: Prinada, p. 274, pl. 16, figs. 1–6; text-fig. 72. (Siberian specimens; discussion, Heer's *A. paniculatus* and *Ginkgo grandiflora* included)
1963 *Ixostrobus heeri* Vasilevskaya & Pavlov, pl. 18, fig. 7. (Cretaceous; USSR)
1963 *Ixostrobus laxus* Vasilevskaya & Pavlov, pl. 43, figs. 7, 8. (Cretaceous; USSR)
1966 *Ixostrobus laxus* Vasilevskaya & Abramova, pl. 8, figs. 6, 7. (Lower Cretaceous; Lena Basin)
1968 *Ixostrobus* ex gr. *heeri* Prinada: Krassilov, p. 944, pl. 1, figs. 8–16. (Isolated microsporophylls, discussion)
1970 *Ixostrobus*, Krassilov, p. 13. (General description and discussion in English)

Ixostrobus whitbiensis sp. nov.

Pl. 8, figs. 2–11; Text-fig. 40

DIAGNOSIS. In fully expanded state cone up to 100 mm long and 15 mm broad but probably sometimes smaller. Lower 30 mm of cone axis bare, forming peduncle. Cone axis and microsporophylls originally stiff and composed of substantial tissue, microsporophylls borne in irregular whorls of 6–8 members, whorls about 1 mm apart. Microsporophylls typically at right angles to axis (but angle sometimes 70°), 5 mm–7 mm long. Stalk about 0·5 mm wide near cone axis, gradually increasing to 1 mm wide at its head, head bearing oval pollen sacs 1 mm (?) long and minute terminal appendage 1 mm long. In fertile part of cone a ridge from each microsporophyll runs down past the next microsporophyll whorl; peduncle marked above by 10–12 longitudinal ribs but ribs eventually dying out and lower part of peduncle smooth.

Cuticle of all parts delicate, about 1μ thick. Peduncle and lower part of sporophylls showing elongated cells with straight finely marked walls. Heads of sporophylls with large isodiametric cells with straight, very finely and faintly marked walls. Sporangia lined by granular cuticle-like membrane. Adherent pollen grains 35μ–40μ long, broadly oval, with broad and conspicuous colpus extending almost whole length. Wall of grain thin (nearly 1μ thick), consisting almost entirely of sexine, nexine (if recognized) merely smooth basal layer. Surface of sexine minutely verrucose, apparently composed of rounded capita united with one another and separating pits. Capita and pits each about 1μ wide.

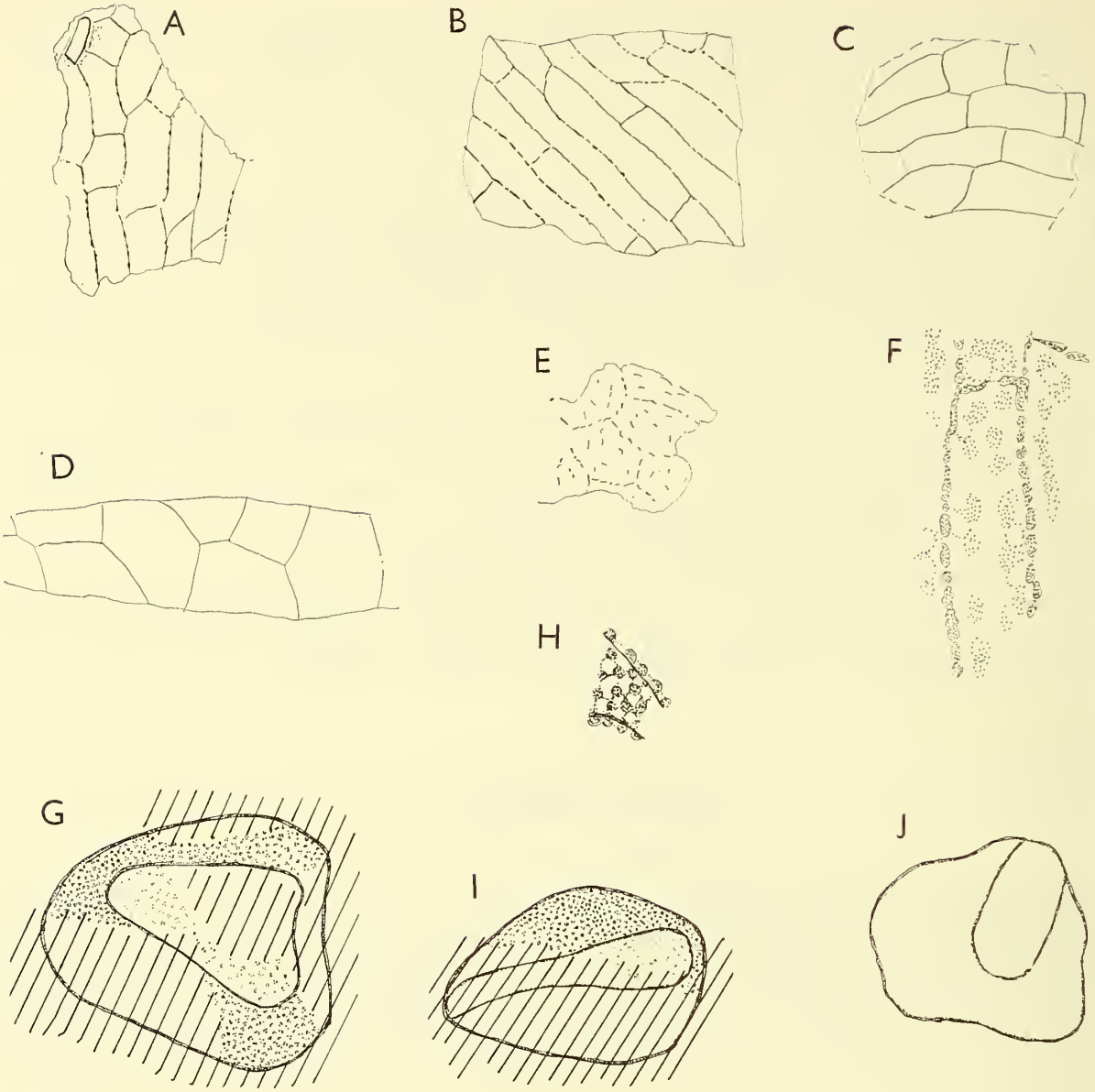


Fig. 40. **Ixostrobus whitbiensis** sp. nov.

A, cuticle of cone axis with possible stoma, top left, magnification ×200. V.56396*a* (from specimen in Pl. 8, fig. 11). B, cuticle of peduncle from specimen in Pl. 8, figs. 7, 8, magnification ×200. V.56394*a*. C–E, cuticle fragments from sporophyll heads (or microsporangia?) of specimen in Pl. 8, fig. 3, magnification ×200. V.56392*a*. F, cell of peduncle illuminated to show surface sculpture, magnification ×500. V.56518. G–J, pollen grains adhering to granular membrane of open pollen sac. In G and I the parts too much obscured to show the sculpture are cross ruled. From specimen in Pl. 8, fig. 3, magnification ×1,000. V.56392*a*. H, details of edge of grain and of colpus from I, drawn freehand, magnification × about 2,500. Figs. A, C–E, G–J Saltwick Waterfall. figs. B, F, Whitby Jump Down Bight.

HOLOTYPE. V.56390 (Pl. 8, figs. 5, 6).

DESCRIPTION. The better Saltwick and Jump Down Bight specimens make handsome fossils for their coaly substance is striking, but their cuticles are difficult to prepare. The associated plants are well preserved and coherent, but the *Ixostrobus* cones are crossed by fine cracks and only small pieces, of area less than 1 mm^2, can be removed and these in maceration break into dust-like fragments less than 100μ long. It was the same when a transfer was attempted, the cone substance crumbled away. Then when these tiny particles were macerated, their cuticles proved very delicate and so transparent as to be almost invisible until stained. Some success was later achieved when the crumbs, after gentle maceration in the acid mixture, were finished individually on a microscope slide, using minute drops of ammonia and performing all manipulations with moving liquids. The great majority of preparations were useless. It was possible that there might be stray fragments of equally delicate cuticles next to our *Ixostrobus* fragments, so we rejected a few things which we could not repeat. Only one group of preparations, from a single sporophyll head, gave the granular membrane supposed to line the pollen sac and to which spores were adherent. All the spores look alike but it is possible that the preparations have nothing to do with *Ixostrobus*. Krassilov (1970) gives no details but states that his cuticles were delicate and the spores poorly preserved. Harris (1935) failed to produce either cuticles or spores from the Greenland specimens and this may have been partly due to a tertiary basalt sill near the bed which had heated and damaged the cuticles.

It will be impossible to describe *I. whitbiensis* satisfactorily till specimens are found giving good transfers and good cuticles. Most of our sporophylls are just denuded stumps. A few have appendages and these may be of two sorts. On the upper side are oval bodies presumed to be sporangia about 1·6 mm × 0·7 mm. These point upwards or upwards and inwards from the head, and not more than one was seen on one head. It was not proved that these were sporangia. A few heads bear an extension pointing downwards and outwards which is about 1·0 mm × 0·5 mm and pointed and this may be the sterile extension, but again without confirmation. Even if both appendages are rightly interpreted they give no help in deciding between Harris's interpretation of *I. groenlandicus* and Krassilov's *I. heeri*.

Heer described many catkins from the Amur region and these are cited on p. 130. A number of these may be species of *Ixostrobus*. We can only compare *I. whitbiensis* in its gross aspect with Heer's specimens and the most similar are those he called *Ginkgo sibirica* male catkins, renamed *Ixostrobus heeri* by Prinada (1962). These indeed look almost the same but their sporangia may be more obvious and more strongly divergent. Other similar specimens are Raciborski's (1892) *I. siemiradzkii*, though it is perhaps a little smaller and less robust; his earlier specimen (1891) is larger and more similar. *I. groenlandicus* Harris (1935) also is similar but a little smaller and less robust.

Other species or species groups figured from East Siberia may be picked out as follows:

(1) *Ginkgo grandiflora*, *Czekanowskia rigida* male, and perhaps *Antholithus schmidtianus* and *A. paniculatus*, all of Heer. Catkins large and stout in all parts. Prinada (1962) names these *Antholithes schmidtianus*.

(2) Heer's *Ginkgo huttoni* male catkin; also Seward's (1912, 1912*a*) *Stenorhachis lepida*. Axis long, sporophylls short and very stout and stiff.

(3) Heer's *Baiera longifolia* male cone. Sporophylls thinner, extension beyond sporangia long. Included in *Sorosaccus sibiricus* by Prinada (1962).

(4) Heer's *Baiera czekanowskiana* male catkin. Sporophylls very slender, no extension beyond sporangia. Very possibly not an *Ixostrobus* but included by Prinada (1962) in *Sorosaccus sibiricus*. The more delicate specimens look like *Ginkgo* male cones, as do some of those figured by Prinada.

Genus appended to *Ixostrobus* but not included in the Czekanowskiales

Genus DESMIOPHYLLUM Lesquereux 1878

Type Species. *Desmiophyllum gracile* Lesquereux 1878, p. 133 (Pennsylvanian).

Desmiophyllum is one of several names that have been used for ribbon-shaped Mesozoic leaves found in isolation from any stem. Most of these generic names (some older than *Desmiophyllum*) are based on scanty information and they are scarcely to be distinguished from one another. Florin (1936*a*, p. 48) used *Desmiophyllum* when he described the cuticles of four such Mesozoic leaves, previously described under this or other names. He attempted no general revision but still his work is the best we have. He found that all four have cuticles of Gymnosperm type, with haplocheilic stomata. He considered their affinities among the Gymnosperms, particularly in relation to the Cordaitales, but decided that the evidence available justified no conclusion at all. We agree. We merely add that our Yorkshire species *D. gramineum* is unlikely to belong to the Czekanowskiales with which it has no points of agreement special to that family. There are some differences, for the leaf base is not contracted and its cuticle is altogether thinner than in any Czekanowskialean leaf known to us. Since it has a cuticle rather like those of Florin's leaves, particularly *D. imhoffi* (Heer), we include it in *Desmiophyllum*.

Desmiophyllum is described in this volume next to *Ixostrobus* for the convenience of workers who wish to disentangle the associations. But as explained above (p. 127) we consider the evidence for preferring to link *Ixostrobus* with either *Czekanowskia* or with *Desmiophyllum* ambiguous and inadequate at present. Whichever link is the real one, *Desmiophyllum* is out of its right taxonomic position in this volume. If *Ixostrobus* belongs to *Czekanowskia* then *Desmiophyllum* is just an isolated Gymnosperm leaf of unknown classification. But if *Ixostrobus* and *Desmiophyllum* belong to one plant then both genera are wrongly placed.

A possibility considered but rejected is that the Yorkshire *Desmiophyllum* might be a *Phoenicopsis*. Our *Desmiophyllum* leaves though seeming well preserved never occur in bundles. The cuticle also is very delicate but in most leaves of the *Phoenicopsis* group it is robust and also rather different in organization. Fragments of leaves looking rather like ours have sometimes been placed in *Phoenicopsis* (for example Seward's (1912) specimens from Afghanistan) but without discussion.

Desmiophyllum gramineum sp. nov.

Pl. 8, figs. 1, 2, 5, 6, 9–11; Text-fig. 41

Cf. 1935 '*Desmiophyllum* Type 2', Harris, p. 98, pl. 17, fig. 15.

Diagnosis. Leaves found detached. Length 100 mm to over 150 mm, width typically 3–4 mm, rarely less in middle region, widest leaves 5 mm. Lower and middle regions of almost uniform width (or base slightly narrowed), upper part tapering gradually to under 1 mm but then ending abruptly; lower part flat, upper part often with incurved margins. Veins 6–10 often 8 (marginal zones not being counted as veins). Veins not known to branch or to anastomose or to end in lamina, number remaining uniform over most of leaf (but not observed near apex). No veins ending in margins. Veins rather slender as preserved, usually thinner in substance than intervenal zones and paler and more translucent. Veins marked on surface of under side by few longitudinal files of elongated cells with conspicuous longitudinal walls; in intervenal zones epidermal cells shorter and walls inconspicuous. On upper side all cells elongated and veins inconspicuous. Veins and also leaf margins showing few elongated internal cells (fibres or tracheids), no mesophyll cells present. Intervenal zones often showing closely placed small mesophyll cells tending to form transverse plates, also vaguely defined sunken areas presumed to be formed by collapse of internal cells. Mesophyll showing (by transmitted light) numerous rounded or oval cells and few elongated cells (?fibres) situated near veins. No interstitial ducts present and no hypodermal cells except possibly along veins.

Cuticles thin on both sides, probably less than 1μ originally; leaf margin not sharp but showing numerous crushed cells. Leaf probably with stomata confined to intervenal zones and mostly on lower side. Upper side showing elongated epidermal cells with more or less transverse ends, those along veins slightly longer and narrower than those between veins. Lateral walls finely but fairly clearly marked, straight but tending to be minutely puckered or appearing moniliform. Occasional cells with whole surface more darkly staining (?thicker). Surface wall densely and fairly conspicuously mottled, markings evenly scattered or forming few obscure longitudinal striations. Trichome bases doubtfully present (occasional ring-like marks on an ordinary cell possibly trichome bases, but possibly injuries caused in preservation). Occasional stomata present on upper epidermis, details as on lower cuticle, but cells near stomata having thicker surface.

Lower cuticle showing veins with narrow elongated cells 10μ wide (as on upper side), intervenal zones with broader epidermal cells, often about 50μ long × 25μ wide, nearly all with rather thickened (i.e. darker stained) surface. Stomata scattered in intervenal zone, always longitudinal. Guard cells exposed in long narrow pit often about 80μ × 12μ, aperture about 50μ long. Pit probably very shallow, margins not overhanging. Subsidiary cells often four, two elongated lateral ones and two scarcely specialized terminal ones, or two lateral ones on each side. Encircling cells probably absent. Surface of lateral subsidiary cells always rather thickened and probably forming ridge parallel with stomatal pit. Epidermal cell walls similar to those of upper side except in shape, anticlinal walls finely puckered or slightly moniliform, surface walls thickly mottled.

The name is from *gramineus*, grassy.

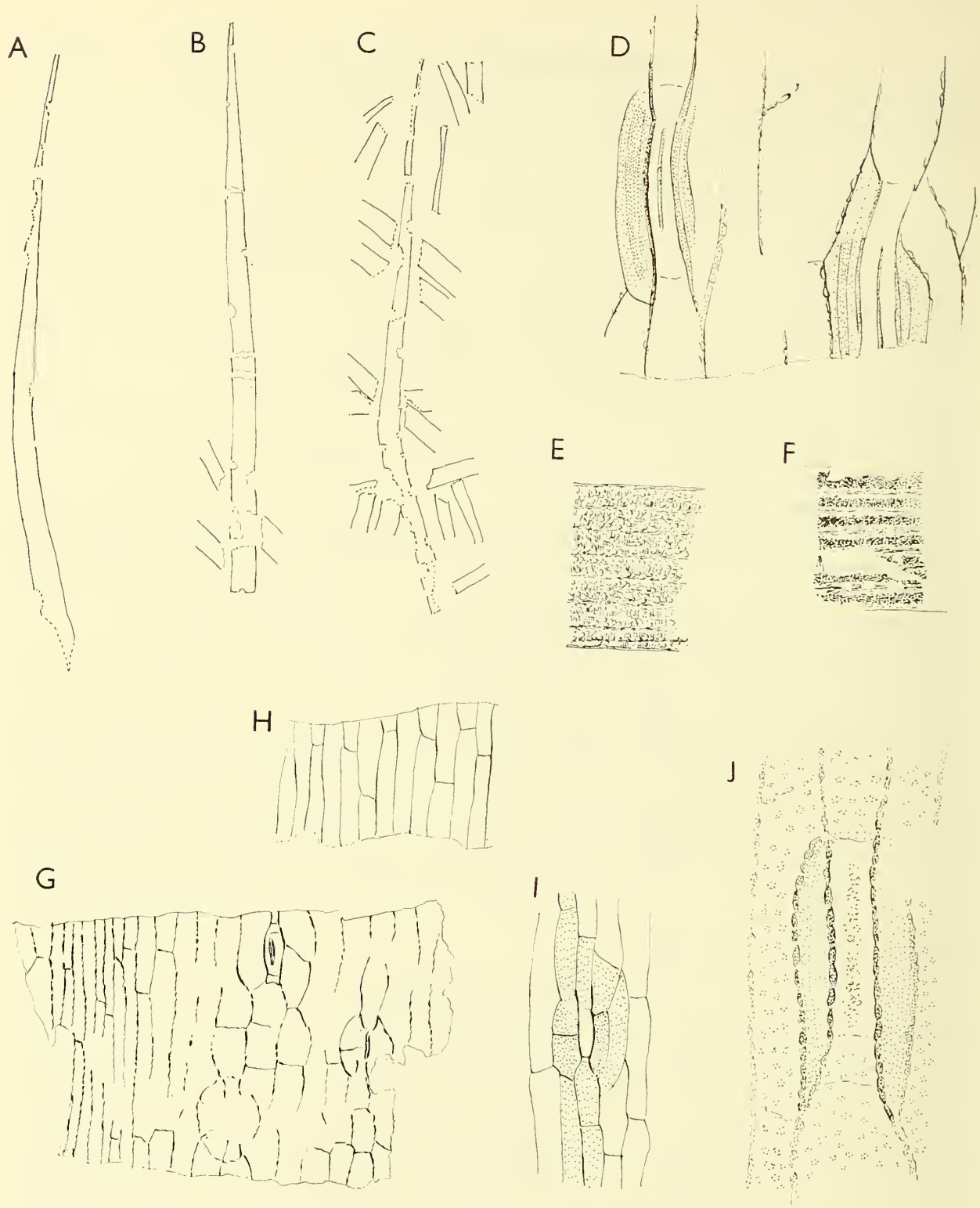


Fig. 41. **Desmiophyllum gramineum** sp. nov.

A, upper part of leaf, veins 9 or 10, actual size. Holotype V.56401. B, short, nearly complete leaf with 10 veins, actual size. V.56402. C, upper part of leaf, veins 7 or 8, actual size. V.56403. A–C all from R. Derwent 'Grass' Bed. D, two stomata on lower (?) side, magnification ×400. V.56520. E, sketch of leaf surface as seen illuminated from above and left, magnification ×10. V.56404. F, sketch of naturally cleared leaf in celloidin transfer, by transmitted light, magnification ×10. V.56521. In E and F no attempt is made to represent cells individually. G, lower cuticle with vein on the left, magnification ×200. V.56522. H, upper cuticle showing uniform cells, magnification ×200. V.56523. I, upper cuticle showing darker cells near a stoma, magnification ×200. V.56524. J, stoma of upper cuticle showing details of surface, magnification ×500. V.56525. D–J are from Saltwick.

HOLOTYPE. V.56401 (Text-fig. 41 A).

DESCRIPTION AND OCCURRENCE. A great number of leaves of this species were seen. As a rule they are so crowded that they interfere with one another and at Saltwick, where the rock gave few slabs more than 100 mm across, it was rarely possible to follow a leaf to either end. However a few showed their attenuated apices satisfactorily. Others showed transverse bases but these could have been leaves broken across before preservation. We have little material from Jump Down Bight, but again a great deal from the R. Derwent where much larger slabs of rock occur but the fine details of the leaves were less well preserved. The veins are only clearly seen in the better preserved specimens, and even there they are lost before the apex.

Fortunately a few leaves preserved in a fine matrix from Saltwick show the epidermal cells and some others, from the same locality, which had suffered oxidative decay before preservation were translucent enough to show some of the internal structure. The mesophyll was helpful in settling a point on which we had some doubt. In view of the extreme delicacy of the leaf cuticle we wondered if *D. gramineum* might be a more or less submerged aquatic, but the compact mesophyll is clearly against that.

For reasons unknown many mesophyll cells survive in some of our cuticle preparations as a layer adhering to the lower cuticle. These cells are better preserved than in the cleared leaves just mentioned. They are often 20μ–30μ long, 50μ–60μ broad, and are in contact with their neighbours transversely and fairly close also to neighbours longitudinally. They tend to form transverse rows. Their walls look simple, without involutions such as are seen in *Pinus*.

Most specimens yielded no cuticles at all and indeed their surfaces are covered with fine cracks making it certain that no continuous cuticle could be obtained. The best of the Saltwick leaves gave preparations but then only with great difficulty. The cuticle is very thin (perhaps 1μ originally) and fragile. Preparations were only obtained when we used the methods mentioned for *Ixostrobus*. Few cuticle fragments exceed 200μ × 50μ and most are smaller.

Apart from the leaf margins where the upper and lower cuticles remain together, we had to deal with separate fragments of the upper and lower side. The fragments are of two kinds:

(1) All the epidermal cells are elongated, the veins are only weakly marked by narrower cells, stomata are few. This we took to be the upper side.

(2) Epidermal cells are elongated and narrow along the veins, but broad, sometimes isodiametric, between them. Stomata are frequent. This we took to be the lower side.

There is no observed difference between the thickness of the two cuticles but the cells of the lower, between the veins, take stain more than do most cells of the upper.

DISCUSSION. *Desmiophyllum gramineum* is described here because of the possibility that it, and not *Czekanowskia*, is the leaf of the plant with *Ixostrobus* (see also p. 133). Its association with *Ixostrobus* in Yorkshire is discussed under *I. whitbiensis*. There is evidence of agreement in the cuticles but it is not impressive. The cuticles of both are equally thin, but this is scarcely evidence because in one plant different kinds of organ commonly have cuticles of very uneven thickness. What is more suggestive is that the epidermal cells of the peduncle of *I. whitbiensis* do resemble the leaf cells in being elongated, having straight finely

marked anticlinal walls which appear finely moniliform or finely puckered, and have a similar mottled surface wall. These points of agreement would be impressive if they were rarely met, but unfortunately they are rather common. Even had we a stoma of *Ixostrobus* it would not help much if it were like that of *D. gramineum* because the stoma of *Czekanowskia* is also rather similar. We need much more information.

No attempt has been made to review possible references, for recognition from published figures is too indefinite. A good many narrow leaf fragments identified as *Podozamites* might however belong to it. One leaf '*Desmiophyllum* Type 2' (Harris 1935) from East Greenland is however mentioned because it is known to have very long leaves (up to 270 mm), similar looking veins and a cuticle 'impossible to prepare' as with nearly all leaves of *D. gramineum*. Another leaf (as fragments) is '*Desmiophyllum* sp.' Daber (1962) from the Lias of N. Germany. Its substance must be thicker since it peels off the rock and its cuticle though rather similar is thicker and more coherent. Its subsidiary cells are papillate. *D. gothani* Florin (Weber 1968) has a similar, broad base but is a much wider leaf. Prinada (1962) mentions '*Desmiophyllum* sp. A' and '*Desmiophyllum* sp. B' (p. 299, pl. 20, fig. 3; pl. 25, fig. 1) in the East Siberian flora, and there are leaf fragments identified as a species of *Phoenicopsis*, e.g. *P. stobieckii* Raciborski which might have been included in *Desmiophyllum*. *Desmiophyllum* sp. A and *P. stobieckii* may be like *D. gramineum* but *Desmiophyllum* sp. B has coarser veins.

REFERENCES

Archangelsky, S. 1965. Fossil Ginkgoales from the Ticó Flora, Santa Cruz Province, Argentina. *Bull. Br. Mus. nat. Hist.* (Geol.) **10**: 121–137, pls. 1–5.

Barnard, P. D. W. 1967. Flora of the Shemshak Formation. Part 2. Liassic Plants from Shemshak and Ashtar. *Riv. ital. Paleont.*, Parma, **73**: 539–588, pls. 46–49.

Bartholin, C. T. 1894. Nogle i den bornholmske Juraformation forekommende Planteforsteninger. *Bot. Tidsskr.*, Kjobenhavn, **19**: 87–115, pls. 1–6.

Benda, L. 1964. Die Jura-Flora aus der Saighan-Serie Nord-Afghanistans. *Beih. geol. Jb.*, Hannover, **70**: 99–152, pls. 1–8.

Black, M. 1929. Drifted Plant-Beds of the Upper Estuarine Series of Yorkshire. *Quart. J. geol. Soc. Lond.*, **85**: 389–437, figs. 1–22.

Boureau, Ed., Furon, R. et Roset, L. F. 1950. Contribution à l'Étude des Flores Jurassiques d'Asie. *Mém. Mus. Nat. Hist. Nat.*, Paris (n.s.) **30**, 2: 207–242, pls. 1–8.

Braun, C. F. W. 1843. Beiträge zur Urgeschichte der Pflanzen. *In* Münster Graf. G. zu: *Beiträge zur Petrefactenkunde*, **6**: 5–25, pls. 12, 13. Bayreuth.

Brongniart, A. 1828–1838. *Histoire des Végétaux fossiles, ou Recherches botaniques et géologiques sur les Végétaux renfermes dans les divers couches du globe.* **1**. (1828–1837) xii+488 pp., 171 pls. **2**. (1837–1838) 72 pp., 28 pls. Paris.

—— 1849. *Tableau des genres de végétaux fossiles considerés sous le point de vue de leur classification botanique et de leur distribution géologique.* 127 pp. Paris.

Bunbury, C. J. F. 1851. On some fossil plants from the Jurassic Strata of the Yorkshire Coast. *Quart. J. geol. Soc. Lond.*, **7**: 179–194, pls. 12, 13.

Cahoon, E. J. 1960. *Sphenobaiera ikorfatensis* f. *papillata* from the Lakota Formation of the Black Hills. *Bull. Torrey bot. Cl.*, New York, **87**: 247–257, pl. 17.

Chapman, F. 1927. Monograph on the Triassic Flora of Baldhill, Bacchus Marsh, Victoria. *Victoria Natl. Mus. Mem.*, **7**: 121–153, pls. 10–14.

Couper, R. A. 1958. British Mesozoic microspores and pollen grains. A systematic and stratigraphic study. *Palaeontographica*, Stuttgart, **103** B: 75–179, pls. 15–31.

Daber, R. 1962. Blattreste im Lias von Nordostdeutschlands. *Paläont. Abh.*, Berlin, **1**, 2: 125–138, pls. 1–4.

Dawson, J. W. 1885. On the Mesozoic floras of the Rocky Mountains region of Canada. *Proc. Trans. Canada Roy. Soc.*, Ottawa, **3**, 4: 1–22, pls. 1–4.

Delle, G. V. 1959. Ginkgoales from Jurassic deposits of the Tkvarchelian coal-bearing basin in Transcaucasia. *Bot. Zh.*, Moscow, **44**: 87–91, pls. 1, 2. [In Russian.]

—— 1967. The Middle Jurassic flora of the Tkvarchelian coal-basin (Transcaucasia). *Palaeobotanika*, Leningrad, **6**: 51–132, pls. 1–25. [In Russian with English Summary.]

Dobruskina, I. A. 1965. Revision of the Jurassic flora described by O. Heer from the river Amur. *Paleont. Zh.*, Moscow, **3**: 110–118. [In Russian.]

Doludenko, M. P. & Svahidze, Ts. I. 1969. The late Jurassic flora of Georgia. *Traus. Acad. Sci. USSR*, Moscow, **178**: 1–115, pls. 1–81.

Edwards, W. N. 1929. The Jurassic Flora of Sardinia. *Ann. Mag. Nat. Hist.*, London (10) **4**: 385–394, pls. 4, 5.

Eichwald, E. 1865–1868. *Lethaea Rossica ou Paléontologie de la Russie*, **2**. xxxv+1,304 pp., atlas, 40 pls. Stuttgart.

Ettingshausen, C. von. 1852. Begründung einiger neuen oder nicht genau bekannten Arten der Lias- und der Oolithflora. *Abh. geol. Reichsanst. Wien*, **1**, 3: 1–10, pls. 1–3.

Florin, R. 1936. Die fossilen Ginkgophyten von Franz-Joseph-Land nebst Erörterungen über vermeintliche Cordaitales mesozoischen Alters, I. Spezieller Teil. *Palaeontographica*, Stuttgart, **81** B: 71–173, pls. 11–42.

—— 1936*a*. Die fossilen Ginkgophyten von Franz-Joseph-Land nebst Erörterungen über vermeintliche Cordaitales mesozoischen Alters, II. Allgemeiner Teil. *Palaeontographica*, Stuttgart, **82** B: 1–72, pls. 1–6.

—— 1949. The morphology of *Trichopitys heteromorpha* Saporta, a seed plant of Palaeozoic age, and the evolution of the female flowers in the Ginkgoineae. *Acta Hort. berg.*, Uppsala, **15**: 79–109, pls. 1–4.

FONTAINE, W. M. 1905. *In* Ward, L. F. Status of the Mesozoic Floras of the United States. *Mon. U.S. Geol. Surv.*, Washington, **48**. 616 pp., atlas, 45 pls.

GENKINA, R. Z. 1963. La flore fossile des depôts charbonneux du Jurassique moyen de l'Oural oriental dans les gisements du bassin à houille brune d'Orsk. *Inst. geol. razrab. gor. iskop. Akad. Nauk. SSSR*, Moscow. [In Russian.]

—— 1966. *The fossil flora and stratigraphy of the Lower Mesozoic deposits of the Issyk-Kul trough.* Moscow. [In Russian.]

GEYLER, H. T. 1877. Ueber fossile Pflanzen aus der Juraformation Japans. *Palaeontographica*, Stuttgart, **24**: 221–232, pls. 30–34.

GOEPPERT, H. R. 1841–1846. *Die Gattungeu der fossilen Pflauzen vergleichen mit denen der Jetztwelt und durch Abbildungen erläutert.* 151 pp., 51 pls.

GOLOVA, T. F. 1948. Fossil plants from the Kemchug Brown Coal deposits of the Chulymo-Enissei coal-bearing basin. *Tr. Tomsk State Univ.* (*Geol.*) **99**.

GOMOLITZKY, N. P. 1963. On the structure of the epidermis of *Czekanowskia latifolia* Tur.-Ket. *Bot. Zh.*, Moscow, **48**: 1828–1830, pl. 1. [In Russian.]

—— 1965. New Ferns and Ginkgophytes of the Middle Jurassic of the Gissarsk Mountain Range. *Paleont. Zh.*, Moscow, **1**: 125–132.

HARRIS, T. M. 1926. The Rhaetic Flora of Scoresby Sound. East Greenland. *Medd. Groulaud*, Kjøbenhavn, **68**: 45–148, pls. 1–13.

—— 1935. The fossil flora of Scoresby Sound, East Greenland, 4. *Medd. Grønland*, Kjøbenhavn, **112**: 1–176, pls. 1–29.

—— 1944. Notes on the Jurassic Flora of Yorkshire, 13–15. 13 *Dictyophyllum rugosum* L. & H.; 14 The *Baiera gracilis* complex; 15 *Stenopteris williamsouis* (Brongn.). *Ann. Mag. Nat. Hist.*, London (11) **11**: 661–690, 10 figs.

—— 1945. Notes on the Jurassic Flora of Yorkshire, 16–18. 16 *Baiera furcata* (L. & H.) Braun; 17 *Sphenobaiera pecten* sp. n. 18 *Equisetites lateralis* (Phillips) and its distinction from *E. columnaris* (Brongn.). *Ann. Mag. Nat. Hist.*, London (11) **12**: 213–234, 7 figs.

—— 1946. Notes on the Jurassic Flora of Yorkshire, 19–21. 19 *Klukia exilis* (Phillips) Raciborski; 20 *Otozamites bunburyanus* Zigno; 21 A coprolite of *Caytonia* pollen. *Ann. Mag. Nat. Hist.*, London (11) **12**: 357–378, 6 figs.

—— 1946*a*. Notes on the Jurassic Flora of Yorkshire, 28–30. 28 *Czekauowskia microphylla* (Phillips) Seward; 29 *Nilssoniopteris vittata* (Brongn.) Florin and *N. major* (L. & H.) Florin; 39 *Ginkgoites lougifolius* (Phillips) n. comb. *Ann. Mag. Nat. Hist.*, London (11) **13**: 1–24, figs. 1–7.

—— 1948. Notes on the Jurassic Flora of Yorkshire, 37–39. 37 *Todites priuceps* (Presl) Gothan; 38 *Ginkgo huttoni* (Sternberg) Heer; 39 *Ginkgo digitata* (Brongn.) Heer. *Aun. Mag. Nat. Hist.*, London (12) **1**: 181–213, figs. 1–8.

—— 1951. Notes on the Jurassic Flora of Yorkshire, 49–51. 49 *Solenites vimineus* (Phillips) n. comb.; 50 *Ginkgo whitbiensis* sp. n.; 51 *Elatides divaricatus* (Bunbury) n. comb. *Ann. Mag. Nat. Hist.*, London (12) **4**: 915–937, figs. 1–5.

—— 1951*a*. The fructification of *Czekanowskia* and its allies. *Phil. Trans. Roy. Soc. Loud.* (B) **235**: 483–508, pls. 18, 19.

—— 1964. *The Yorkshire Jurassic Flora*, **2**. *Caytoniales, Cycadales and Pteridosperms.* viii+191 pp., 7 pls. Brit. Mus. (Nat. Hist.), London.

HEER, O. 1876. Beiträge zur Jura-Flora Ostsibiriens und des Amurlandes. *Mém. Acad. Imp. Sci. St Pétersb.* (7) **22**: 1–122, pls. 1–31. (*Fl. Foss. Arctica*, **4**, 2.)

—— 1878. Beiträge zur Fossilen Flora Sibiriens und des Amurlandes. *Mém. Acad. Imp. Sci. St Pétersb.* (7) **25**, 6: 1–58, pls. 1–15. (*Fl. Foss. Arctica*, **5**, 2).

—— 1880. Nachträge zur Jura-Flora Sibiriens. *Mém. Acad. Imp. Sci. St Pétersb.* (7) **27**, 10: 1–34, pls. 1–9. (*Fl. Foss. Arctica*, **6**, 1.)

—— 1881. Zur Geschichte der Ginkgo-artigen Bäume. *Eugler's Bot. Jahrb.*, Leipzig, **1**: 1–13.

HOLLICK, A. 1930. The Upper Cretaceous Floras of Alaska. *Prof. Pap. U.S. geol. Surv.*, Washington, **159**: 1–123, pls. 1–86.

JOHANSSON, N. 1922. Die Rätische Flora der Kohlengruben bei Stabbarp und Skromberga in Schonen. *K. sveuska VetenskAkad. Handl.*, Stockholm, **63**, 5: 1–78, pls. 1–8.

JOHNSON, T. 1920. The male flower or microstrobilus of *Ginkgoanthus Phillipsi. Rep. Yorks. Phil. Soc.*, **1919**: 1–6, pl. 1.

KASYERNOV, M. V. & others. 1962. Biostratigraphy of the Mesozoic and Tertiary deposits of Western Siberia. *Tr. Sniigims*, Leningrad, **22**, 1: 1–591, atlas, 128 pls. (22, 2.) [In Russian.]

KAWASAKI, S. 1925. Some Older Mesozoic Plants in Korea. *Bull. geol. Surv. Chosen* (*Korea*), Keijo, **4**, 1: 1–71, pls. 1–47.

—— 1926. Additions to the Older Mesozoic Plants in Korea. *Bull. geol. Surv. Chosen* (*Korea*), Keijo, **4**, 2: 1–35, pls. 1–11.

—— 1939. Second Addition to the Older Mesozoic Plants in Korea. *Bull. geol. Surv. Chosen* (*Korea*), Keijo, **4**, 3: 1–69, pls. 1–16.

KHAKLOV, V. A. 1929. Contribution à l'Étude de l'Age des dépots à charbon du bassin de Kouznetzk. *Bull. Fil. Sibér. Ouest. Com. Géol.*, **8**, 4: 1–32, pls. 1–5. [In Russian.]

—— 1931. The Jurassic Flora from the Kuznetsk Coal Basin. *Trans. Coal Sci. Invest. Vostugol* (G) **3**.

KIMURA, T. 1959. Mesozoic Plants from the Kotalei Coal-field, the Kuruma Group, Central Honshu, Japan. *Bull. Sen. High Sch., Tokyo Univ. Educ.*, **3**: 61–79, pls. 1, 2.

—— 1959*a*. On the Tetori flora (Part II). Addition to the Mesozoic plants from the Kuzuryu sub-group Tetori Group, Japan. *Bull. Sen. High Sch. Tokyo Univ. Educ.*, **3**: 104–117, pl. 1.

KIMURA, T. & SEKIDO, S. 1965. Some interesting Ginkgoalean leaves from the Hoshiro sub-group, the Tetori Group, Central Honshu, Japan. *Mem. Meijiro Gakuen Woman's Jun. Coll.*, **11**: 1–4, pls. 1, 2.

KNOWLTON, F. H. 1914. The Jurassic Flora of Cape Lisburne, Alaska. *Prof. Pap. U.S. Geol. Surv.*, Washington, **85**, D: 39–64, pls. 5–8.

KRASSER, F. 1905. Fossile Pflanzen aus Transbaikalien der Mongolei und Mandschurei. *Denkschr. Ak. Wiss. Wien*, **78**: 589–634, pls. 1–4.

—— 1913. Die fossile Flora der Williamsonien bergenden Juraschichten Sardiniens. *Anz. Ak. Wiss. Wien*, **50**: 31–36.

KRASSILOV, V. A. 1968. A new group of Mesozoic gymnosperms—Czekanowskiales. *Dokl. Acad. Nauk SSSR.*, Moscow, **168**: 942–945. [In Russian.]

—— 1968*a*. A study of plants from the Czekanowskiales group. *Acad. Sci. USSR., geol. Inst. Nauk.*, Moscow, **191**: 31–40, pls. 1, 2. [In Russian.]

—— 1970. Approach to the classification of Mesozoic "Ginkgoalean" plants from Siberia. *Palaeobotanist*, Lucknow, **18**, 1: 12–19, pls. 1–3.

KRÄUSEL, R. 1943. Die Ginkgophyton der Trias von Lunz in Nieder-Österreich und von Neuwelt bei Basel. *Palaeontographica*, Stuttgart, **87** B: 59–93, pls. 1–15.

—— 1955. Die Keuperflora von Neuewelt bei Basel (Part 1). Koniferen und andere Gymnospermen. *Schweiz. Palaeont. Abh.*, Basel, **71**: 1–27, pls. 1–9.

—— 1961. Ein Fund fruchtender Gymnospermenreste im Keuper von Neuewelt bei Basel. *Eclogae geol. Helv.*, Basel, **53**: 693–694.

KRYSHTOFOVICH, A. N. 1910. Jurassic Plants from Ussuriland. *Mém. Com. géol. St Péterb.* (n.s.) **56**: 1–23, pls. 1–3. [In Russian with English summary.]

—— 1912. Mesozoic Plant-remains from the Eastern Ural. *Bull. Com. géol. St Pétersb.*, **31**: 489–498, pl. 15.

—— 1915. Jurassic Plants from the river Tyrma (Amurland). *Trav. Mus. Géol.-Min. Acad. Imp. Sci. Petrograd*, **8**: 79–124, pls. 1–7.

—— 1915*a*. Plant-remains from Jurassic lake-deposits of Transbaikalia. *Mém. Soc. Imp. Russe Min.*, Petrograd (2) **51**: 77–98, pl. 6.

—— 1916. Material for the Jurassic Flora of Ussuriland. *Trav. Mus. Géol.-Min. Acad. Imp. Sci. Petrograd*, **2**, 4: 81–140, pls. 7–11.

—— 1926. Some fossil plants from the Jurassic slate of the North Caucasus. *Bull. Com. géol. Leningrad*, **45**: 597–608, pls. 12, 13. [In Russian with English summary.]

—— 1927. Contribution to the Jurassic Flora of Middle Siberia. *Bull. Com. géol. Leningrad*, **46**: 559–570, pl. 31. [In Russian with English summary.]

—— 1933. Baikal Formation of the Angara Group. *Trans. geol. Prosp. Serv. USSR.*, Moscow, **326**: 1–136, pls. 1–17.

KRYSHTOFOVICH, A. N. & PRINADA, V. 1932. Contribution to the Mesozoic Flora of the Ussuriland. *Bull. geol. Prosp. Serv. USSR.*, Moscow, **51**: 363–373, pls. 1, 2.

—— —— 1933. Contribution to the Rhaeto-Liassic Flora of the Cheliabinsk Brown-Coal Basin, Eastern Urals. *Trans. geol. Prosp. Serv. USSR.*, Moscow, **346**: 1–40, pls. 1–5.

LANE, G. 1910. Notes on the Jurassic Flora of Cleveland. *Proc. Cleveland Nat. Fld Cl.*, Middlesbrough, **2**: 206.

LEBEDEV, E. L. 1965. Late Jurassic Flora of the Zeia River and the Jurassic-Cretaceous Boundary. *Tr. geol. Inst. Akad. Nauk. USSR.*, Moscow, **125**: 1–142, pls. 1–36. [In Russian.]

LECKENBY, G. 1864. On the Sandstones and Shales of the Oolites of Scarborough, with Descriptions of some New Species of Fossil Plants. *Quart. Jl. geol. Soc. Lond.*, **20**: 74–82, pls. 8–11.

LESQUEREUX, L. 1878. On the *Cordaites* and their related generic divisions in the Carboniferous formation of the United States. *Proc. Amer. phil. Soc.*, Philadelphia, **17**: 315–355.

LEUTHARDT, F. 1903. Die Keuper Flora von Neuewelt bei Basel. *Abh. schweiz. paläont. Ges.*, Zurich, **30**: 1–23, pls. 1–10.

LINDLEY, J. & HUTTON, W. 1831–1837. *The Fossil Flora of Great Britain: or Figures and Descriptions of the Vegetable Remains found in a Fossil State in this country.* 3 vols. London. Vol. 1, li+223 pp., pls. 1–79 (1831–1833); Vol. 2, xxviii+208 pp., pls. 80–156 (1833–1835); Vol. 3, 208 pp., pls. 157–230 (1835–1837).

LUNDBLAD, B. 1957. On the presence of the Genus *Pseudotorellia* (Ginkgophyta) in the Rhaetic of N.W. Scania. *Geol. För. Stockh. Förhandl.*, **79**: 759–765, pl. 12.

—— 1959. Studies in the Rhaeto-Liassic floras of Sweden, 11, 1. Ginkgophyta from the mining district of N.W. Scania. *K. svenska VetenskAkad. Handl.*, Stockholm (4) **6**, 2: 1–38, pls. 1–6.

—— 1968. The present status of the genus *Pseudotorellia* Florin (Ginkgophyta). *J. linn. Soc. Lond.* (*Bot.*) **61**: 189–195.

MAKAREWICZOWNA, A. 1928. Flora dolno-liasowa okolic Ostrowca. Étude sur la flore fossile du Lias inférieur des environs d'Ostrowiec, Pologne. *Trav. Soc. Sci. Lett. Wilno*, **4**: 97–145, pls. 10–13. [In Polish with French résumé.]

MANUM, S. 1968. A new species of *Pseudotorellia* Florin from the Jurassic of Andöya, Northern Norway. *J. linn. Soc. Lond.* (*Bot.*) **61**: 197–200, figs. 1, 2.

MEHTA, K. R. & SUD, J. D. 1955. On some Ginkgoalean leaf impressions from the Rajmahal Hills. *Palaeobotanist*, Lucknow, **2**: 51–54, pl. 1.

MENENDEZ, C. A. 1951. La flora mesozoica de la formación Llantenes (Provincia de Mendoza). *Rev. Inst. Invest. Mus. argent. Cienc. nat. Bot.*, Buenos Aires, **2**: 147–261, pls. 1–15.

MÖLLER, H. 1903. Bidrag till Bornholms fossila flora (Rhät och Lias). Gymnospermar. *K. svenska VetenskAkad. Handl.*, Stockholm, **36**, 6: 1–56, pls. 1–7.

NATHORST, A. G. 1878, 1879, 1886. Om floran i. Skånes kolforande Bildningar 1. Floran vid Bjuf. *Sverig. geol. Unders. Afh.*, Stockholm (C) **27, 33, 85**: 1–131, pls. 1–26.

—— 1880. Berättelse, afgifven till Kongl. VetenskapsAkademien, om en med understöd af allmänna medel utförd vetenskaplig resa till England. *Ofvers. VetenskAkad. Forh.*, Stockholm, **5**: 23–84.

—— 1900. Fossil Plants from Franz Josef Land. *The Norwegian Polar Expedition* 1893–1896. *Scientific Results* (*ed. F. Nansen*), *II.* 26 pp., 2 pls. London & Christiania.

—— 1906. Om några *Ginkgo* växter fran Kolgrufvorna vid Stabbarp i Skåne. *Lunds Univ. Arrskrift.* (n.f.) **2**, 2, 8: 1–15, pls. 1, 2.

—— 1919. *Ginkgo adiantoides* (Unger) Heer im Tertiär Spitzbergens nebst einer kurzen übersicht der übrigen fossilen Ginkgophyten desselben Landes. *Geol. För. Stockh. Förhandl.*, **41**: 234–248, pls. 1–4.

NEUBURG, M. F. 1936. On the Stratigraphy and Age of Carboniferous deposits of the Tannu-Tuva People's Republic. *Trav. geol. Inst. Akad. Nauk. SSSR*, Leningrad, 5: 129–159, pls. 1–4. [In Russian with English summary.]

OISHI, S. 1930. On the cuticles of some fossil Ginkgoacean leaves. *Proc. Imp. Acad. Sci.*, Tokyo, **6**, 3: 109–112, pls. 1–3.

—— 1931. Fossil Plants from Japan and Korea. *Sci. Rep. Tohoku Univ.*, Sendai (2, Geol.) **14**, 2 A: 107–118, pl. 36.

—— 1931*a*. On the Upper Triassic formation in the Nariwa District, Bitchu. *J. geol. Soc. Tokyo*, **38**: 1–8.

—— 1931*b*. Mesozoic Plants from Kita-Otari, Prov. Shinano, Japan. *J. Fac. Sci. Hokkaido Univ.*, Sapporo (4) **1**: 223–255, pls. 16–18.

—— 1932. The Rhaetic Plants from the Nariwa District, Prov. Bitchu (Okayama Prefecture), Japan. *J. Fac. Sci. Hokkaido Univ.*, Sapporo (4) **1**: 257–379, pls. 19–53.

—— 1932*a* The Jurassic Plants from Shitaka (The Maizuru Coal-field), Prov. Tango (Kyoto Prefecture), Japan. *J. Fac. Sci. Hokkaido Univ.*, Sapporo (4) **2**: 1–13, pls. 1–3.

—— 1932*b*. Rhaetic Plants from Province Nagato (Yamaguchi Prefecture), Japan. *J. Fac. Sci. Hokkaido Univ.*, Sapporo (4) **2**: 51–67, pls. 9, 10.

—— 1933. A Study of the Cuticles of some Mesozoic Gymnospermous Plants from China and Manchuria. *Sci. Rep. Tohoku Imp. Univ.*, Sendai (2, Geol.) **12**, 239–252, pls. 36–39.

—— 1940. The Mesozoic Floras of Japan. *J. Fac. Sci. Hokkaido Univ.*, Sapporo (4) **5**: 123–480, pls. 1–48.

OISHI, S. & HUZIOKA, K. 1938. Fossil Plants from Nariwa. A Supplement. *J. Fac. Sci. Hokkaido Univ.*, Sapporo (4) **4**: 69–101, pls. 7–12.

OISHI, S. & TAKAHASI, E. 1936. The Rhaetic Plants from Province Nagato. A Supplement. *J. Fac. Sci. Hokkaido Univ.*, Sapporo (4) **4**: 113–133, pl. 10.

Orlovskaya, E. R. 1962. The finds of *Pseudotorellia* and *Eretmophyllum* in the Jurassic deposits of Kazakhstan. *Bot. Zh.*, Leningrad, **47**: 1437–1445, pls. 1–4. [In Russian with English summary.]

—— 1968. The Lower Mesozoic Flora of Eastern Kazakhstan. *Tr. Inst. geol. Acad. Nauk. SSSR*, Moscow, **23**: 64–75, pl. 20. [In Russian.]

P'an, C. H. 1936. Older Mesozoic Plants from North Shensi. *Palaeont. sinica*, Peking (A) **4**, 2: 1–49, pls. 1–15.

Pant, D. D. 1959. The classification of gymnospermous plants. *Palaeobotanist*, Lucknow, **6**: 65–70.

Phillips, J. 1829. *Illustrations of the Geology of Yorkshire: or, a description of the strata and organic remains of the Yorkshire Coast.* xvi+192 pp., 14 pls. York.

—— 1875. *Illustrations of the Geology of Yorkshire: or, a description of the strata and organic remains. Part I, The Yorkshire Coast.* 3rd edit. Edited by R. Etheridge. xii+354 pp., 28 pls.

Pomel, A. 1849. Matériaux pour servir à la flore fossile des terrains jurassiques de la France. *Amtl. Ber. Versamml. deutsch. naturf. Ärzte*, Aachen, **25** (1847): 332–354.

Potonié, R. 1962. Synopsis der Sporae in situ. *Beih. geol. Jb.*, Hannover, **39**: 1–204, pls. 1–19.

Prinada, V. D. 1928. Sur des restes de plantes des depôts mésozoiques de la Samarskaya Louka. *Bull. Com. géol. Leningrad*, **46**: 965–978, pl. 1. [In Russian with French résumé.]

—— 1931. Contribution towards the knowledge of the Mesozoic flora of Central Asia. *Trans. geol. Prosp. Serv. USSR*, Moscow, **122**: 1–59, pls. 1–6. [In Russian with English summary.]

—— 1938. Jurassic Flora of the Emba Region. *Problems Palaeont.*, Moscow, **4**: 363–405, pls. 1–5. [In Russian with English summary.]

—— 1951. Flore mésozoique de Siberie orientale et de Transbaikalie. *Trav. Univ. Irkoutsk*, **6**: 1–37. Atlas. [In Russian.]

—— 1962. *Flore mésozoique de Sibérie orientale et de Transbaikalie.* 368 pp., 25 pls. Moscow. [In Russian.]

Prosvirjakova, Z. P. 1966. *La flore jurassique de Mangyšlak et sa signification pour la stratigraphie.* 173 pp., 35 pls. Akad. Nauk. SSSR, Moscow & Leningrad. [In Russian.]

Raciborski, M. 1891. Flora retycka pólnocnego stoku gor Swietokrzyskich. *Rozpr. Wydz. mat.-przyr. Akad. Um.*, Krakow, **23**: 292–326, pls. 1–5.

—— 1892. Przyczynek do flory retyckiej Polski. *Rozpr. Wydz. mat.-przyr. Akad. Um.*, Krakow, **22**: 345–360, pl. 2.

Reymanowna, M. 1963. 1. Review of investigations of Polish Jurassic floras. 2. The Jurassic Flora from Grojec near Cracow in Poland. *Polska Akad. Nauk. Inst. Bot.*, Cracow, **4**, 2: 3–48, pls. 1–9.

Romanova, V. A. 1958. On the Jurassic flora of the Alakal basin. *Akad. Nauk. Kazakhstan SSR., Mat. Hist. Faunes Flores Kazakhstan*, **11**: 143–148, pls. 1, 2.

Sah, S. C. D. 1953. On some species of *Ginkgoites* from the Jurassic of the Rajmahal Hills, Bihar. *Palaeobotanist*, Lucknow, **2**: 55–58, pl. 1.

Sah, S. C. D. & Jain, K. P. 1965. *Ginkgoites rajmahalensis* sp. nov. from the Rajmahal Hills, Bihar, India. *Palaeobotanist*, Lucknow, **13**: 155–157, pl. 1.

Samylina, V. A. 1956. The epidermal structure of the leaves of the genus *Sphenobaiera. Dokl. Acad. Nauk. SSSR.*, Moscow, **106**: 537–539, pl. 3.

—— 1963. The Mesozoic flora of the Lower Course of the Aldan River. *Paleobotanika*, Leningrad, **4**: 59–139, pls. 1–37. [In Russian with English summary.]

—— 1967. The Mesozoic Flora of the area to the west of the Kolyma River (the Zyrianka Coal-basin) II. Ginkgoales, Coniferales. General Chapters. *Paleobotanika*, Leningrad, **6**: 133–175, pls. 1–14. [In Russian with English summary.]

—— 1967*a*. On the final stages of the history of the genus *Ginkgo* L. in Eurasia. *Bot. Zh.*, Leningrad, **52**: 303–316, pls. 1–6. [In Russian.]

Saporta, G. de 1873–1875. *Paléontologie française ou description des fossiles de la France* (2, *Végétaux*), *Plantes Jurassiques, I. II.* I, 506 pp., 70 pls. (1873); II, 352 pp., pls. 71–127 (1875). Paris.

—— 1884. *Paléontologie française ou description des fossiles de la France* (2, *Végétaux*), *Plantes Jurassiques, III.* 672 pp., pls. 129–226. Paris.

—— 1886–1891. *Paléontologie française ou description des fossiles de la France* (2, *Végétaux*), *Plantes Jurassiques, IV.* Pp. 1–177, pls. 1–22 (1886); pp. 178–208, pls. 23–28 (1888); pp. 209–272, pls. 29–40 (1889); pp. 273–354, pls. 41–52 (1890); pp. 355–548, pls. 53–74 (1891). Paris.

Schenk, A. 1865–1867. *Die fossile Flora der Grenzschichten des Keupers und Lias Frankens.* xxiv+232 pp., atlas 45 pls. Wiesbaden. Pp. 1–32, pls. 1–5 (1865); pp. 33–96, pls. 6–15 (1866); pp. 97–192, pls. 16–30 (1867); pp. 97–128 (repeated), 193–232, pls. 31–45 (1867).

—— 1871. Beiträge zur Flora der Vorwelt, IV. Die fossile flora der nordwestdeutschen Wealdenformation. *Palaeontographica*, Stuttgart, **19**: 201–276, pls. 22–43.

SCHIMPER, W. P. 1869–1874. *Traité de Paléontologie Végétale, ou la Flore du monde primitif dans ses raports avec les formations géologiques et la flore du monde actuel.* 3 vols. & atlas. Paris. **1**, 738 pp., pls. 1–53 (1869); **2**, 522 pp., pls. 54–75 (1870); pp. 522–968, pls. 76–90 (1872); **3**, iv+896 pp., pls. 91–110 (1874).

SEWARD, A. C. 1900. *The Jurassic Flora, I. The Yorkshire Coast. Catalogue of the Mesozoic Plants in the Department of Geology, British Museum (Natural History)*, **3**. xii+341 pp., 21 pls. London.

—— 1900*a*. Notes on some Jurassic plants in the Manchester Museum. *Mem. Manchr. lit. phil. Soc.* **44**, 8: 1–28, pls. 1–4.

—— 1904. *The Jurassic Flora, II. Liassic and Oolitic Floras of England. Catalogue of the Mesozoic Plants in the Department of Geology, British Museum (Natural History)*, **4**. xvi+192 pp., 13 pls. London.

—— 1907. Jurassic Plants from Caucasia and Turkestan. *Mém. Com. géol. St Pétersb.* (n.s.) **38**: 1–48, pls. 1–8.

—— 1911. Jurassic Plants from Chinese Dzungaria, collected by Professor Obrutschew. *Mém. Com. géol. St Pétersb.* (n.s.) **75**: 1–61, pls. 1–7.

—— 1911*a*. The Jurassic Flora of Sutherland. *Trans. Roy. Soc. Edinb.*, **47**: 643–709, pls. 1–10.

—— 1912. Mesozoic plants from Afghanistan and Afghan-Turkistan. *Palaeont. indica*, Calcutta (n.s.) **4**, 4: 1–57, pls. 1–7.

—— 1912*a*. Jurassic plants from Amurland. *Mém. Com. géol. St Pétersb.* (n.s.) **81**: 1–34, pls. 1–3.

—— 1917. *Fossil Plants. A Text-Book for Students of Botany and Geology, III.* xviii+656 pp., figs. 377–629. Cambridge.

—— 1919. *Fossil Plants. A Text-Book for Students of Botany and Geology, IV.* xvi+534 pp., figs. 630–818. Cambridge.

—— 1926. II. The Cretaceous Plant-bearing Rocks of Western Greenland. *Phil. Trans. Roy. Soc. Lond.* (B) **215**: 57–175, pls. 4–12.

SEWARD, A. C. & BANCROFT, N. 1913. Jurassic Plants from Cromarty and Sutherland, Scotland. *Trans. Roy. Soc. Edinb.*, **48**: 867–888, pls. 1, 2.

SEWARD, A. C. & GOWAN, J. 1900. The Maidenhair Tree (*Ginkgo biloba* L.). *Ann. Bot.*, London, **14**: 109–154, pls. 8–10.

SEWARD, A. C. & THOMAS, H. H. 1911. Jurassic Plants from the Balagansk district, Government of Urkutsk. *Mém. Com. géol. St Péterb.* (n.s.) **73**: 1–23, pls. 1–3.

SIXTEL, T. A. 1960. *Stratigraphy of the continental deposits of the Upper Permian and Trias of Central Asia.* 101 pp., 19 pls. Tashkent. [In Russian.]

STANISLAVSKY, F. A. 1957. *Jurassic plants from the Don Basin and Dnieper-Donetz region.* Akad. Sci. Ukraine SSR., Kiev. 128 pp., 18 pls. [In Russian.]

STERNBERG, C. VON 1820–1838. *Versuch einer geognostich-botanischen Darstellung der Flora der Vorwelt.* Leipzig & Prag. Pt. 1 (1820) 24 pp., pls. 1–13; Pt. 2 (1821) 33 pp., pls. 14–26; Pt. 3 (1823) 39 pp., pls. 27–39; Pt. 4 (1825) 42 pp., pls. 40–49, A-E; Pts. 5, 6 (1833) 80 pp., pls. 1–26; Pts. 7 (1838) 220 pp., pls. 27–68, A, B; Pt. 8 (1838) 71 pp.; Testamen, viii pp.

STOPES, M. C. 1907. The flora of the Inferior Oolite of Brora (Sutherland). *Quart. Jl. geol. Soc. Lond.*, **63**: 375–382, pl. 27.

SVESHNIKOVA, I. N. & BUDAHTSOV, L. Y. 1969. *Florulae fossiles arcticae. Florulae palaeozoicae ac Mesozoicae Insularum Spetsbergiae occidentalis Sibiriae Novae et Terrae Franz-Joseph dictae.* 129 pp., 46 pls. Leningrad.

SZE, H. C. 1931. Beiträge zur Liassische Flora von China. *Mem. Nat. Res. Inst. Geol.*, Nanking, **12**: 1–85, pls. 1–10.

—— 1933. Beiträge zur mesozoischen Flora von China. *Palaeont. sinica*, Peking (A) **4**: 1–68, pls. 1–12.

—— 1933*a*. Mesozoic Plants from Kansu. *Mem. Nat. Res. Inst. Geol.*, Nanking, **13**: 65–76, pls. 8–10.

—— 1949. Die mesozoische Flora aus der Hsiangchi Kohlen Serie in West Hupeh. *Palaeont. sinica*, Peking (n.s., A) **2**: 1–71, pls. 1–15.

TATEIWA, I. 1929. *Geological Atlas of Chosen (Korea) No.* 10, *Keishu-Eisen-Taikyu and Wakwan Sheets* [1/50,000 Survey—geol. maps+sect.] 3 pp., 7 pls. Chosen.

TEIXEIRA, C. 1948. *Flora mesozoica portuguesa, I.* 118 pp., 45 pls. (Serv. Geol. Portugal) Lisboa.

TESLENCO, Y. V. 1960. Contributions to the study of the Middle Jurassic flora of the neighbourhood of Krasnoyarsk. *Tr. Sniggims*, Leningrad, **8**: 3–235, pls. 1–13. [In Russian.]

THOMAS, H. H. 1911. The Jurassic Flora of Kamenka in the District of Isium. *Mém. Com. géol. St Pétersb.* (n.s.) **71**: 1–95, pls. 1–8.

—— 1913. The Fossil Flora of the Cleveland District of Yorkshire: 1. The Flora of the Marske Quarry. *Quart. Jl. geol. Soc. Lond.*, **69**: 223–251, pls. 23–26.

—— 1913*a*. The Jurassic plant beds of Roseberry Topping. *Naturalist*, London, **1913**: 198–200.

—— 1913*b*. On some new and rare Jurassic Plants from Yorkshire: *Eretmophyllum*, a new type of Ginkgoalean leaf. *Proc. Cambr. phil. Soc.*, **17**: 256–262, pls. 6, 7.

Toit, A. L. du 1927. The Fossil Flora of the Upper Karroo Beds. *Ann. S. Afr. Mus.*, Cape Town, **22**: 289–420, pls. 16–32.

Toyama, S. & Oishi, S. 1935. Notes on some Jurassic plants from Chalai-nor Prov., North Hsingan, Manchoukuo. *J. Fac. Sci. Hokkaido Univ.*, Sapporo (4) **3**: 61–77, pls. 3–5.

Tralau, H. 1968. Evolutionary trends in the genus *Ginkgo*. *Lethaia*, Oslo, **1**: 63–101, 14 figs.

Turutanova-Ketova, A. I. 1930. Jurassic flora of the chain Kara-Tau (Tian-Shan). *Trav. Mus. géol. Leningrad*, **6**: 131–172, pls. 1–6. [In Russian with English summary.]

—— 1931. Contributions to the study of the Jurassic flora of Lake Issyk-Kul basin in the Kirgiz ASSR. *Trav. Mus. geol. Leningrad*, **8**: 311–356, pls. 1–5. [In Russian with English summary.]

—— 1936. Materials for the stratigraphy of the Chakpak Coal region in South Kazakhstan. *Tr. Inst. Geol. Acad. Nauk. SSSR*, Moscow, **5**: 85–116, pls. 1–3.

—— 1944. Contributions on the question of the stratigraphy and age of the coal-bearing deposits of Mangystau in the Kazakh SSR. *Ann. Leningr. Univ.*, **70**: 67–90, pl. 4.

Vachrameev, V. A. 1958. Stratigraphy and fossil flora of the Jurassic and Cretaceous deposits of the Vilyiusk Basin and of the adjoining part of the Upper Verkhoyansk foredeep trough. *Regional Stratigraphy of the USSR*, **3**. 136 pp., 32 pls. Acad. Nauk. SSSR Geol. Inst., Moscow-Leningrad. [In Russian.]

Vachrameev, V. A., Dobruskina, I. A., Zaklinskaya, E. D. & Meyen, S. V. 1970. Palaeozoic and Mesozoic floras of Eurasia and Phytogeography of this time. *Tr. Inst. Geol. Acad. Nauk. SSSR*, Moscow, **208**: 1–428. [In Russian.[

Vachrameev, V. A. & Doludenko, M. P. 1961. Upper Jurassic and Lower Cretaceous floras of the Burenska Basin. *Tr. Inst. Geol. Acad. Nauk. SSSR*, Moscow, **54**: 1–136, pls. 1–60. [In Russian.]

Van Konijnenburg-Van Cittert, J. H. A. 1971. In situ Gymnosperm Pollen from the Middle Jurassic of Yorkshire. *Acta Bot. Neerl.*, Wageningen, **20**: 1–80, pls. 1–16.

Vasilevskaya, N. D. 1959. Gymnospermes des gisements houillers de la region de Sangar (bassin houiller de la Lena). *Sb. Stat. Paleont. Biostrat. Izd. Inst. Geol. Arktiki*, Leningrad, **15**: 65–88. [In Russian.]

—— 1960. Ginkgoales from the Lower Cretaceous deposits of the lower reaches of the river Lena. *Tr. Inst. Geol. Arktiki*, Leningrad, **3**.

—— 1963. Ginkgoales. *In* Handbook for Palaeontologists and Geologists of USSR. *Osnovy Palaont., Acad. Nauk. SSSR*, Moscow, **15**: 168–196, pls. 4–8.

—— 1966. Some Early Cretaceous plants of Zhigansk area. *Uch. zap. Nauchno-issled. Inst. Geol. Arktiki*, Leningrad, **15**: 49–76, pls. 1–7.

Vasilevskaya, N. D. & Abramova, L. N. 1966. Materialȳ k poznaniyu rannemeloroi florȳ Lenskogo Basseina. *Uch. zap. Nauchno-issled. Inst. Geol. Arktiki*, Leningrad, **16**.

Vasylevskaya, N. D. & Pavlov, V. V. 1963. Stratigraphy and flora of the Cretaceous deposits of the Lena-Olenek section of the Lenskii coal-bearing basin. *Tr. Inst. Geol. Arktiki*, Leningrad, **128**: 1–96, pls. 1–49. [In Russian.]

Vladimirovich, V. P. 1959. On the study of the post-Triassic and Early Jurassic floras of the East Urals. *Bot. Zh.*, Moscow, **44**: 457–466, pls. 1–3. [In Russian.]

Walkom, A. B. 1917. Mesozoic Floras of Queensland, Part I concluded. d. Ginkgoales, e. Cycadophyta, f. Coniferales. *Publ. geol. Surv. Qd.*, Brisbane, **259**: 1–30, pls. 1–9.

—— 1919. Mesozoic Floras of Queensland, Parts III and IV. The Floras of the Burrum and Styx River Series. *Publ. geol. Surv. Qd.*, Brisbane, **263**: 1–64, pls. 1–7.

—— 1924. On fossil plants from Bellevue, near Esk. *Mem. Qd. Mus.*, Brisbane, **8**: 77–92, pls. 15–21.

Watson, J. 1969. A revision of the English Wealden flora, I. Charales—Ginkgoales. *Bull. Br. Mus. nat. Hist.* (*Geol.*) London, **17**, 5: 209–254, pls. 1–6.

Weber, R. 1968. Die fossile Flora der Rhät-Lias-Uebergangs-schichten von Bayreuth (Oberfranken) unter besonderer Berücksichtigung der Coenologie. *Erlanger geol. Abh.*, **72**: 1–73, pls. 1–17.

Yabe, H. 1908. Jurassic Plants from T'ao-chia-T'un, China. *Bull. Imp. geol. Surv. Japan*, Tokyo, **21**: 5–12, pls. 1,2.

—— 1922. Notes on some Mesozoic Plants from Japan, Korea and China, in the Collection of the Institute of Geology and Palaeontology of the Tohoku Imperial University. *Sci. Rep. Tokyo Univ.* (2, Geol.) **7**: 1–28, pls. 1–6.

YABE, H. & ENDO, S. 1934. Strobilus of *Schizolepis* from the Lycoptera-Beds of Jehol. *Proc. Imp. Acad. Japan*, Tokyo, **10**: 658–660, 3 figs.

YABE, H. & OISHI, S. 1928. Jurassic Plants from the Fang-tzu Coal-field, Shantung. *Japan J. Geol. Geogr.*, Tokyo, **6**: 1–14, pls. 1–4.

—— —— 1933. Mesozoic plants from Manchuria. *Sci. Rep. Tokyo Univ.* (2, Geol.) **12**: 195–238, pls. 30–35.

YOKOYAMA, M. 1889. Jurassic Plants from Kaga, Hida and Echizen. *J. Coll. Sci. Imp. Univ. Tokyo*, **3**: 1–66, pls. 1–14.

—— 1906. Mesozoic Plants from China. *J. Coll. Sci. Imp. Univ. Tokyo*, **21**, 9: 1–39, pls. 1–12.

ZALESSKY, M. D. 1918. The Palaeozoic flora of the Angara series. *Mém. Com. géol. St Pétersb.* (n.s.) **174**: 1–76, pls. 1–63.

INDEX

Principal taxonomic names and the page numbers of the principal references are printed in **bold** type. An asterisk (*) indicates a figure.

Allicospermum xysteum, 71
Angariella, 86
Antholithus, 71
  kraschenninikovii, 131
  paniculatus, 130, 131, 133
  schmidtianus, 130, 131, 133
  wettsteini, 72
Araucariacites australis, 123
Arctobaiera, 80, 111

Baiera, 2, 3, 5, 26, **29,** 30, 57, 73*, 79, 84
  amalloidea, 40, 110
  caniculata, 3, 21–23, 25, 26
  cretosa, 52
  czekanowskiana, 78, 130, 134
  digitata, 5
  furcata, 2, 19, 20, 26, **30,** 31*, 32, 33*, 34, 35*, 36, 37*, 38, 39, 42, 47, 71, 73*, 74–76; Pl. 1, figs. 1, 2
  gracilis, 2, 20, **30,** 32, 34, 36, 38, 71, 74
    forma *münsteriana*, 26, 30, 38
  guilhaumati, 21
  huangi, 56
  leptophylla, 82, 110
  lindleyana, 30, 38, 97
  longifolia, 20, 21, 43, 47, 48, 78, 130, 134
    var. *czekanowskiana*, 48
  microphylla, 97
  muensteriana, 71
  multipartita, 9
  paucipartita, 40, 80, 110
  phialophora, 40
  phillipsi, 11, 20, 21
  scalbiensis, 3, 30, 32, 36–38
  spectabilis, 11, 13, 39
  viannai, 38
Beania (*Sphaereda*) *parvula*, 116
Beast Cliff, 19, 42, 63, 117
  Bed B, 125
  Otozamites Bed, 65, 66
  Sphenobaiera pecten Bed, 42
Bernettia phialophora, 72
Bilsdale, 53, 62, 66, 95
Black Nab, 50
Blea Wyke, 91, 125
Bloody Beck, 13
Brachyphyllum mamillare, 123
Brora, Scotland, 56
Brown Rigg Beck, 12
Burniston Long Nab, 109
  Wyke, 39

Cayton Bay, 26, 62
Caytonanthus, 5, 71
  arberi, 71
Caytonia, 85
  sewardi, 75
Cedrus, 82
Clitherbeck Coalpits, 62
Cloughton Wyke, 8, 11, 59, 62, 91, 123
  Drifted Plant Bed, 8, 11
  Eretmophyllum Bed, 62
  Quinqueloba Bed, 26
  Solenites Bed, 88–92, 115–117, 119, 122, 123, 125
Coniopteris, 85
Ctenis sp., 57, 62
Culgoweria, 80
Cyclopteris digitata, 5, 9, 11
  huttoni, 11
  incisa, 9
  longifolia, 21, 24
Czekanowskia, 39, 56, 78–87, 91, **92,** 100, **106,** 107–110, 112, 124–130, 134, 137
  blacki, 81, 82, 84, **102,** 104, 105*, 106, 107, 112; Pl. 6, figs. 2, 3; Pl. 7, figs. 3, 12, 13
  furcula, 83, 84, 87, 89, 91, **92,** 93*, 94, 95*, 96*, 97, 106, 129; Pl. 5
  grandiflora, 130
  hartzi, 81, 106, 107, 123–125
  latifolia, 106, 110
  microphylla, 83, 84, 89, **97,** 98*, 99*, 100, 106; Pl. 4, fig. 3
  murrayana, 83, 86
  nathorsti, 106, 107, 128
  rigida, 81, 83, 91, 102, 106, 107, 123–126, 133
  setacea, 83, 92, 106, 107
  thomasi, 84, 87, 89, **100,** 101*, 102, 103*, 106; Pl. 4, fig. 4

sp. A, 108, 109*; Pl. 6, figs. 1, 4, 7
sp. B, 109
sp. C, 109
sp. D, 110
sp. E, 110
Czekanowskiales, 2, 3, **79–85**

Danby, 62
Derwent River, 12, 74, 137
Ginkgo Bed, 13, 73
Grass Bed, 129, 130, 136
North Plant Bed, 12
Desmiophyllum, 127, 128, 130, **134**
gothani, 138
gracile, 134
gramineum, 128, 129, 134, **135,** 136*, 137, 138; Pl. 8, fig. 1
imhoffi, 134
spp. A, B, 138
Type 2, 128, 135, 138
Dicropteris longifolia, 43

Eretmophyllum, 3, **56,** 57, 67, 82
baikonuricum, 61, 62
lovisatoi, 61
pubescens, 11, 47, 55, **57,** 58*, 59–62, 66; Pl. 3, fig. 4
pulchellus, 62
saighanense, 61
tetonense, 61
thomasi, 62
whitbiense, 55, 57, 60, 61, **62,** 63, 64*, 65, 66; Pl. 3, figs. 1–3; Pl. 7, fig. 2

Farndale, 53, 62, 71
Fieldenia, 70
nordenskioldi, 67
Flabellaria, 86
viminea, 86, 87, 89
Fylingdales, 66

Ginkgo, 2, 3, **4,** 5, 26, 29, 40, 57, 71–73*, 78–80, 82, 84, 85, 127, 131, 134
acosmia, 20
adiantoides, 6, 10
amgaensis, 55
antarctica, 10
biloba, 4, 5, 40, 56, 67, 71, 72, 74, 76, 78, 82, 128
digitata, 4, **5,** 6, 7*, 8–10, 13, 15, 19, 29, 53, 55, 56, 71
var. *huttoni*, 9, 10
flabellata, 20, 29
glandulosum, 55
gracile, 55
grandiflora, 130, 131, 133
hermelini, 10, 20, 21, 128
huttoni, 4, 5, 8–10, **11,** 12*, 13, 14*, 15, 16*, 19, 26, 29, 55, 56, 61, 71–73*, 74, 76, 77*, 78, 129, 130, 133; Pl. 7, fig. 9
iutegriuscula, 10
lepida, 19–21, 38, 130
longifolius, 4, 5, 15, 19, 20, **21,** 22, 23*, 24*, 25*, 26, 30, 47, 61
marginatus, 20, 21, 26, 47, 128
paradiantoides, 10
pilifera, 10
pleuripartita, 10, 11, 15
polaris, 10, 29
pusilla, 29
reniformis, 10
schmidtiana parvifolia, 9, 20
sibirica, 9, 10, 19–21, 110, 130, 133
sp. cf. **sibirica,** 4, 9, 15, **17,** 18*, 19–21, 26, 29, 38, 47, 61
taeniata, 20, 26
whitbiensis, 3, 5, 6, 15, **27,** 28*, 29
zerauschanicum, 55
Ginkgoales, **2,** 3, **71**
Ginkgoanthus phillipsi, 71
Ginkgodium, 5, 55, 56
digitata, 9
longifolium, 56
nathorsti, 55, 56
Ginkgoites, 2, 4, 5
lepidus, 21
longifolius, 21, 23
phillipsi, 21
scarburgensis, 11, 13, 16
sibirica, 20, 21, 26
tigrensis, 72
sp., 21
Gnipe Howe, 42, 50
Goathland, Darnholm Coalpits, 62
Gristhorpe, 6, 8, 12, 62, 86, 89
Bed, 7, 8, 10, 11, 15, 22, 23, 26, 58–60, 62, 88–91, 99, 100–103, 116, 125
Series, 8, 10, 11, 15, 26, 29, 39, 62, 92, 97, 125

Hagg Beck, Bed D, 62
Haiburn Gorse, 62
Wyke, 6, 7, 11, 16, 33, 34, 36, 39, 42, 90, 94, 110, 117, 125
Haiburnia blacki, 78
Hancock Museum, Newcastle, 12, 13
Hartzia, 79, 80, 87, 124
tenuis, 81
Harwood Mill, 104
Hasty Bank, 17, 19, 20, 44, 47, 54, 56, 63, 66, 104, 109
Hawsker, 49, 51, 91, 110, 125
Helmsdale, Scotland, 9
High Whitby, 50–52
Hillhouse Nab, Farndale, 69, 71

Inaperturopollenites, 123
Ingleby Arncliffe Beacon Scar, 42
Isoetes, 86
murrayana, 86, 87
Ixostrobus, 78–80, 85, 122, **126,** 127–130, 133, 134, 137, 138
groenlandicus, 126, 131, 133
heeri, 127, 131, 133
laxus, 131
siemiradzkii, 131, 133
whitbiensis, 126, **131,** 132*, 133, 137; Pl. 8, figs. 2–11

Jeanpaulia lindleyana, 30
longifolia, 43
Jugger Howe, 104
Jump Down Bight, 47, 129, 132, 133, 137

Karkenia incurva, 72

Langdale, 16, 73
Leakholm Hole i' th' Ellers Coalpit, 62, 66
Leeds University, 36
Leptosrobus, 71, 79, 84, 85, 91, **114,** 116, 118, 121, 122, 124–126, 128, 129
angustifolius, 86
cancer, 87, **114,** 115*, 116, 117*, 118, 119*, 121, 122*, 123–125; Pl. 7, figs. 4–8, 10, 11, 14, 15
crassipes, 118, 124, 126
laxiflora, 114, 116, 118, 123, 124, 126
limbatus, 123
longus, 116, 121, 123–125
marginatus, 123, 125
microlepis, 124
rigida, 86
Lockwood Gill Head, 71

Manchester Museum, 12, 16
Marske Quarry, 8, 11, 22, 26, 44–47, 91, 94, 102, 104
Maw Wyke, 110
May Beck, 73, 75, 76
Microcheiris enigma, 79
Middlesbrough Museum, 45
Millepore Bed, 15

Neill Cliff Liverwort Bed, 126, 128
Nilssonia compta, 71

Penny Holme, 14
Petard Point, 17, 19, 20
Phoenicopsis, 56, 57, 62, 79, 80, 84, 85, 125, 127, 128, 131, 134, 138
angustifolia, 123, 125, 126
stobieckii, 138
tenuis, 81
Picea, 82
Pinus, 40, 56, 82, 91, 137
Podozamites, 128, 138
stobieckii, 128
Pseudoctenis sp. A, 62, 65
Pseudotorellia, 3, 55, 57, 62, **66,** 67, 69, 70, 72
angustifolia, 70
ensiformis, 70
ephela, 70
grojecensis, 67, 70
heeri, 67, 70
heterophylla, 67
longifolia, 70
minuta, 70
nordenskioldi, 70
tibia, 67, 68, 69*, 70, 71
vachrameevi, 70

Ravenscar, 53, 125
Roseberry Topping, 17–20, 44–47, 91, 94, 101
Rosedale Head, 27, 29
Knottside, 42
Rye R. Bed, 4, 42

Salisburia digitata, 5
huttoni, 11
lepida, 38
Saltwick, 50, 51, 53, 94, 128, 129, 132, 133, 136, 137
Samaropsis, 75
Sandsend Alum Pit, 66, 104
Scalby, 12, 15, 33, 34, 36, 39, 71–78, 82, 104, 105, 108, 109, 112, 113
Schizolepis jeholensis, 127
Schizopteris gracilis, 30
Sedgwick Museum, Cambridge, 14, 16, 37
Snilesworth, 42
Solenites, 42, 79–82, **86,** 87, 91, 92, 95, 97, 104, 108, 116, 118, 120, 121, 124, 125, 129
furcatus, 30
murrayana, 86, 87
vimineus, 84, 86, **87,** 88*, 89, 90*, 91, 92, 100, 125; Pl. 4, figs. 1, 2
Sorosaccus sibiricus, 78, 134
Sphaereda parva, 116
parvula, 116
Sphaerococcites muensterianus, 29
Sphenarion, 40, 79, 80, 83, 106, **110–112**
latifolia, 110, 112
leptophylla, 110, 112
muiriae, 84, **111–113***; Pl. 6, figs. 5, 6; Pl. 7, fig. 1
Sphenobaiera, 2, 3, 29, **39,** 40, 42, 57, 72, 79, 80, 110
angustifolia, 47
boeggildiana, 55, 110
czekanowskiana, 47, 48
flabellata, 110
furcata, 32, 40, 71

gyron, 9, 15, 47, 52, **53,** 54*, 55–57, 61
horniana, 40, 110
ikorfatensis, 47, 52, 53
forma *papillata*, 52
longifolia, 22, **43,** 44, 45*, 47, 48, 52, 61; Pl. 1, figs. 3–5
ophioglossum, 42, 43, 47, **48,** 49*, 50, 51*, 52, 53, 61; Pl. 2
paucipartita, 82, 110, 112
pecten, 38, **40,** 41*, 42, 43, 47, 52
pulchella, 53
spectabilis, 40, 52, 72, 82, 110
Sphenopteris latifolia, 11, 12
longifolia, 21
Stachyopitys, 71
presli, 71
Stainsacre Beck, 15, 73, 74
Staphidiophora, 79, 124
secunda, 124
Stenopteris williamsoni, 99
Stenorhachis, 127
konianus, 128, 131
lepida, 78, 128, 131, 133
paradoxa, 131
Stephanophyllum, 80, 82, 127
Stockholm Museum, 27, 28, 47
Sycarham Series, 15, 39, 62, 92, 97, 125

Taxites siemiradzkii, 126, 130
Todites williamsoni, 94
Torellia, 67, 70
Trichopitys, 84
Tripsdale Kay Nest, 53
Tsugipollinites lucidus, 123

Umaltolepis, 67, 72
Utrecht University Botanical Museum, 76, 77

Voltzia, 79

Westerdale Stockdale Waterfall, 66
Whitby, 8, 44, 46, 47, 53, 63–66, 89, 94, 97, 128
Jump Down Bight, 47, 129, 132, 133, 137
Long Bight, 47, 93, 95, 96
Lower Sandstone, 50, 53
New Layer, 29
Scar, 66
Zamites Bed, 129
White Nab, 13, 16
Whitestone Point, 8, 13, 14, 49–51
Windwardia, 80, 124
Windy Gully, 107

Yons Nab, 12
Yorkshire Museum, 7, 12, 16, 26, 35, 41, 42, 98, 116, 125

Zamites gigas, 129

BRITISH MUSEUM
GENERAL
20 JAN 1975
LIBRARY
NATURAL HIS. ORY

PLATES

PLATE 1

Baiera furcata (L. & H.)

FIG. 1. Lower cuticle. Magnification ×100.

FIG. 2. Upper cuticle. Magnification ×100.

Both from Scalby Wyke Drifted Plant Bed, previously known as *Baiera scalbiensis* Black.

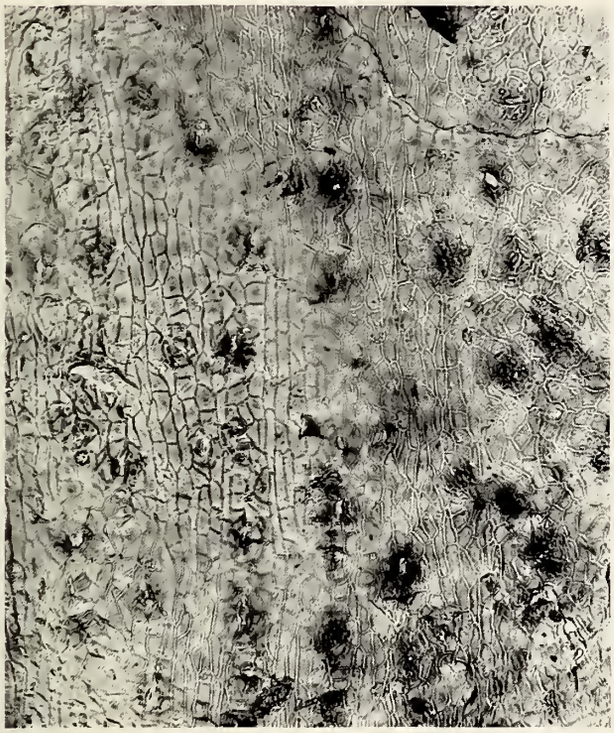
Sphenobaiera longifolia (Pomel)

FIG. 3. Lower cuticle. Magnification ×100. Marske. V.56627.

FIG. 4. Upper cuticle. Magnification ×400. Roseberry Topping. V.56628.

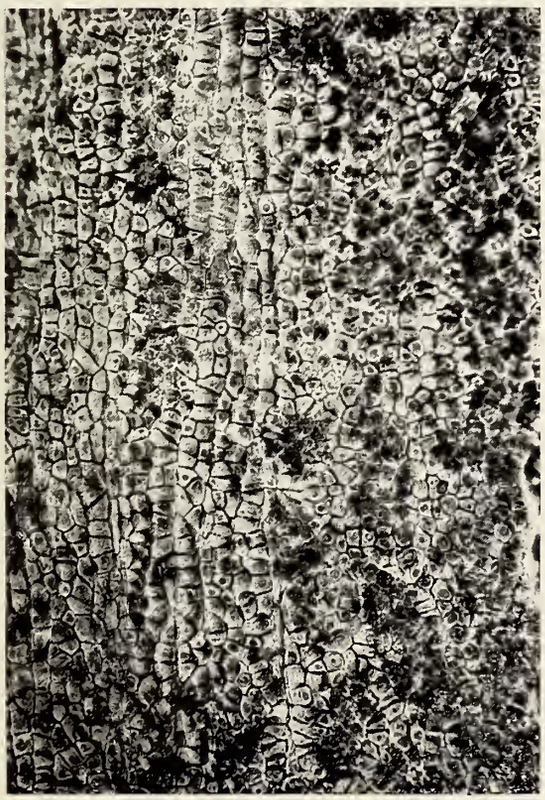
FIG. 5. Upper cuticle. Magnification ×100. Marske. V.56629.

1



2

3



4

5

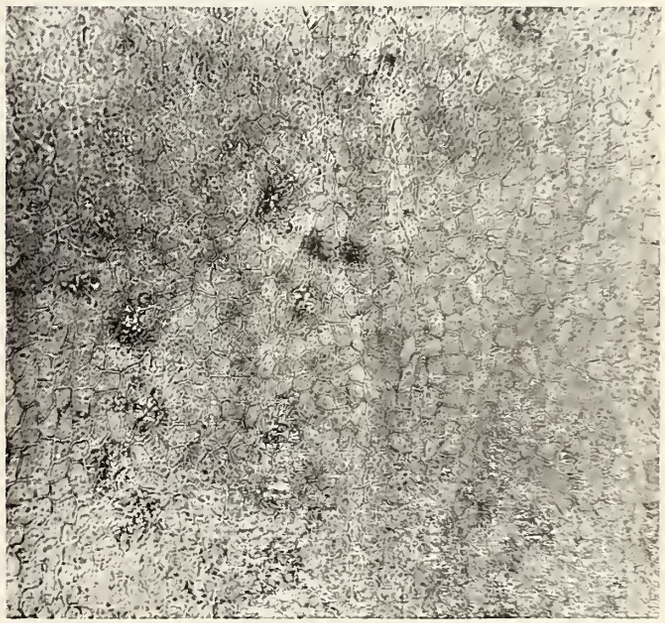


PLATE 2

Sphenobaiera ophioglossum sp. nov.

Hawsker, Whitestone Point

FIG. 1. Lower epidermis. Magnification ×100.
FIG. 2. Upper epidermis. Magnification ×100.
} V.56630.

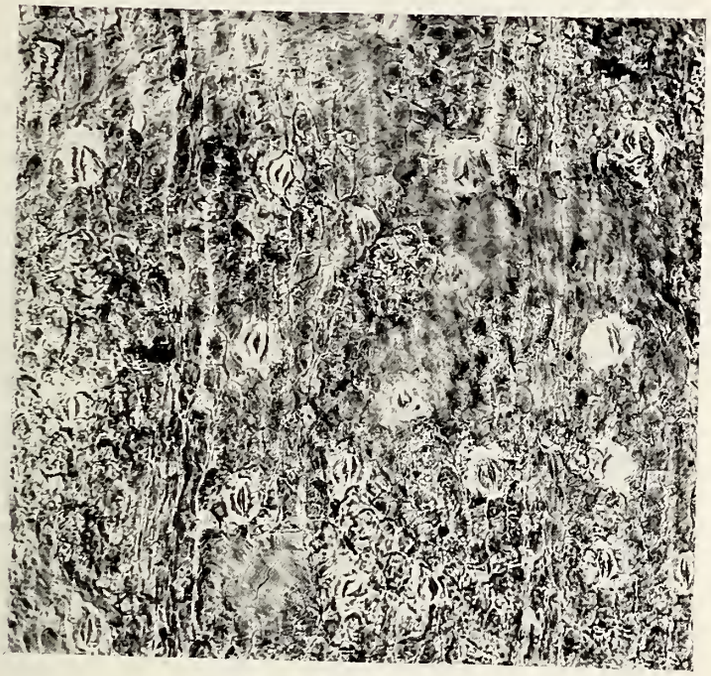
FIG. 3. Lower epidermis. Magnification ×200. V.56631.

FIG. 4. Lower epidermis with stoma. Magnification ×500. V.56632.

Hawsker, High Whitby (fallen block)

FIG. 5. Upper epidermis with stoma. Magnification ×500. V.56633.

1



2

3

4

5

PLATE 3

Eretmophyllum whitbiense Thomas

Whitby (fallen block)

FIG. 1. Lower cuticle. Magnification ×100. V.56634.

FIG. 2. Lower cuticle. Magnification ×100.

FIG. 3. Upper cuticle. Magnification ×100.

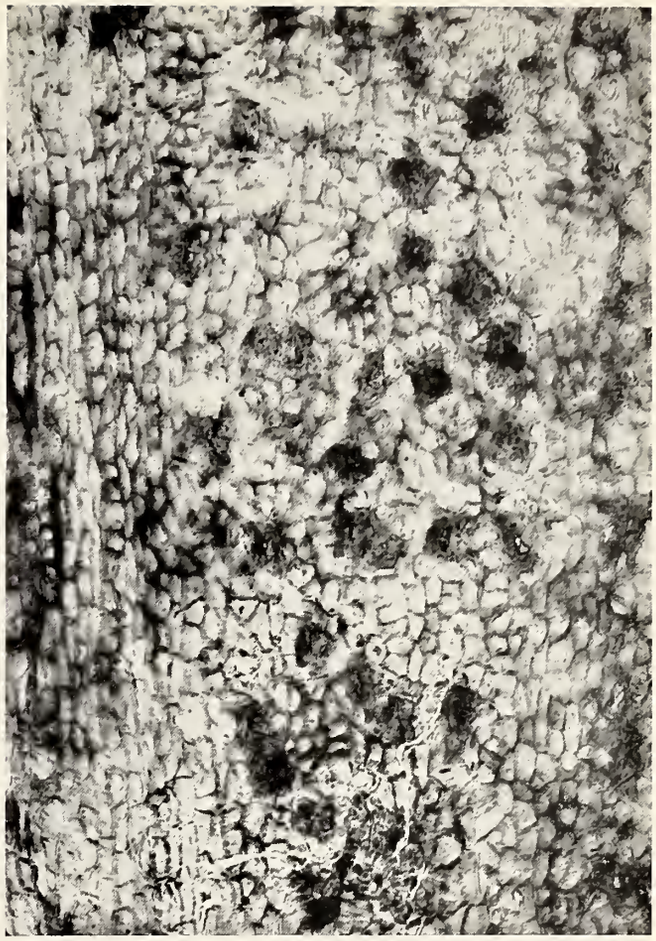
} V. 56635.

Eretmophyllum pubescens Thomas

Gristhorpe Bed

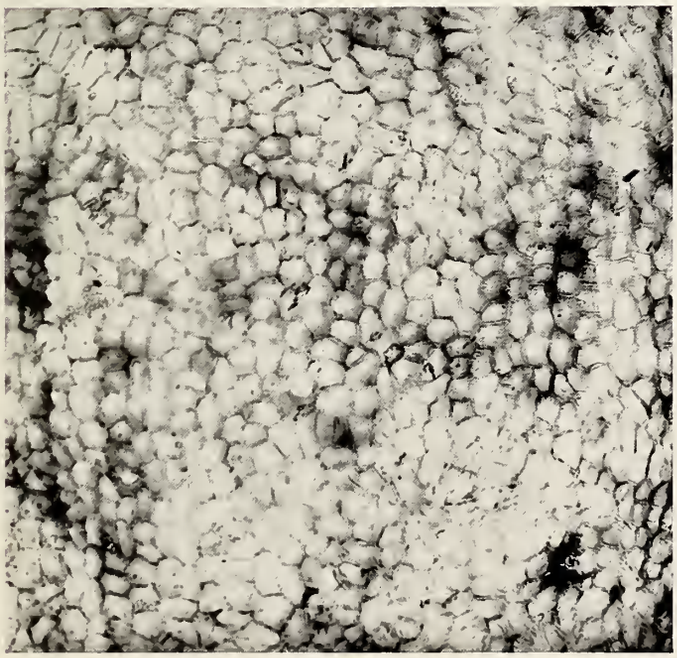
FIG. 4. Upper cuticle. Magnification ×100. V.56636.

1



2

3



4

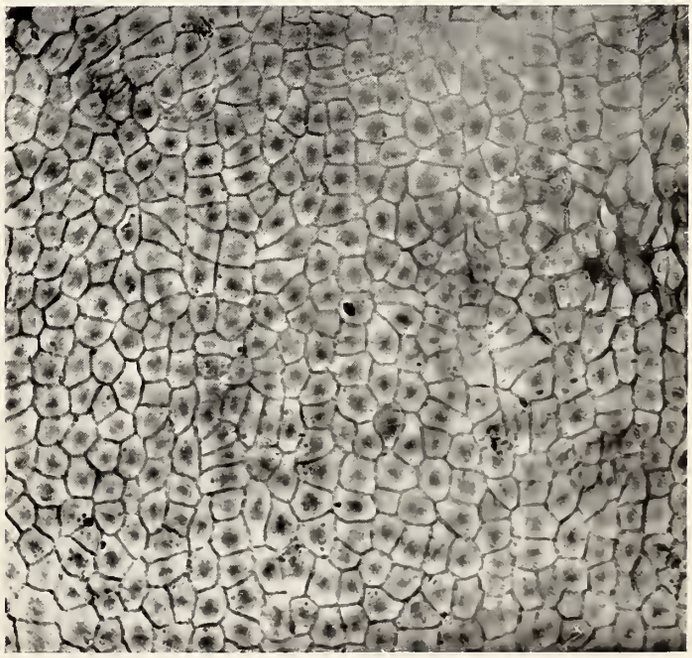


PLATE 4

Solenites vimineus (Phillips)

FIG. 1. Leaf cuticle showing typical stomata. Magnification × 500. V.56476. Cloughton Wyke *Solenites* Bed.

FIG. 2. Leaf cuticle. Stomata tending to have unusually well developed rims. Magnification × 500. V.56477. Gristhorpe Bed.

Czekanowskia microphylla (Phillips)

Gristhorpe Bed

FIG. 3. Two fragments of leaf cuticle showing stomatal pits occluded by papillae from subsidiary cells. Magnification × 500. V.56483.

Czekanowskia thomasi sp. nov.

Gristhorpe Bed

FIG. 4. Leaf cuticle from holotype. Magnification × 500. V.56420*a*.

1

2

3

4

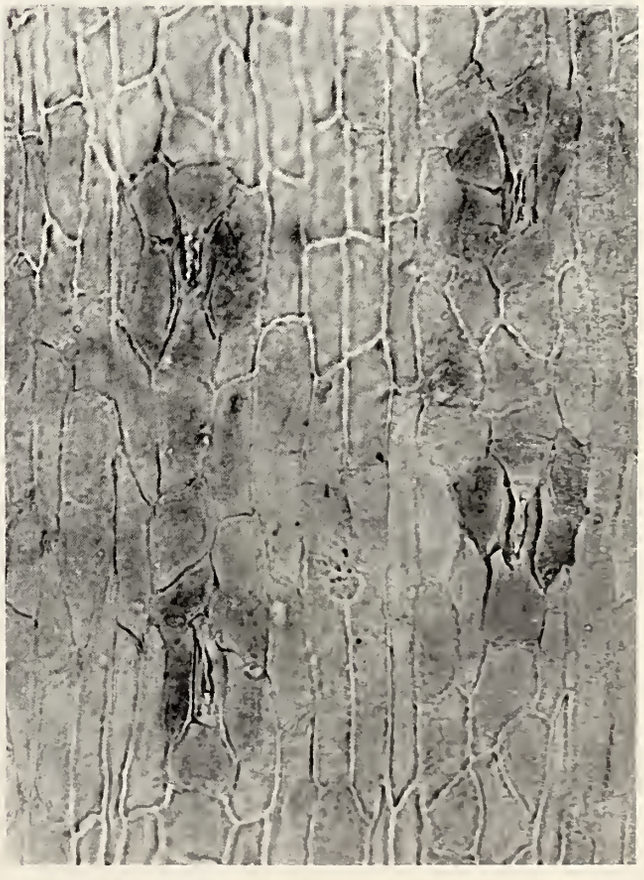


PLATE 5

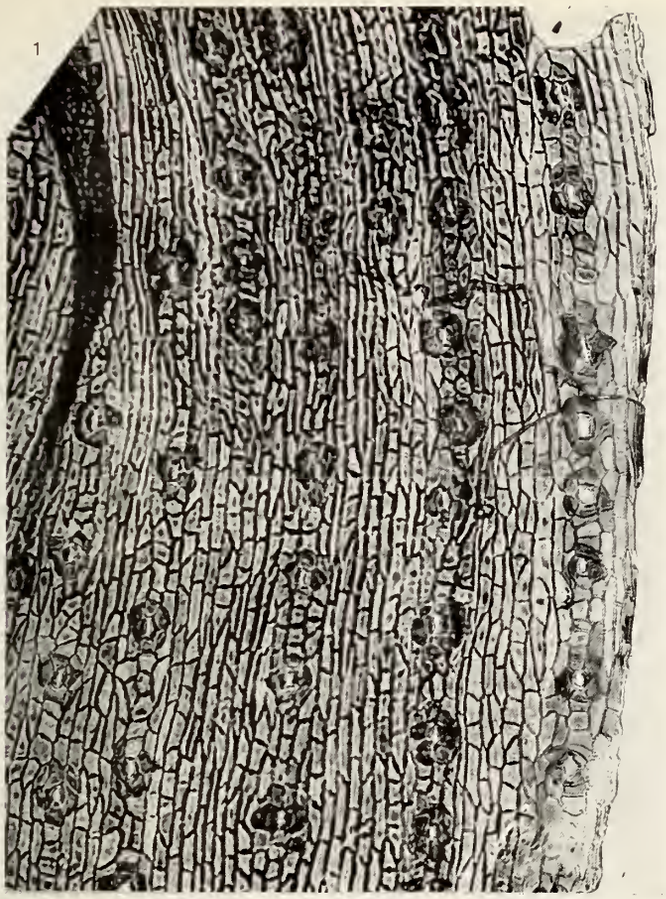
Czekanowskia furcula sp. nov.

FIG. 1. One side of leaf cuticle. Pads visible on cell surface. Magnification ×180. V.56488. Farndale Crag Pond, Upper black shale.

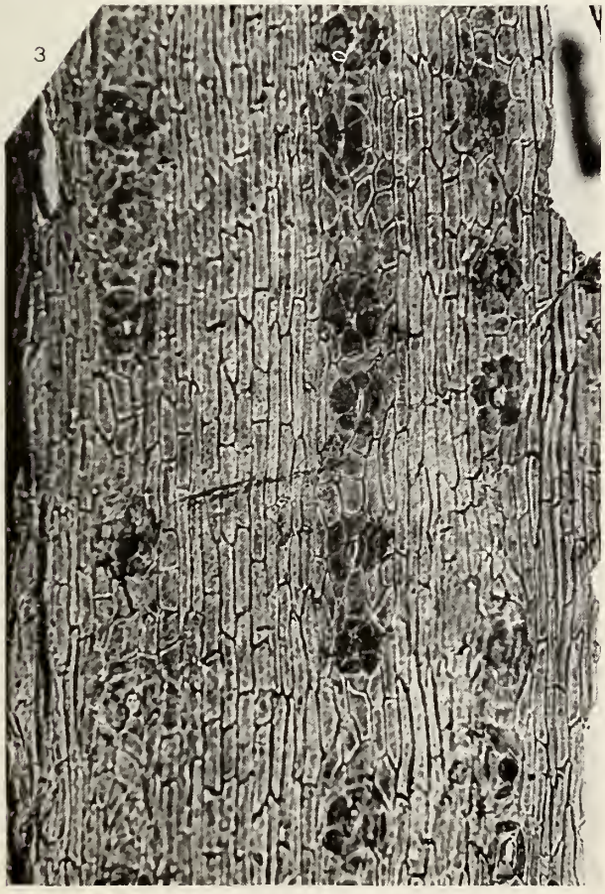
FIG. 2. Portion of leaf cuticle from the holotype showing many stomatal apertures more or less round, but all with very well developed rims. Magnification ×500. V.28393*a*. Whitby Long Bight (fallen block).

FIG. 3. One side of leaf cuticle slightly atypical with fewer rows of larger stomata. Magnification ×180. V.56489. Marske Quarry.

FIG. 4. Portion of cuticle. Magnification ×500. V.56489. Marske Quarry.


1

2


3

4

PLATE 6

Czekanowskia sp. A

Fig. 1. V.56592. Magnification × 130.

Figs. 4, 7. Stomata (seen from within) with subsidiary cells projecting over striated epidermal cells. Magnification × 500. V.56592.

Czekanowskia blacki sp. nov.

Fig. 2. Stomata showing subsidiary cells only slightly thickened. Magnification × 500. V.56497.

Fig. 3. Cuticle. Magnification × 500. V.56496.

Sphenarion muiriae sp. nov.

Fig. 5. Stoma. Magnification × 500. V.56499.

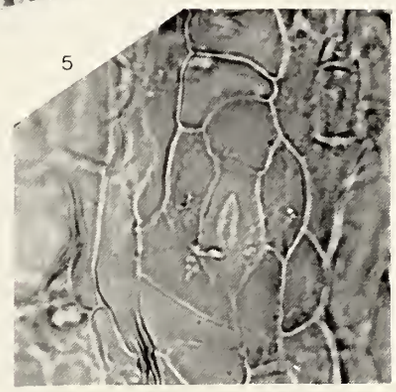
Fig. 6. Stomata. Magnification × 500. V.56499.

All the specimens are from Scalby Ness *Ginkgo* Bed.

1

2

3


5

4

7

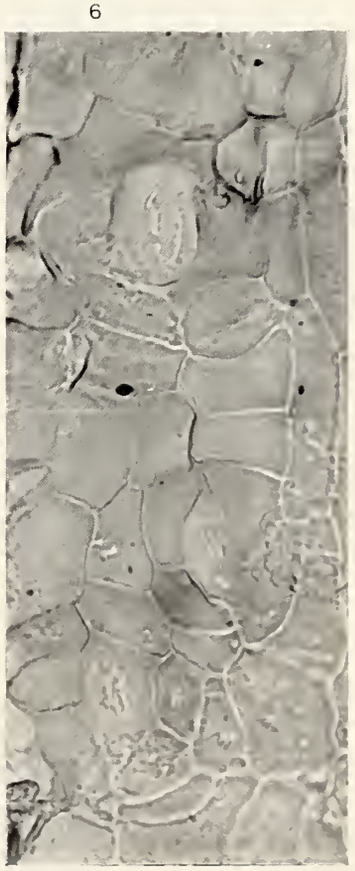

6

PLATE 7

Sphenarion muiriae sp. nov.

Fig. 1. Cuticle, thicker side. Magnification ×130. V.56499. Scalby Ness.

Eretmophyllum whitbiense Thomas

Fig. 2. Complete leaf base. Magnification ×1. V56465. Whitby.

Czekanowskia blacki sp. nov.

Scalby Ness

Fig. 3. Naturally cleared leaf. The single vein is held in position by mesophyll plates. Magnification ×25. V.56494.

Figs. 12, 13. Upper and lower halves of a piece of naturally cleared leaf. In the middle region the vein has shifted and below it has disintegrated into separate fibrovascular elements. Magnification ×10. V.56494.

Leptostrobus cancer Harris

Cloughton Wyke *Solenites* Bed

Fig. 4. Scale leaves thought to belong to cone base (specimen destroyed in preparation) Magnification ×4. From V.56503.

Fig. 5. Inner side of valve with pimply band (two black bodies are extraneous). Magnification ×10. V.56505.

Figs. 6, 7. Separated inner rim of valve. Fig. 6 ×10, Fig. 7 ×30. In Fig. 7 at the top 10 mm of dark tissue is the thick cuticle near the outer margin, blacker regions are caused by folds. Then about 7 mm of pale cuticle is of the trench (delimited above by fold 1-2 mm broad and below by fold 4 mm broad), finally the pimply zone (torn away on right). This is seen separately below but overlaps the trench fold above. V.56506.

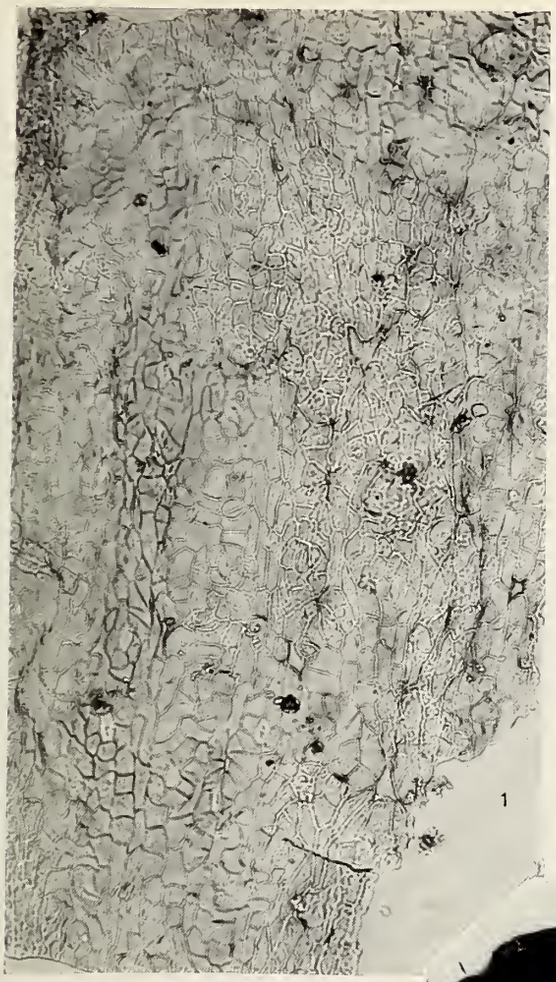
Fig. 8. Valve cuticle, the pimply zone is just visible. A dark oval body may be a minute abortive seed. Magnification ×10. V.56507.

Figs. 10, 11. Cone fragment, part and counterpart (see Text-fig. 36 D). Magnification ×1. V.56379.

Figs. 14, 15. Cone fragment, part and counterpart (see also Text-fig. 36 E). Magnification ×1. V.56378.

Ginkgo huttoni (Sternberg)

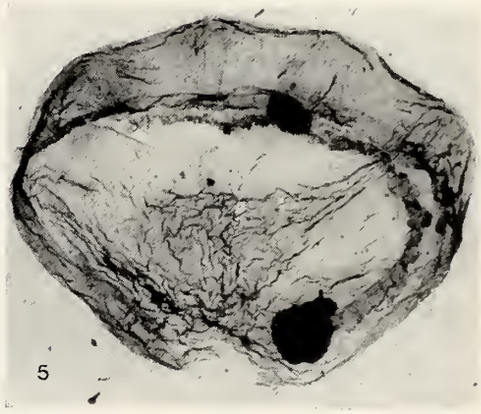
Fig. 9. Two pairs of seeds, the lower pair is more complete. Almost everything but the cuticles has vanished through decay. See also Text-figs. 22 P and 23 I. Actual size. V.56411. Scalby Ness *Ginkgo* Bed.


1

2

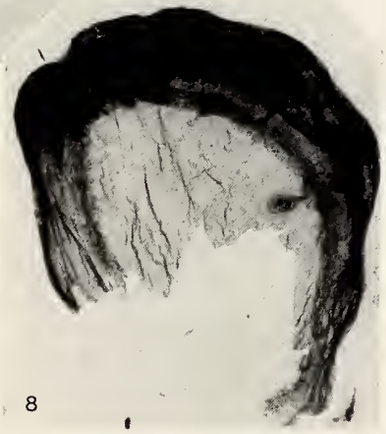
3

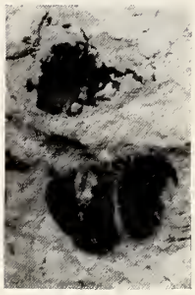
4

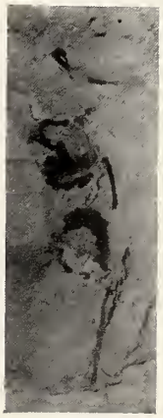

5

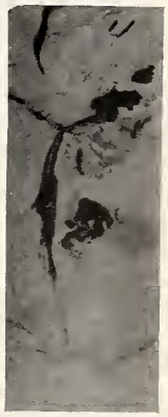
6

7


8


9


10


11

12

13

14

15

PLATE 8

Desmiophyllum gramineum sp. nov.

Fig. 1. Fragments from the Type locality of *Ixostrobus whitbiensis*. Actual size. V.56400. Whitby, Jump Down Bight.

Ixostrobus whitbiensis sp. nov.

Fig. 2. Slender form (with *Desmiophyllum*). Actual size. V.56391. Saltwick waterfall.

Fig. 3. Sporangia. The cuticles shown in Text-fig. 40 were obtained from this specimen. Magnification ×2. V.56392. Saltwick waterfall.

Fig. 4. Slender form. Magnification ×2. V.56393. Whitby Jump Down Bight.

Figs. 5, 6. Holotype. Black matter to the left may be the edge of a *Zamites* 'flower' peduncle and on the right is a fragment of *Desmiophyllum*. Fig. 5 ×2; Fig. 6. actual size. V.56390. Whitby Jump Down Bight.

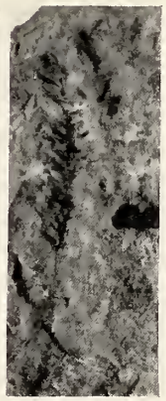
Figs. 7, 8. Photographed dry in Fig. 7, under oil in Fig. 8. Actual size. V. 56394. Whitby Jump Down Bight.

Fig. 9. Cone fragment with *Czekanowskia furcula* and *Desmiophyllum* (top right) Actual size. V.56395. Saltwick waterfall.

Fig. 10. Cone fragment, with *Desmiophyllum*. Magnification ×2. V.56397. R. Derwent 'Grass' Bed.

Fig. 11. Two cone fragments, with *Desmiophyllum*. Magnification ×2. V.56396. Saltwick waterfall.

1


2

3

4

6

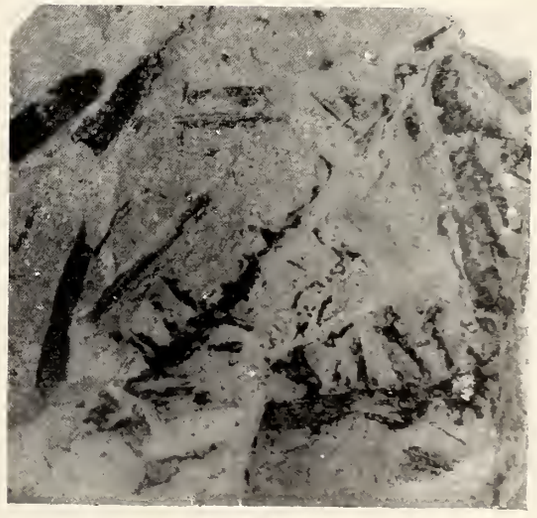
7

8

9

5

10


11

BRITISH MUSEUM
GENERAL
20 JAN 1975
LIBRARY
NATURAL HISTORY