



THE YORKSHIRE JURASSIC FLORA

II. CAYTONIALES, CYCADALES & PTERIDOSPERMS

BRITISH MUSEUM (NATURAL HISTORY)

THE YORKSHIRE JURASSIC  
FLORA

II

CAYTONIALES, CYCADALES & PTERIDOSPERMS

*By*

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With seven plates  
and sixty-seven figures in the text

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## PREFACE

IT was originally intended to complete this work on the Yorkshire Jurassic Flora in two volumes, but this has not proved feasible, and in this second volume the author has limited his attention to the Caytoniales, Cycadales and Pteridosperms, covering a total of fifty-two species belonging to fifteen genera. It is hoped to complete the work on the remaining groups, the Bennettiales, Ginkgoales and Coniferales, in two further volumes presently in hand.

As in the first volume, much of the material under examination has been collected by Professor Harris himself and again the Department is indebted to him for another important series of hand-specimens and slide preparations, including type and figured material, which he has generously presented to the National Collections. And once more, the very informative figures in the text are from the author's skilful pen, this time reinforced by seven plates.

To Mr. F. M. Wonnacott both the author and myself are yet again indebted for the firm but discreet exercise of his editorial skill.

*July* 30, 1963

ERROL WHITE  
*Keeper of Palaeontology*

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## INTRODUCTION

As first planned, this volume was to include the Caytoniales, the Cycads, the Bennettiales and various other Gymnosperms with leaves of more or less pinnate construction. This comprises that vague assemblage often called the 'Cycadophyta'. However, the Bennettiales have been excluded to expedite publication. I would like to take this opportunity to acknowledge the generosity of Mrs. Hamshaw Thomas who placed her late husband's very large collection of Yorkshire fossils at my disposal. The new specimens have made it possible for me to reorganise the descriptions of several species and numerous specimens of his are figured here.

TOM M. HARRIS

## SYSTEMATIC DESCRIPTIONS

### Class Caytoniales

This isolated class is still no more than an isolated genus and this genus has still no name, though it has been called 'The *Caytonia* plant' for informal purposes. It is better with no name because however strongly supported it is essentially an inference rather than a fossil. The separate parts are named, the leaf being *Sagenopteris*, the fruit and seed being *Caytonia* and the microsporophyll being *Caytonanthus*. Dispersed pollen agreeing with that of *Caytonanthus* has been described under the names *Alisporites* Daugherty, *Vitreisporites* Leschik and *Caytonisporites* Couper. Since other plants also produced pollen of this general type it is unsafe to identify dispersed grains as Caytonialean.

The affinities of the Caytoniales have from the first been regarded as open. Thomas (1925) emphasised points of agreement with both the Pteridosperms and with the Angiosperms. On the whole, work since that date has made the Caytoniales seem even more isolated; the fruit in particular is strictly Gymnospermous in pollination. The general organisation of the sporophylls seems Pteridosperm-like (though the fruit is still to be explained); the seeds are like those of certain Bennettitales, and to a less extent the Angiosperms and the leaves, while unusual in their form, have a distinctly Angiosperm-like epidermis (see Thomas 1925; Harris 1951).

Two organs tentatively referred to the Caytoniales are the isolated seed *Amphorispermum* (included here) and the microsporophyll *Pramelreuthia* Kräusel (1949). This, however, may be nearer *Harrisothea* Lundblad (1961) which belongs to a very different plant.

The evidence for attributing the various organs to one genus is the combination of the evidence of association and the evidence of agreement in structure since no specimen showing continuity has yet been discovered.

#### 1. Evidence of Association

This is now overwhelming. It was at first untidy since the incompletely resolved suites of organs of two species were mixed in the Gristhorpe Bed (Thomas 1925, 1931). However in the Basal Liassic rocks of East Greenland a single species is involved and this is represented by the same suite of organs in three localities (Harris 1932a, 1937). A *Caytonia*-like fruit is associated with a *Sagenopteris* in the Swedish Rhaetic (Lundblad 1948). Then in Yorkshire the two species of the Gristhorpe Bed have now been fully separated. One of these (leaf and fruit) apparently occurs in Sardinia (Edwards 1929) and also in a second locality in Yorkshire. A third Yorkshire species is now known though not yet fully distinguished and its leaf and reproductive organs are associated in several localities. If the Caytoniales were among the

commonest Yorkshire fossils such association would have little significance but they are by no means common and fruits and anthers in particular are scarcely ever met without leaves. At present Caytonialean leaves and reproductive organs are known associated in nine different localities.

The occurrence of pollen grains of *Caytonanthus* inside the micropyles or nucellar beaks of *Caytonia* seeds is intimate association. All suitable seeds of all four species show them and no other kind of pollen has been recognised in this position. Even *Caytonia* seeds taken from a coprolite showed this pollen.

## 2. Agreement in Structure

Thomas (1925) emphasised the resemblance between the cuticle of *Sagenopteris* petioles and the rachises of both *Caytonia* and *Caytonanthus* from the Gristhorpe Bed, but as the separate species were not fully discriminated the resemblance was generic rather than specific. Now that the difference in the epidermal cells of the two Yorkshire species is realised, it is possible to recognise the species of origin of each organ. In *Sagenopteris colpodes* of the Gristhorpe Bed the cells have fine, sinuous walls on the lamina and jagged thickenings on the petiole where sac-like trichomes are numerous. In *S. phillipsi* the cells have broad, straight walls throughout and trichomes are rare. Just the same features are recognisable in the fruiting rachises and probably in the microsporophyll rachises (though the evidence for *Caytonanthus oncodes* is less perfect). Additional support is given by the Greenland species which has glandular trichomes on fruit and leaf (Harris 1933).

## Genus SAGENOPTERIS Presl, 1838 : 164

EMENDED DIAGNOSIS. Leaf petiolate, petiole normally bearing two pairs of leaflets at its apex, petiole and leaflets shed by absciss layers. Leaflet lanceolate with a main vein at a greater or less distance distal to the mid-line; lateral veins arising at a small angle, but curving outwards, forking and anastomosing to form obliquely elongated meshes, ultimate veins ending freely at the margin.

Lamina cutinised; stomata confined to lower side, oval, guard cell surface flat but with a sunken region around aperture, stoma surrounded by a perigenous ring of subsidiary cells.

TYPE SPECIES. *Filicites nilssoniana* Brongniart (1825 : 218).

DISCUSSION. The name applies to normal foliage leaves but is extended to cover small leaves and minute scale leaves. For convenience also a twig is described here under the same name but were the stem better known it would deserve a separate name.

*Petiole.* The following points have been noted. The petiole base is only slightly expanded and shows a clean abscission surface. On the shoot (of *S. phillipsi*) there is a clearly marked imprint of a single curved vascular strand on the leaf base scar. At the top of the petiole, the scars of the four leaflets are in two clearly marked pairs and are on the upper surface (reaching but not going below the petiole margin). There are two strong ridges (in *S. colpodes*) beginning at the lower pair of leaflet scars and passing down the upper surface of the petiole, so as to delimit a median groove. The back of the petiole is smooth, but in *S. phillipsi* it is ribbed. The leaflets are abscised from clean scars which show the imprint of a single median bundle.

*Sagenopteris colpodes* Harris

## Text-figs. 1-3

1. Yorkshire specimens of similar form but unknown cuticle structure except where stated.

- 1833 *Glossopteris phillipsi* Brongniart (in part): Lindley & Hutton, p. 177, pl. 63, fig. 1. (Crude drawing of whole leaf.)  
 1900 *Sagenopteris phillipsi* (Brongn.): Seward (in part), p. 162, text-fig. 25 and text-fig. 26 (= var. *major*). Fig. 25 is Lindley & Hutton's leaf redrawn.  
 1900a *Sagenopteris phillipsi* (Brongn.): Seward, p. 11, pl. 3, fig. 8 only. (var. *major*.)  
 1913 *Sagenopteris phillipsi* (Brongn.) var. *major* Thomas, p. 226, pl. 25, fig. 2. (Good fragment from Marske.)  
 1925 *Sagenopteris phillipsi* (Brongn.): Thomas, p. 334, pl. 15, figs. 49, 51 only. (Not text-fig. 12 c, d.) (Small complete leaf and cuticle of petiole.)  
 1940 *Sagenopteris colpodes* Harris, p. 250, text-figs. 1, 2, 6 F-H. (Holotype, cuticle.)

2. Leaves of similar shape from other regions. Cuticles unknown.

- 1894 *Sagenopteris goeppertiana* Raciborski, p. 214, pl. 20, figs. 13-18. (Poland.)  
 1902 *Sagenopteris rhoifolia* Presl: Möller, p. 11, pl. 6, figs. 5-7. (Bornholm.)  
 1904 *Sagenopteris phillipsi* (Brongn.): Seward, p. 94, pl. 9, fig. 3. (English Midlands.)  
 1913 *Sagenopteris nilssoniana* (Brongn.): Grandori, p. 68, pl. 5, figs. 14, 15; pl. 6, figs. 16-19; text-figs. 4-8. (Upper Lias, N. Italy.)  
 1955 *Sagenopteris phillipsi* (Brongn.): Pantic, p. 221, pl. 3, fig. 4. (Jurassic, Serbia.)  
 1962 *Sagenopteris phillipsi* (Brongn.): Teslenko, p. 126, pl. 17, fig. 4; text-fig. 30.  
 1963 *Sagenopteris phillipsi* (Brongn.) var. *cuneata* Baranova, Burakova & Bekasova, p. 178, pl. 38, figs. 3-7; text-fig. 74. (Jurassic, Central Asia.)

*Sagenopteris colpodes* is regarded here as the aggregate of two very similar species which are imperfectly distinguishable on present evidence, though the corresponding fruits differ considerably.

EMENDED DIAGNOSIS. Upper leaflets almost symmetrical, lower pair with midrib considerably nearer the distal margin. Leaflets varying from small ones of broadly ovate shape and twice as long as broad to large ones of long lanceolate shape and five times as long as broad. Apex of leaflet obtuse, margins entire, base minutely stalked. Midrib usually disappearing considerably below the apex. Vein meshes 0.75-nearly 1.0 mm. wide on larger leaves. Hairs not obvious on lamina. Cuticle rather thin (upper about  $1.5\mu$ , lower thinner). Upper showing cells of somewhat rectangular shape, often transversely elongated between veins and occasionally forming longitudinal rows; over veins elongated along the vein. Cell outlines rather obscurely marked, usually sinuous but occasionally showing disconnected jagged thickenings, rarely appearing as isolated beads. Cell surface showing parallel striations along the veins but obscurely mottled between veins, never papillate. Trichome bases absent. Lower cuticle showing cell outlines very indistinctly between the veins. Cells along the veins elongated, walls often nearly straight; cells between veins often of irregular shape, walls coarsely waved; cells along veins showing parallel longitudinal striations, other cells smooth. Stomata oval, outline finely marked but distinct. Subsidiary cells unspecialised, cuticle not extending over or under guard cells. Surface of stoma sometimes showing radiating striations. Trichomes frequent along veins, occasional between veins, base a small thickened cell bearing a ring shaped scar; free part missing. Cuticle of adaxial side of petiole showing two longitudinal ribs (extending down from pinnae); cells often shorter than broad, arranged in longitudinal files, lateral walls showing jagged thickenings, end walls usually smooth and finely marked. Trichomes rare. Abaxial side without ribs; cells elongated, in less definite rows, lateral walls and end walls

similar, with jagged thickenings. Trichomes numerous especially near margin, free part forming a thinly cutinised sac  $50\mu$  long.

HOLOTYPE. V.26441, figured by Harris (1940, text-fig. 6 G).

OCCURRENCE. *Sagenopteris* leaves are so delicate that their cutinised fragments are seldom recognisable in macerations of rock in bulk. All the following records therefore refer to hand specimens, in every case confirmed by a cuticle preparation.

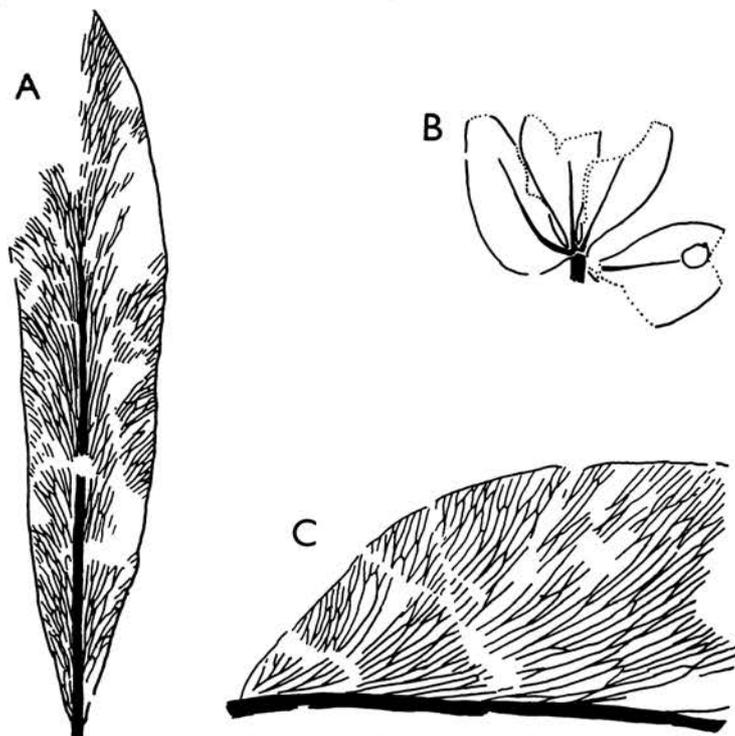


Fig. 1. *Sagenopteris colpodes* Harris

A, leaflet from Hasty Bank, V.34656,  $\times 1$ . B, leaf with three attached leaflets and one perhaps originally attached. The round outline represents a fruit of *Caytonia sewardi*, V.2186,  $\times 1$ . C, fragment of a large leaflet from Roseberry Topping, V.34663,  $\times 1$ .

B, Gristhorpe Bed, previously figured (apart from the detached leaflet) by Harris (1940).

Middle Deltaic Gristhorpe Series. (Mostly small leaves.)

Gristhorpe Bed.

Cloughton Wyke *Solenites* Bed.

Lower Deltaic. (Mostly large leaves.)

Hasty Bank.

Ryston Nab Quarry.

Roseberry Topping.

Boulby Alum Quarry, Bed 2 A.

Eston Moor Quarry (1).

Whitby, Long Bight Plant Bed.

Marske Quarry.

Farndale, Hillhouse Nab.

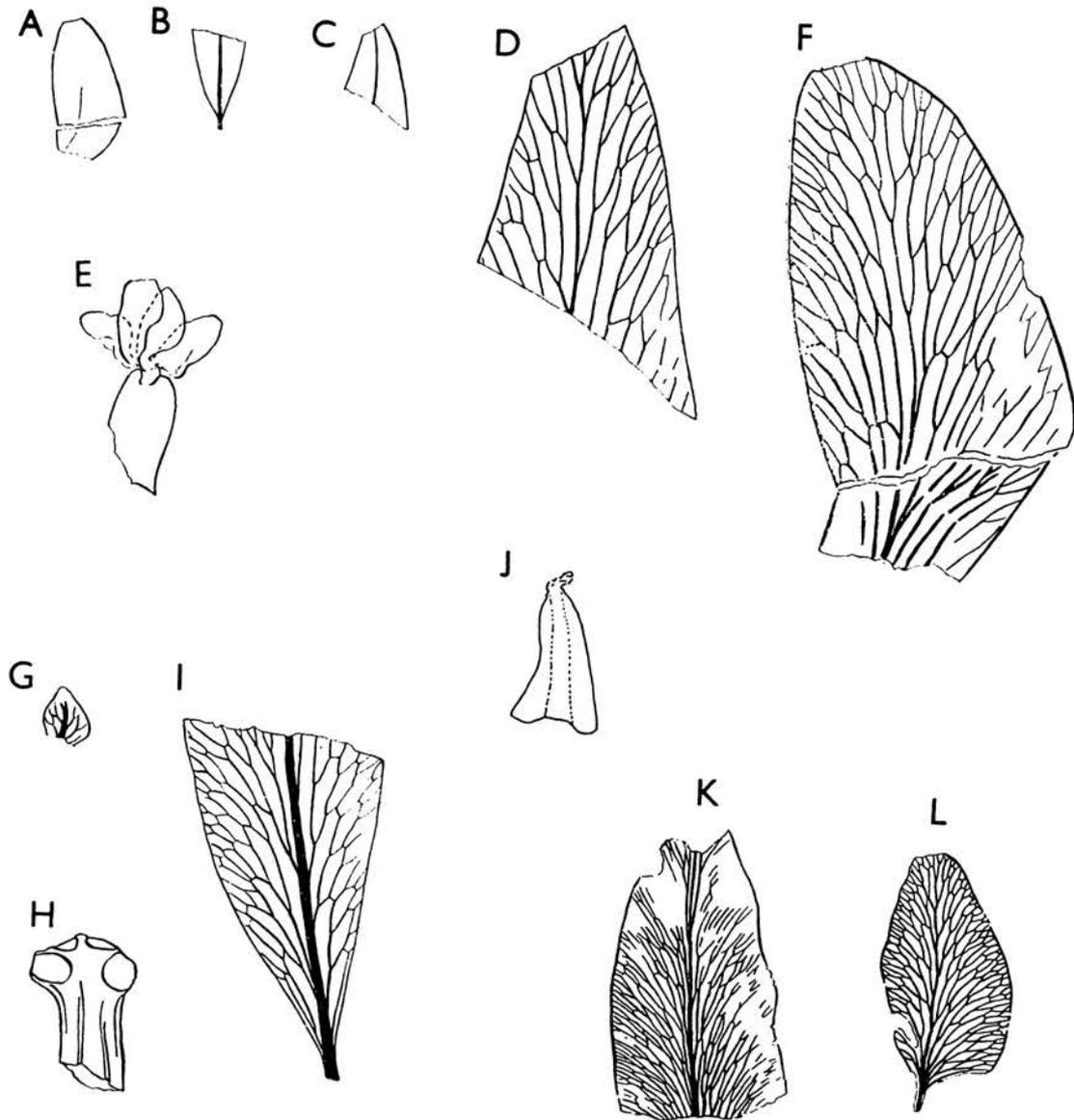


Fig. 2. *Sagenopteris colpodes* Harris. Leaf and scale leaf

A, leaflet fragment shown also in F, V.24708,  $\times 1$ . B, leaflet fragment shown also in I, V.26434,  $\times 1$ . C, leaflet fragment shown also in D, V.26434,  $\times 1$ . D, as C,  $\times 4$ . E, small leaf from a bulk maceration (cuticle only), V.26435,  $\times 4$ . F, as A,  $\times 4$ . G, small leaflet from bulk maceration (cuticle only), V.26436,  $\times 4$ . H, petiole showing four leaflet scars, from bulk maceration, V.26437,  $\times 8$ . I, as B,  $\times 4$ . (Some of the finest veins in D, F, G and I have probably been missed.) J, scale leaf, V.45564,  $\times 4$ . K, holotype, V.26441,  $\times 1$ . L, V.26440,  $\times 1$ .

All the specimens are from the Gristhorpe Bed except J which is from Boulby Alum Quarry. All the figures except J are from Harris (1940).

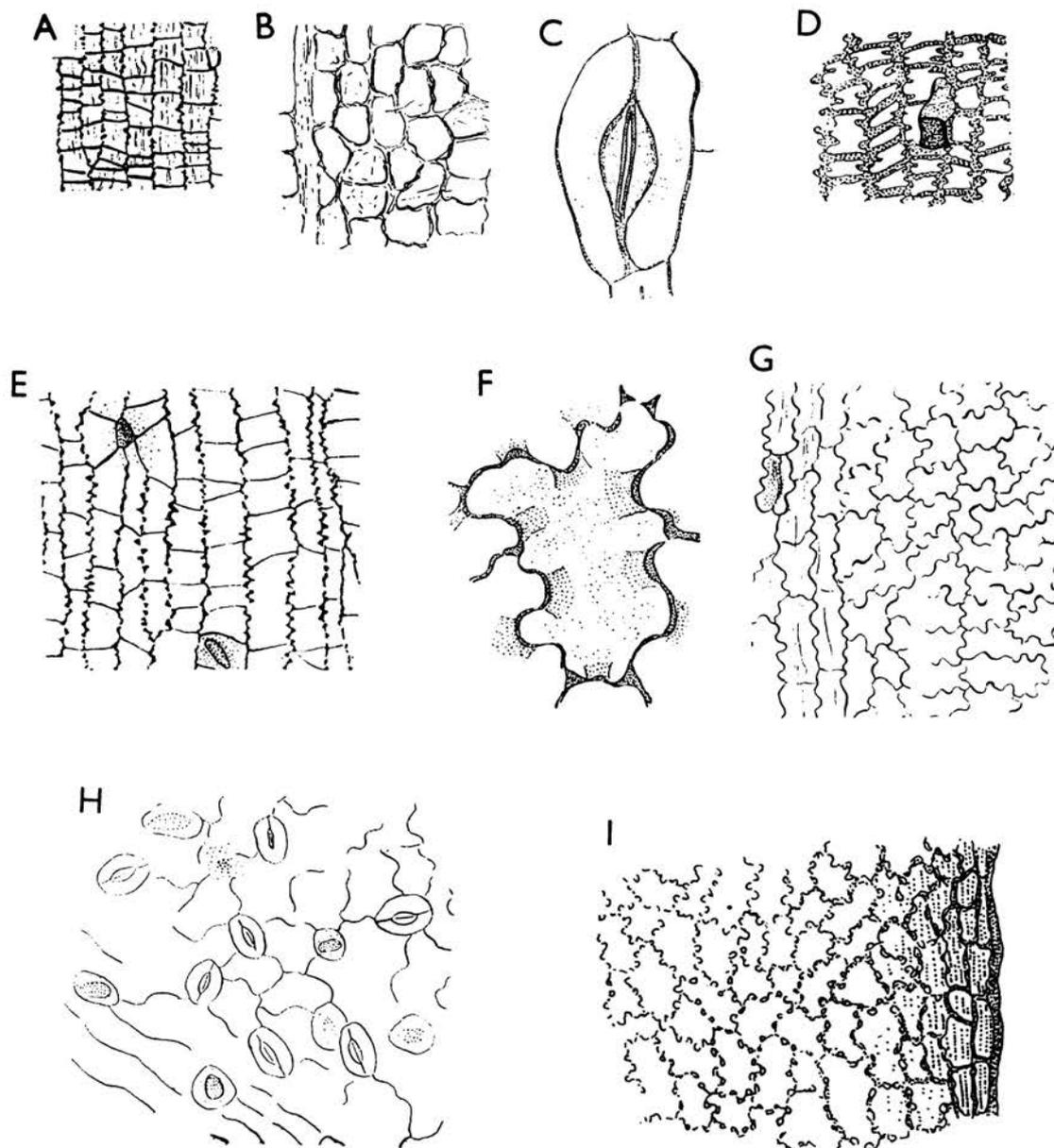


Fig. 3. *Sagenopteris colpodes* Harris (cuticle)

A, small leaf base, underside, V.26435 (Text-fig. 2 E),  $\times 200$ . B, palisade cells (adhering to upper cuticle), V.24708a,  $\times 100$ . C, stoma of foliage leaf, V.26438,  $\times 800$ . D, small leaf base, upper side, showing a hair, V.26435,  $\times 200$ . E, petiole, underside, V.26437,  $\times 200$ . F, G, foliage leaf, upper cuticle, V.26438, F,  $\times 800$ , G,  $\times 200$ . H, foliage leaf, lower cuticle (a vein runs on the left), V.26438,  $\times 200$ . I, foliage leaf, lower cuticle near margin, V.34663a,  $\times 200$ .

All the specimens are from the Gristhorpe Bed except I which is from Roseberry Topping. All the figures except I are from Harris (1940).

DISCUSSION. There are two forms:

- (a) Small form (Middle Deltaic). Leaflet seldom over 5 cm. long; cell outlines appearing continuous.
- (b) Large form (Lower Deltaic). Leaflet often over 10 cm. long; cell outlines often interrupted.

The original specimens were a few small leaves from the Middle Deltaic Gristhorpe Bed, and further small leaves have been found there and also a few large ones. In several Lower Deltaic localities there are many large leaves and also some small ones; the range of form is the same, but the mean size is perhaps twice as large in the Lower Deltaic localities. There appears to be a difference in cuticle also, but this is not secure because the cuticle is so delicate that half the specimens (from all localities) gave no useful preparations. Some of the Lower Deltaic specimens have cuticles just like the Gristhorpe Bed specimens but in most the walls either appear nearly straight with nodular thickenings from which jagged extensions run on to the cells, or the nodular thickenings are separate and form a row of beads. Some variation occurs in a single leaf. In the associated minute scale leaves, the walls are straight with slight jagged thickenings.

This variation would have been treated as unimportant were it not that the reproductive organs with the larger Lower Deltaic form are different from those with the Middle Deltaic form. It appears that we are dealing with two distinct plant species in which the fruit and seeds are satisfactorily distinguishable; the less known pollen producing organs are imperfectly distinguished and the leaves are very imperfectly distinguished indeed. It seems unpractical and wrong in principle to distinguish the leaves as two species until there are clear morphological characters to distinguish them. Such characters as I tried to use failed and left many specimens indeterminate. A new character is needed and there is obvious room for progress.

Certain of the Gristhorpe specimens show their mesophyll cells as bulges on the upper surface or as dark marks by transmitted light or as resinous casts after maceration. On the lower side there may be transverse ridges caused by the spongy mesophyll, which evidently, as in many other plants, is arranged in parallel strands or plates running from vein to vein. *S. phillipsi* shows the mesophyll less clearly, if at all.

*Scale leaves.* There are scale leaves associated with *S. colpodes* at the Lower Deltaic Boulby Alum Quarry locality. They are like those of *S. phillipsi* but have more trichomes and cell walls with more or less developed jagged thickenings.

### *Sagenopteris phillipsi* (Brongn.) Presl

Text-figs. 4-6

#### 1. Yorkshire specimens.

- 1829 *Pecopteris paucifolia* Phillips, p. 148.
- 1829 *Pecopteris longifolia* Phillips, p. 189, pl. 8, fig. 8. (Inaccurate drawing.)
- 1830 *Glossopteris phillipsi* Brongniart, p. 255, pl. 61 bis, fig. 5; pl. 63, fig. 2. (Drawings by Phillips and by Murray, veins inaccurate.)
- 1833 *Glossopteris phillipsi* Brongn.: Lindley & Hutton (in part), pl. 63, figs. 2, 3 only. (Whole leaf and a fragment, veins diagrammatic.)
- 1835 *Otopteris cuneata* Lindley & Hutton, pl. 155. (Small leaves with two leaflets.)
- 1875 *Glossopteris phillipsi* Brongn.: Phillips, p. 203, pl. 8, fig. 8. (1829 figure emended to show vein meshes.)

- 1900 *Sagenopteris phillipsi* (Brongn.): Seward (in part), p. 162, pl. 18, figs. 2-4 (Normal leaf and small ones with 1 or 2 lobes); text-fig. 24 (Lindley & Hutton's *G. phillipsi* redrawn.)  
 1900a *Sagenopteris phillipsi* (Brongn.): Seward, p. 11, pl. 3, fig. 7 only. (Lindley & Hutton's *O. cuneata* refigured.)  
 1925 *Sagenopteris phillipsi* (Brongn.): Thomas (in part), p. 334, pl. 15, figs. 50, 52, 53; text-figs. 11 C, D; 12 C, D. (Good leaves, cuticle of petiole.)  
 1939 *Sagenopteris phillipsi* (Brongn.): Darrah, p. 339, text-fig. 174. (Yorkshire leaf.)  
 1940 *Sagenopteris phillipsi* (Brongn.): Harris, p. 256, text-figs. 3-5, 6 H-E. (Various forms of leaf, cuticle, shoot.)  
 1951 *Sagenopteris phillipsi* (Brongn.): Harris, p. 30, text-fig. 1. (Discussion.)

2. Specimens of rather similar form from other regions (in no case confirmed by cuticle).

- 1892 *Sagenopteris phillipsi* (Brongn.): Bartholin, p. 13, pl. 5, figs. 7, 8. (Bornholm.)  
 1894 *Sagenopteris phillipsi* (Brongn.): Raciborski, p. 214, pl. 20, figs. 19, 20. (Poland.)  
 1902 *Sagenopteris phillipsi* (Brongn.): Möller, p. 52, pl. 6, figs. 1-7. (Bornholm.)  
 1905 *Sagenopteris paucifolia* (Phillips) Ward, p. 85. (Name revived; specimens illustrated on pl. 15, figs. 1-3 have broader leaflets and are probably distinct.)  
 1911 *Sagenopteris phillipsi* (Brongn.): Seward, p. 655, pl. 1, figs. 1-4; pl. 6, figs. 3-5; pl. 7, fig. 19 s; text-fig. 1. (Upper Jurassic, Scotland. Some of the leaflets are too broad for *S. phillipsi*.)  
 1913 *Sagenopteris paucifolia* (Phillips): Halle, p. 85, pl. 15, figs. 1-3. (Graham Land.)  
 1928 *Sagenopteris phillipsi* (Brongn.): Makarewiczówna, p. 12, pl. 4, fig. 6. (Lias, Poland; but very like her pl. 4, fig. 7 determined as *S. nilssoniana*.)  
 1940 *Sagenopteris paucifolia* (Phillips): Oishi, p. 362, pl. 41, figs. 6, 7. (Leaflets from Jurassic of Japan, form approaching *S. colpodes*.)

DIAGNOSIS. Upper leaflets symmetrical, lower pair only slightly enlarged on lower side. Leaflets typically long-lanceolate to linear-lanceolate, length 5 to 10 times width. Apex of leaflet acute, margins entire, base sessile or minutely stalked. Midrib extending almost to apex. Vein meshes about 0.5 mm. wide in larger leaflets. Petiole smooth above, ribbed below.

Cuticle moderately thick, upper about  $3\mu$ , lower  $1.5\mu$ . Upper cuticle showing small isodiametric cells. Cell outlines well marked, sides straight, often flanked by a broad border, never sinuous, or with jagged thickenings. Cell surface obscurely mottled, not papillate, not striated along veins. Trichomes absent, stomata absent.

Lower cuticle showing isodiametric cells with straight, clearly marked walls, cells along veins rectangular and in rows. Cell surface obscurely sculptured, not papillate; stomata frequent, subsidiary cells unspecialised, or occasionally bulging over the guard cells, encircling cells occasional or absent. Edges of subsidiary cells often forming distinct ridges underneath the guard cells.

Trichome bases rare or occasional on midrib, consisting of a thickened cell with a bulging surface.

Upper cuticle of petiole showing short cells in longitudinal files, lateral cell walls thick, straight. Lower cuticle showing longer cells, lateral walls straight, occasionally interrupted by pits. Trichome bases rare (free part unknown).

LECTOTYPE. Specimen figured by Brongniart (1830, pl. 61 bis, fig. 5).

OCCURRENCE.

Middle Deltaic Gristhorpe Series

Gristhorpe Bed

Farndale, in the tips of old coal pits from Swinacle Ridge to Ouse Gill.

Lower Deltaic (determinations less secure.)

?Ryston Nab Quarry (ill preserved)

Farndale, Hillhouse Nab plant bed.

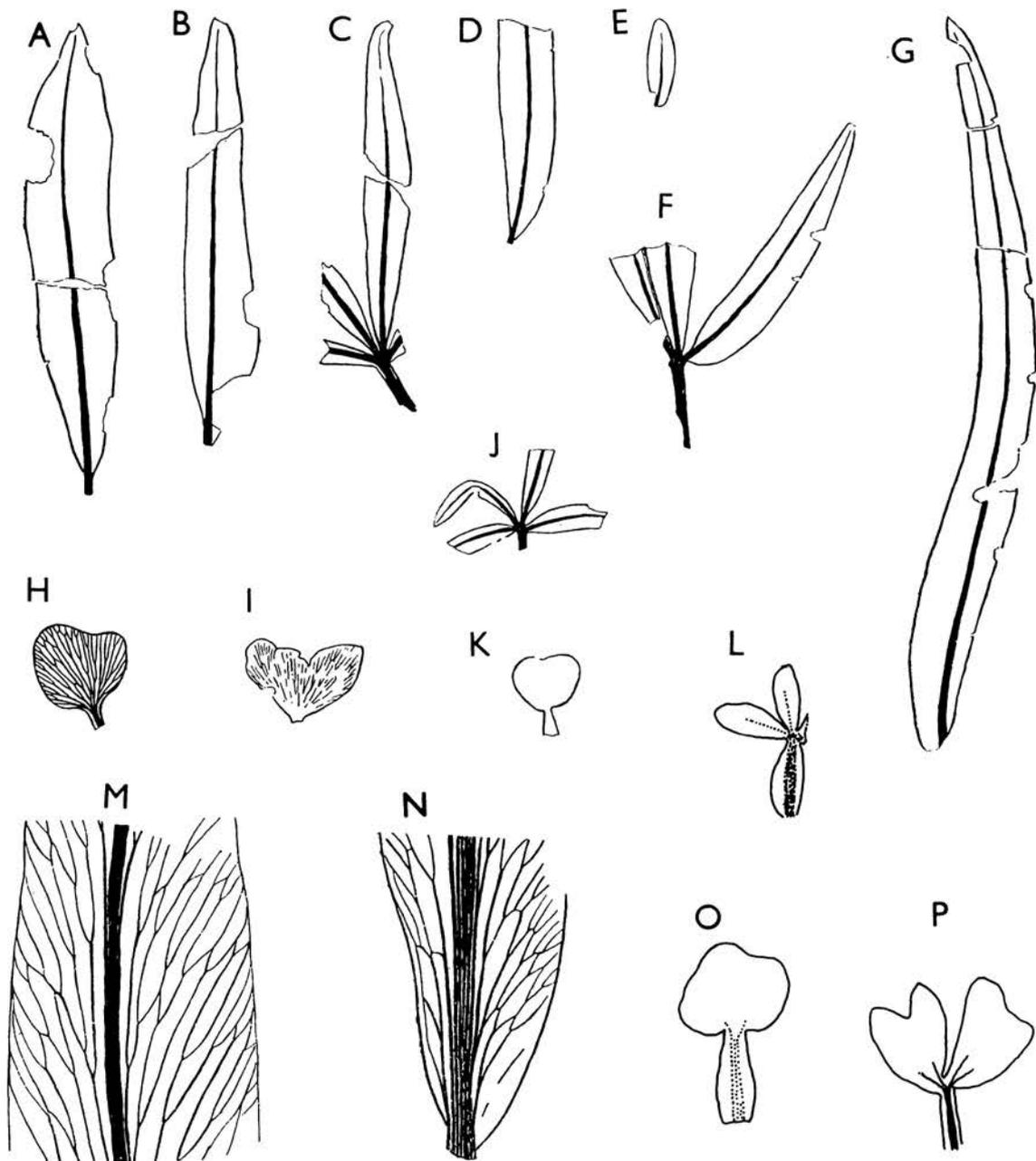


Fig. 4. *Sagenopteris phillipsi* (Brongniart)

A-G, portions of foliage leaves, all  $\times 1$ ; M is part of B,  $\times 4$ ; N is part of A,  $\times 4$ . H-L, O, P, organs transitional to scale leaves, all  $\times 1$ , except L and O which are  $\times 2$ . A, N, V.26429. B, M, V.23935. C, V.24716. D, V.24673. E, F, V.26427. G, V.24677. H, V.25853. I, V.21401. J, V.24676. K, V.26460. L, V.28489. O, V.31870. P, V.28489.

All the specimens are from the Gristhorpe Bed and all the figures except L, O, P are from Harris (1940).

DISCUSSION. Almost our whole knowledge of *S. phillipsi* is based on specimens from the Gristhorpe Bed where it is locally common. Among the normal leaves there is a series of small leaves with a short petiole and a lamina imperfectly divided into four, or even with a single broad lobe: these have been called *S. cuneata* but their cuticles are just the same as in normal leaves and I consider they are merely the leaves produced in a particular region of the

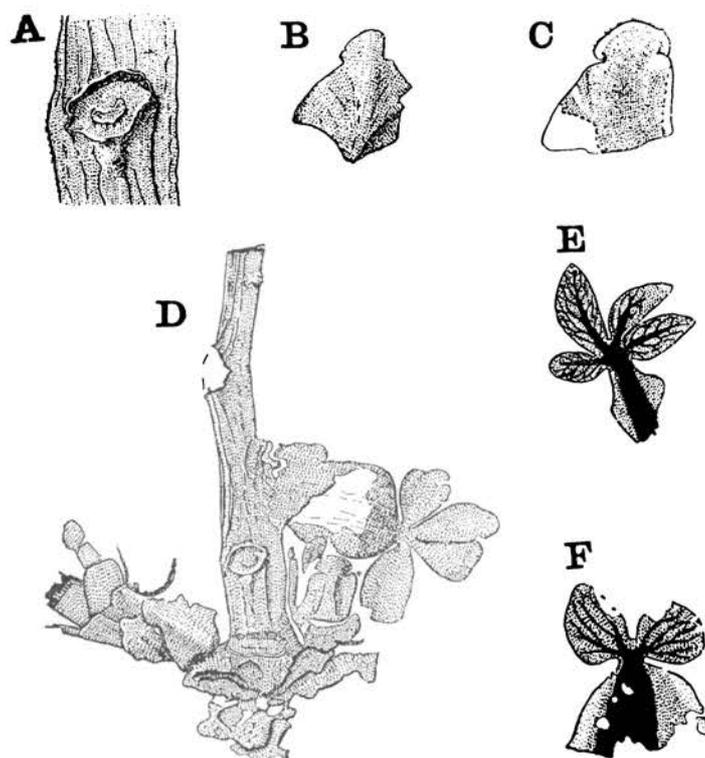


Fig. 5. *Sagenopteris phillipsi* (Brongniart). Stem, small leaf and bud-scale

A, leaf scar of stem shown in D, V.26427,  $\times 8$ . B, bud-scale (shown to left of D under different lighting), V.26427,  $\times 8$ . C, bud-scale (shown to right of D), stippled part detached and viewed by transmitted light, V.26427b,  $\times 8$ . D, shoot with small leaf and bud-scales, drawn immersed in paraffin, V.26427,  $\times 4$ . E, small leaf (by transmitted light, transfer preparation), V.25872,  $\times 4$ . F, small leaf, transfer, by transmitted light, V.25878,  $\times 4$ .

All the figures are from Harris (1940).

stem. There is also a series of leaves ranging from broad bud-scales to narrower bud-scales with four tiny leaflets, again their cuticles are normal but trichomes may be abundant along the margins.

The twig shown in Text-fig. 5 shows a series of rather varied bud-scales at the beginning of a year's growth. There is an organ transitional between a bud-scale and a foliage leaf lying over the stem and possibly only slightly displaced and there is a scar of a foliage leaf above. This is still all we know about the stem in the Caytoniales.

COMPARISON. It is likely enough that all species of *Sagenopteris* show a series of organs

ranging from bud-scales to foliage leaves, but it is only the fairly well formed foliage leaves that are compared below. The small leaves can only be determined in relation to the associated normal ones. Even normal leaves are very varied and their cuticles seem more constant than their gross form.

#### Leaflet dimensions

Small	<i>S. colpodes</i> aggregate 2.5 cm. × 1.0 cm.	<i>S. phillipsi</i> 3.0 cm. × 0.5 cm.
Medium	10.0 cm. × 2.0 cm.	5.0 cm. × 0.8 cm.
Large	over 20 cm. × 4.0 cm.	12.0 cm. × 1.3 cm.
Vein meshes in large leaflet	0.75 mm. wide	0.5 mm. wide
Cuticle	Thin. Cell outlines sinuous or with jagged extensions or broken. Trichome bases frequent below.	Moderately thick. Cell out- lines straight, uninterrupted.  Trichome bases rare below.

As indicated above, *S. colpodes* is the aggregate of two similar species.

#### Other species with known cuticles

*S. nilssoniana* (= *S. rhoifolia*) basal Liassic; cuticle like *S. phillipsi* but trichomes known to be long; leaflets usually much broader (see Halle 1910 in part, Harris 1932, Carpentier 1947, Menéndez 1956).

*S. hallei* (basal Liassic); epidermal cells with a papilla, otherwise like *S. phillipsi* (see Harris 1932a, Daber 1962).

*S. undulata* Halle; pinnule margins often wavy; cuticle like *S. nilssoniana* (see Halle 1910, Lundblad 1950).

Comparison with *Sagenopteris* leaves from other floras described without cuticles is of little value but lists of fairly similar specimens are given above.

No doubt Phillips' (1829) sketch, bad as it is, figures this species. Its name was given as *Pecopteris longifolia* in the explanation of the plate, but elsewhere listed as *P. paucifolia*. He sent a different drawing to Brongniart who published it the following year as *Glossopteris phillipsi*, and cited both of Phillips' specific names as synonyms but did not say why he changed the name. Later Phillips (1875) included *P. paucifolia* as a synonym and dropped all mention of *P. longifolia*. The name *paucifolia* was revived by Ward (1905) and used by Halle (1913) and by Oishi (1940), but others have used *phillipsi*. The specific name *longifolia* seems to me to have only a weak claim to validity and the name *paucifolia* an even weaker one. The customary name *phillipsi* is here regarded as valid.

The fruit *Caytonia nathorsti* and the microsporophyll *Caytonanthus arberi* are attributed to the same plant as *Sagenopteris phillipsi* (in the strict sense).

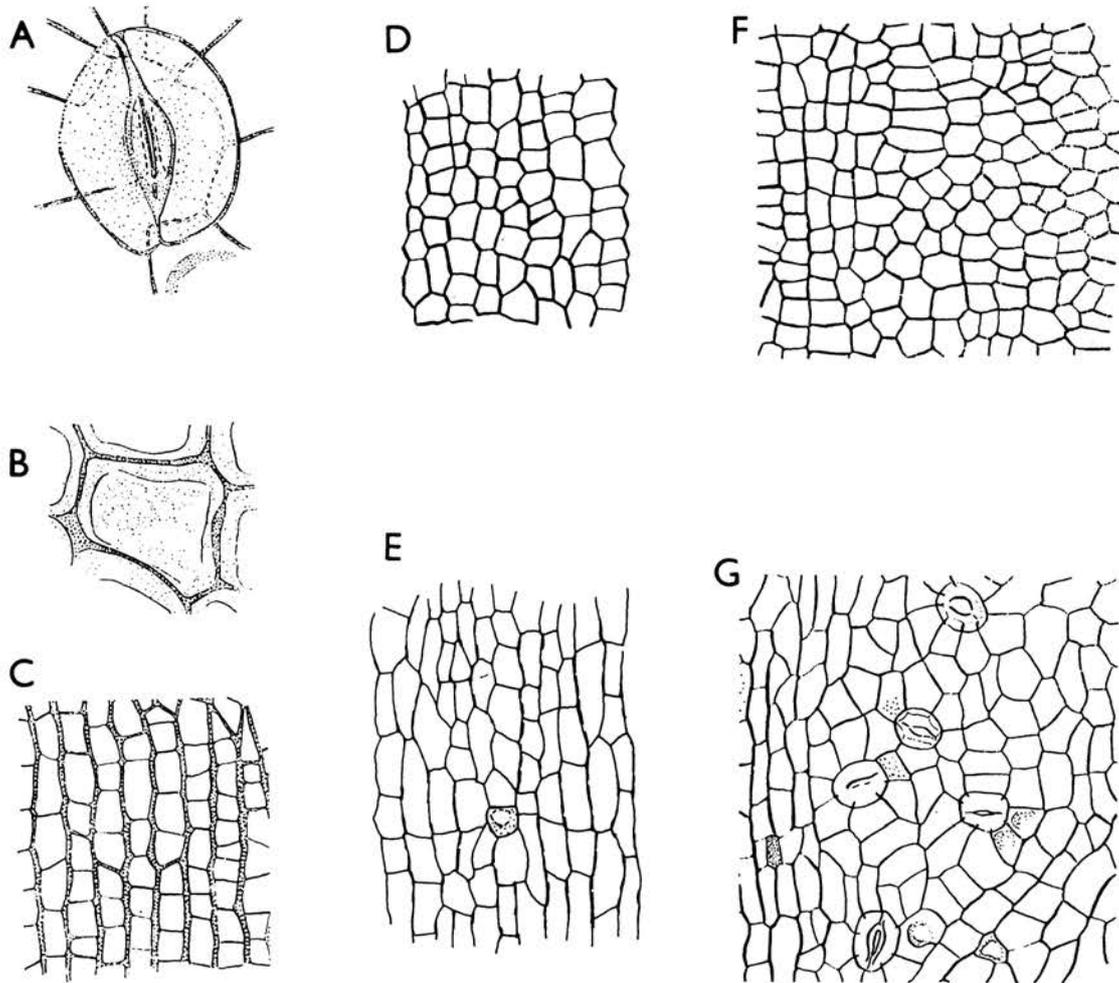


Fig. 6. *Sagenopteris phillipsi* (Brongniart). Cuticle of foliage leaf

A, stoma from lamina, V.26430,  $\times 800$ . B, cell of upper epidermis, V.26430,  $\times 800$ . C, petiole, adaxial side, V.26427a (from the specimen shown in Fig. 4 F),  $\times 200$ . D, petiole, abaxial side, V.26427a,  $\times 200$ . E, petiole, abaxial side with a trichome base, V.34670a,  $\times 200$ . F, upper epidermis of lamina, V.26430,  $\times 200$ . G, lower epidermis of lamina, V.26430,  $\times 200$ .

All the specimens are from the Gristhorpe Bed and all the figures except E are from Harris (1940).

### Genus CAYTONANTHUS Harris 1937: 40

**DIAGNOSIS** (slightly emended). Microsporophyll; main rachis branching in the horizontal plane, branches in more or less opposite pairs but often unequal, branches simple, forked or bearing opposite branches; each ultimate branchlet bearing a single superficial synangium almost terminally. Surfaces of main rachis and its branches dorsiventrally differentiated. Synangia elongated, radially symmetrical, usually composed of 4 (less often 3 or 5) pollen sacs; walls of pollen sacs rigid, separating from one another longitudinally along the axis of the synangium and dehiscent inwards but remaining attached apically and basally. Walls showing a single layer of elongated thick-walled cells without transverse ribs. Microsporophyll and synangia cutinised. Pollen forming a single mass in each loculus, grains disaccate, monolept.

Width of total grain ca.  $20\mu$ , height of sacchi about  $\frac{1}{2}$  width of total grain. Corpus deeper and higher than wide. Roots of sacchi offset distally and free parts pointing distally. Sacchi as deep as corpus, normally inflated. Cappa scarcely thickened, without special ornament. Ornament on sacchi usually plain, on corpus faint or absent.

TYPE SPECIES. *Antholithus arberi* Thomas (1925 : 327).

DISCUSSION. Potonié & Kremp (1956 : 176) recommend that isolated *Caytonanthus*-like grains should be placed in *Alisporites* Daugherty, but Nilsson (1958) prefers *Vitreisporites* Leschik. Townrow (1962a : 38) gives other possible synonyms.

We owe our knowledge of *Caytonanthus* to Thomas (1925) with some later additions (Harris 1937, 1941, 1951; Townrow 1962a). Most of our knowledge is summarised in the diagnosis given above and a few additional points are mentioned below.

The pollen tetrad cannot be seen in the unripe anther but was obtained from some coprolites composed almost entirely of *Caytonanthus* eaten at various stages of maturity. These prove that the furrow is external and disposes of any suggestion that it might have been pointed inwards as in 'pre-pollen'.

The fairly well developed synangial and rachis cuticles, almost as thick as in the leaf, suggest that *Caytonanthus* was a long lived organ. An unexplained fact is that many specimens with ripe synangia have failed to shed their pollen.

Abnormalities noted are the rare occurrence of synangia with 3 or with 5 loculi and the rare occurrence of pollen grains (in the coprolites) with three sacs.

The fragment shown in Text-fig. 7 A, B, gave new information when transferred. The rachis is smooth on the exposed side but shows a single broad ridge on the concealed side (? the adaxial side). It looks as though the lateral branches subdivided in a plane almost at right angles to the one in which the main rachis branches. It may be significant that all the synangia point towards the microsporophyll base. Two scars of detached synangia each show a single minute boss, presumably the vascular strand.

*Caytonanthus* is more like the microsporophyll of various Pteridosperms than any Angiosperm stamen. Its synangia are essentially radial and unlike anthers which have bilateral symmetry. In its pollen it agrees with certain Pteridosperms and fossils of doubtful affinity but differs from all Angiosperms.

The generic name *Caytonanthus* and the specific name *arberi* of the type species are both antedated but for reasons given below I do not accept the earlier binomial *Ginkgoanthus phillipsi* Johnson (1920) as valid. No doubt the Yorkshire specimens crudely figured by Phillips (1829) as 'unknown leaves' represent a *Caytonanthus* though whether the original is the specimen in the Yorkshire Museum or in the Leckenby Collection at Cambridge I cannot say (both claim identity on their labels). Johnson described and figured a Yorkshire Museum specimen which had been previously figured by Seward as '*Ginkgo digitata* flowers' under the name *Ginkgoanthus phillipsi*. I have examined it carefully but I can find no reason to identify it with *Caytonanthus arberi* rather than the species *C. oncodes*. It has lost all the substance of the rachis and the anthers are quite empty of pollen. The isolated fern spore which Johnson figured is unhelpful, I therefore reject the specific name *phillipsi*. The generic name *Ginkgoanthus* I reject because Nathorst had given this to an obscure Spitzbergen fossil which there is no reason to identify with *Caytonanthus*. This rejection is in accordance with article PB 6 of the International rules of nomenclature.

The species of *Caytonanthus* are known unequally and are not fully comparable.

*C. kochi* Harris from the Greenland Lower Lias, has only its ultimate branchlets and synangia known. Its pollen grains are at least as large as those of *C. oncodes* but less clearly pitted.

*C. oncodes* Harris (Yorkshire Middle Jurassic). Main rachis imperfectly known, has fairly large pollen grains (wings averaging  $16.8\mu$  wide) and clearly pitted. Its synangia are perhaps shorter and borne on more divided laterals than in *C. arberi*, but this is not certain as too few specimens have been studied.

*C. arberi* (Thomas) (Yorkshire Middle Jurassic). The most fully known species has smaller pollen grains (wings averaging  $13.5\mu$  wide) and inconspicuously pitted. These averages are only useful in comparing considerable numbers of grains, each group from a single source as there is overlap in the size range of each species. Some imperfectly known Yorkshire specimens mentioned below as *Caytonanthus* sp. A have pollen of intermediate size (wings about  $14.5\mu$  wide) and obviously pitted.

### *Caytonanthus arberi* (Thomas) Harris

Pl. 1, figs. 11, 12, 16–19; Pl. 2, figs. 2, 3; Text-figs. 7 A, B, D, E; 8 C–F, I

- 1925 *Antholithus arberi* Thomas, p. 327, pl. 14, fig. 33, probably also figs. 34, 35, 38, 40, 42. (Sporophyll, synangia, cuticles, restoration, discussion.)  
 1931 *Antholithus arberi* Thomas: Thomas, p. 651. (Discussion.)  
 ?1937 '*Caytonanthus* sp. A', Harris, p. 44, text-fig. 4 A, 6. (Isolated Yorkshire pollen grains.)  
 1941 *Caytonanthus arberi* (Thomas) Harris, p. 51, pl. 2, figs. 2–4; text-figs. 1, 2, 4, 5, 7, 8. (Sporophyll, synangia, pollen, separation from *C. oncodes*; attribution to *Caytonia nathorsti*; 'Thomas' pl. 14, fig. 33 designated as holotype.)  
 1946 'Coprolite of *Caytonia* pollen', Harris, p. 373, text-fig. 6. (Coprolites composed largely of this species.)  
 1951 *Caytonanthus arberi* (Thomas): Harris, p. 31, text-fig. 2. (New restoration, spore tetrads from coprolite, discussion.)  
 1956 Coprolite, Harris, p. 10, pl. 4. (Two groups of coprolites full of *C. arberi*.)

The following references may be to this species or to *C. oncodes*:

- 1829 'Unknown leaves', Phillips, pl. 7, fig. 23. (Crude sketch of synangia.)  
 1875 'Unknown leaves', Phillips, pl. 7, fig. 23. (As 1829.)  
 1880 Catkins of *Ginkgo*, Nathorst, p. 75.  
 1900 '*Ginkgo digitata* (flowers)', Seward, p. 259, text-fig. 45. (Drawing of synangia.)  
 1919 'Male flowers' (of *Ginkgoites*) or '*Antholithus* sp.', Seward, text-fig. 654 A (specimen in Leckenby Collection, Cambridge), text-fig. 645 B. (Phillips' specimen? Drawing of microsporophyll.)  
 1920 *Ginkgoanthus phillipsi* Johnson, p. 1, text-figs. 1–3, 6, 8. (Phillips' specimen? Name, microsporophyll, cuticle; adherent fern spore attributed to it.)  
 1925 *Antholithus arberi* Thomas (in part): Thomas, text-figs. 36, 37, 39. (Fragments of microsporophyll.)  
 ?1937 *Caytonanthus arberi* (Thomas): Harris, p. 41, text-fig. 4 E–G. (Isolated pollen, but more like *C. oncodes*.)  
 1958 *Caytonanthus arberi* (Thomas): Couper, p. 119, pl. 26, figs. 1–6. (Pollen, similar to that of *Caytonisporites pallidus* (Reisinger) Couper, p. 150, pl. 26, figs. 7, 8.)  
 1962a *Caytonanthus arberi* (Thomas): Townrow, p. 21, pl. 2, A, D; text-figs. 3 D, E. (Pollen.)

EMENDED DIAGNOSIS. Microsporophyll rachis bearing short lateral branches, lateral branches lobed but scarcely subdivided, synangia typically about  $3 \times 1$  mm.; pollen grains typically  $22\mu$  from wing to wing (extremes  $18$ – $28\mu$ ), central cell about  $15\mu$  long; wings seldom bulging but often slightly constricted; mean width of wing  $13.5\mu$  (extremes  $9$ – $18\mu$ ), surface of wings pitted, but pitting not very conspicuous.

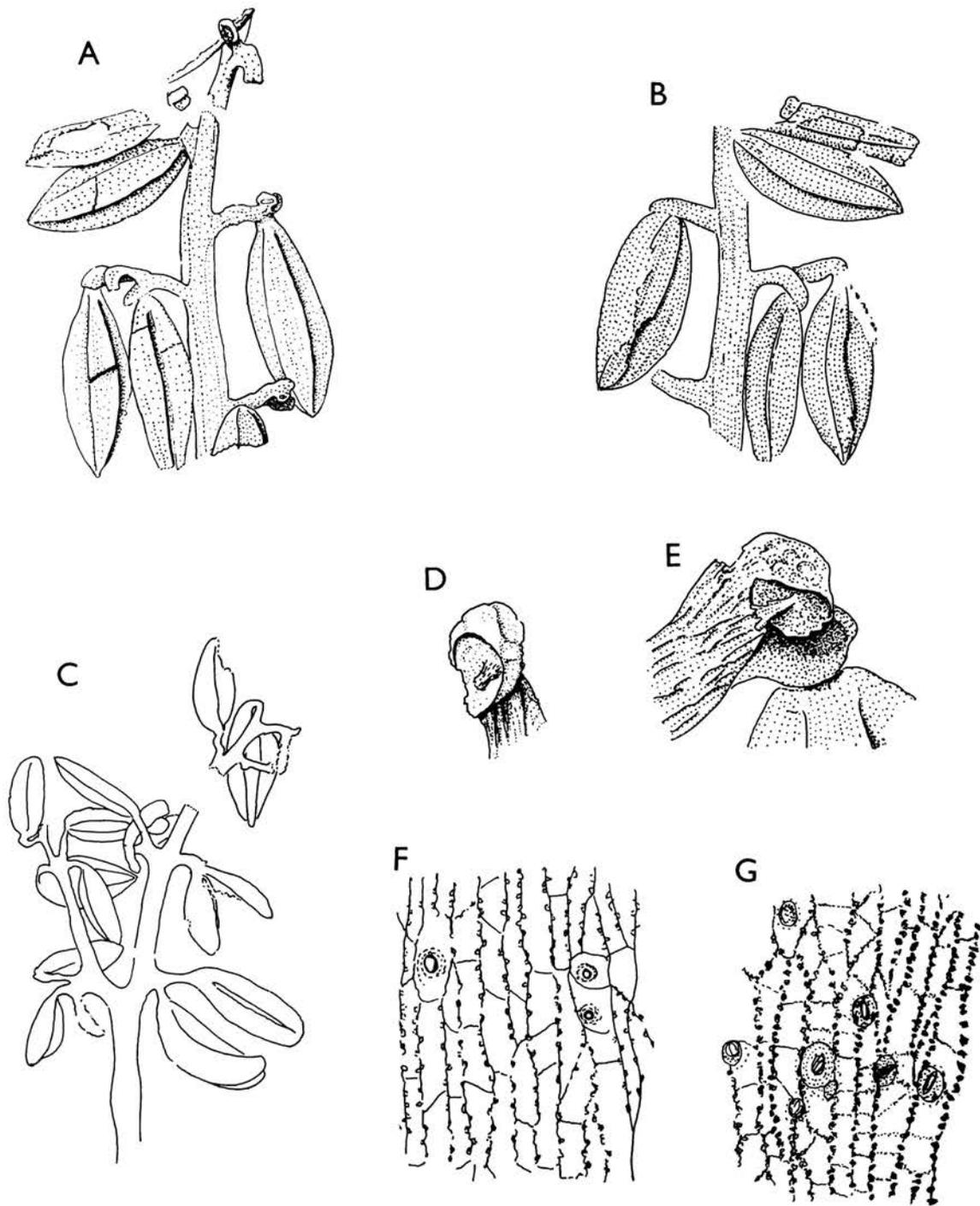


Fig. 7. *Caytonanthus arberi* (Thomas), *C. oncodes* Harris

A, *C. arberi*, transfer of specimen shown in B, V.45567,  $\times 6$ . B, specimen as originally exposed,  $\times 6$ . C, *C. oncodes*, outline drawing of the holotype (see also Harris 1941, text-figs. 5-8, 11 for photographs), V.25897,  $\times 4$ . D, E, bases of detached synangia, seen also in A,  $\times 30$ . F, G, cf. *C. oncodes*, thinner and thicker side of isolated rachis fragment, V.45566,  $\times 200$ .

All the specimens are from the Gristhorpe Bed.

LECTOTYPE. V.18592, figured by Thomas (1925, pl. 14, fig. 33). See Harris (1941 : 51).

DISCUSSION. Both a specimen in the Leckenby collection at Cambridge figured by Seward (1900) and one at York figured by Johnson (1920) have been claimed as the original of Phillips' 'unknown leaves'—a figure so crude as to be indecisive. Both specimens were examined by Nathorst who concluded that they were male flowers of a *Ginkgo* species and this was endorsed by Seward and then by Johnson who gave the name '*Ginkgoanthus Phillipsi*' for the York specimen.

It is compared with the other species under the description of the genus *Caytonanthus*. *C. arberi* is known only from the Middle Deltaic Gristhorpe Bed.

### *Caytonanthus oncodes* Harris

Text-figs. 7 C, F, G; 8 G, H

1941 *Caytonanthus oncodes* Harris, p. 52, pl. 2, figs. 5–11; text-figs. 3, 6. (Microsporophyll, synangia, pollen—see also citations of specimens which could also belong to *C. arberi*.)

1958 *Caytonanthus oncodes* Harris: Couper, p. 119. (Measurements of pollen.)

1962a *Caytonanthus oncodes* Harris: Townrow, p. 22, pl. 2 G; text-figs. 3 B, F, G, K; 8 A. (Pollen.)

DIAGNOSIS. Microsporophyll rachis bearing fairly long lateral branches which subdivide once or twice into finger-like branchlets. Synangia typically broad, about  $2.5 \times 1.5$  mm. Pollen grains typically  $31\mu$  from wing to wing (extremes  $25$ – $35\mu$ ), central cell about  $17\mu$  from end to end, wings bulging slightly, seldom contracted, mean width  $16.5\mu$  (extremes  $10$ – $22\mu$ ). Surface of wings clearly and rather regularly pitted.

HOLOTYPE. V.25897, figured by Harris (1941, pl. 2, figs. 5, 8, 11).

*Cuticle of rachis.* A piece of cuticle which branches in the manner of *Caytonanthus* was isolated from the Gristhorpe Bed by maceration in bulk. It was determined, with some doubt, as the rachis of *Caytonanthus oncodes*, and its cells are illustrated here. The cuticle is of moderate thickness and like the petiole of *S. colpodes* in its cells. One side is distinctly thicker and the epidermal cells have more obvious jagged thickenings on their longitudinal walls. Trichome bases are numerous on both sides, but slightly commoner on the thicker. The free part of the trichome is seen along the margins where it forms a cutinised sac  $20$ – $30\mu$  long.

This cuticle agrees closely with that of *C. arberi* except that the cell walls are jagged and trichomes are numerous.

*C. oncodes* is known only from the Middle Deltaic Gristhorpe Bed, where it is rare. For literature see *C. arberi* above; for comparison, see *Caytonanthus* above.

### *Caytonanthus* sp. A

Text-fig. 8 A, B

Some shale from Boulby Alum Quarry which was full of *Sagenopteris colpodes* and *Brachyphyllum mamillare* but apparently nothing else, when macerated in bulk yielded numerous scale leaves of *Sagenopteris* and a few broken *Caytonanthus* synangia with unripe pollen. Some of the scale leaves were thickly covered with pollen grains of the *Caytonanthus* type, but no other grains, so these grains were studied on the assumption that they belong to the same plant as the associated leaves and synangia. The grains proved to be of intermediate character between *C. oncodes* and *C. arberi*. The wings are obscurely pitted and the mean length from wing to wing is  $25.5\mu$  ( $\sigma$   $2.5\mu$ ) and the width of the wing (measured at its middle) was  $14.5\mu$ .

A piece of shale from Roseberry Topping showing abundant leaves of the large form of *Sagenopteris colpodes* when macerated yielded fruits and seeds of *Caytonia kendalli* and also a synangium agreeing with *Caytonanthus* sp. A. Although it is not yet possible to characterise *Caytonanthus* sp. A the evidence of association suggests that it belongs to the same plant as *C. kendalli* and the large form of *S. colpodes*.

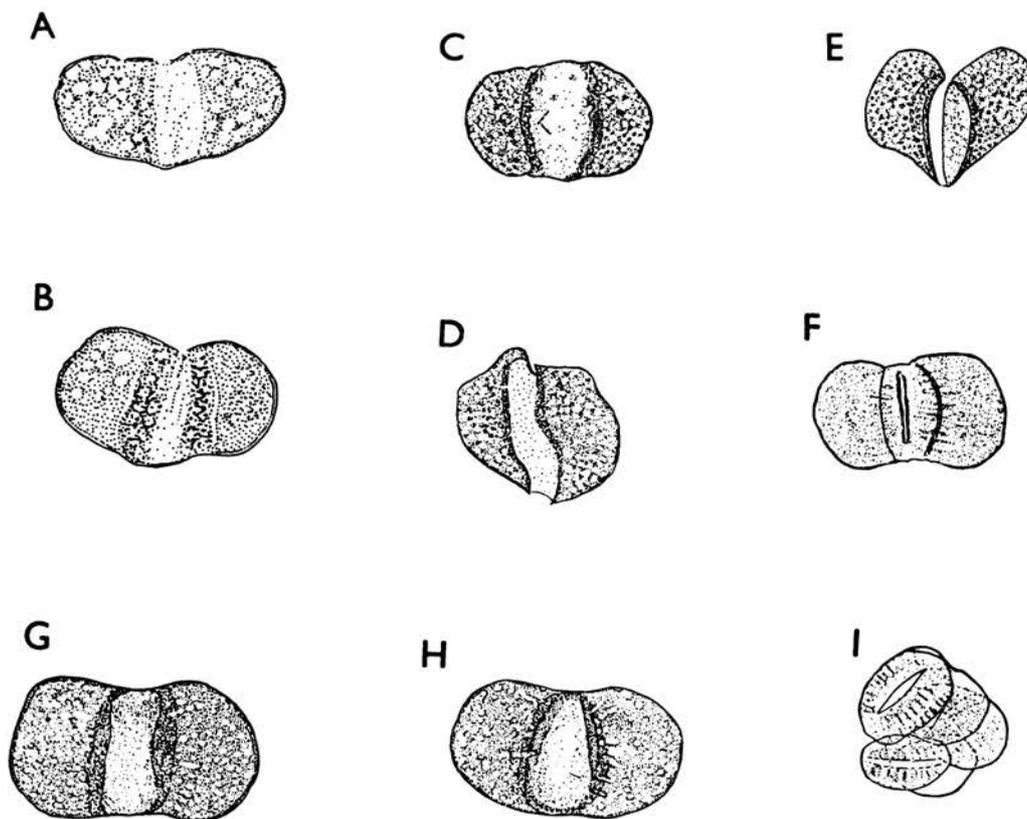


Fig. 8. *Caytonanthus*. Pollen. All  $\times 1000$

A, B, *Caytonanthus* sp. A. A, from pollen sac, V.45569, Roseberry Topping. B, one of many grains sticking to a small leaf of *Sagenopteris colpodes*, V.45570, Boulby Alum Quarry. C-F, I, *C. arberi*. C, from a pollen sac, V.25903k. D, from the micropyle of *C. nathorsti*, V.26724. E, from the micropyle of *C. nathorsti*, V.26722. F, from a coprolite full of *Caytonanthus*, V.29469. G, H, *C. oncodes*. G, from a pollen sac, V.18595f. H, from micropyle of *C. seawardi* seed, V.26654. I, *C. arberi*, immature tetrad from same coprolite as F.

All the specimens of *C. arberi* and *C. oncodes* are from the Gristhorpe Bed. C-E, G, H are from Harris (1941). F, I are from Harris (1951) by permission of the publishers of *Phytomorphology*.

### Genus CAYTONIA Thomas

- 1912 '*Caytonia*' Thomas, p. 469 (*nomen nudum*.)  
 1920 *Lacniella* Krasser, p. 14. (Diagnosis, no figure, regarded below as a *nomen nudum*.)  
 1922 '*Caytonia*' Thomas, p. 452 (*nomen nudum*.)  
 1922 '*Gristhorpia*' Thomas, p. 452 (*nomen nudum*.)  
 1925 *Gristhorpia* Thomas, p. 304.  
 1925 *Caytonia* Thomas, p. 314. (Diagnosis, description, figures and discussion.)  
 1940a *Caytonia* Thomas: Harris, p. 714. (Emended diagnosis; *Gristhorpia* included.)

EMENDED DIAGNOSIS. Megasporophyll, main rachis bearing seed-containing sacs ('fruits') laterally in nearly opposite pairs. Epidermis of rachis cutinised, dorsiventrally differentiated. Mature fruits cut off from rachis by an absciss layer. 'Fruits' shortly stalked, globose, fleshy; mouth strongly contracted and curved back against the stalk, closed at maturity. Seeds numerous, small, flattened, orthotropous, borne in a curved row with their micropyles facing the mouth of the fruit. Micropyle sunken. Integument single, free to base; external cuticle delicate, continuing as micropylar canal. Inner cuticle of integument very delicate, showing broad cells; nucellus strongly cutinised, chalaza minute, apex of nucellus with a small, open beak. Cells of nucellus elongated except at the ends of the seed. Megaspore membrane not cutinised. Pollen grains normally occurring in the beak of nucellus.

TYPE SPECIES. *Caytonia seawardi* Thomas (1925).

*Morphology.* The present account is largely a summary of the accounts of Thomas (1925, 1934) and Harris (1940a, 1941, 1959). The main change since 1925 has been the realisation that pollination was essentially gymnospermous and there have been additions to our knowledge of the seeds.

Thomas (1925) showed that the fruit-bearing organ of *Caytonia* is like the rachis of a pinnate leaf rather than a stem with a raceme of fruits in that it bears organs laterally and in having a dorsiventrally differentiated epidermis. He concluded that it was a sporophyll. This idea is now supported by some additional evidence. In both *C. seawardi* and *C. nathorsti* the fruits are attached slightly above the lateral plane as are the pinnae on rachises of most plants, and in *C. nathorsti* there are strong subepidermal fibrous ridges which run exactly as would be expected in a rachis. In *C. seawardi* there is a specimen which as a result of natural clearing, perhaps through slight oxidation, shows something of its vascular anatomy. The rachis has a single broad, dark strand along its centre and minute bundles pass from the edges of this main strand to the abscissed bases of the fruit stalks, one to each. This resembles the petiole of *Sagenopteris* where there is also a single dark strand which gives off one bundle to each segment, and in the petiole we know that the bundle is C-shaped where it joins the stem.

Some of Thomas' descriptive terms have been changed in the light of further knowledge. His 'central stalk' or 'axis' is called the megasporophyll rachis; his 'carpel' is called the 'fruit', this term 'fruit' being used here in a functional rather than in a morphological sense and his 'stigma' is called the lip of the mouth of the fruit.

The fruits were indeed fleshy and were edible, like berries, for there are little coprolites containing their chewed-up remains (see p. 27). The flesh of the fruit, in addition to a soft pulp of which we know little, contained a large number of solid oval cells about  $100\mu$  wide; they are most conspicuous in *C. seawardi*, but are seen in *C. kendalli* and occasionally in *C. nathorsti*. They appear like the hard cells of which there are many kinds among wild berries. It is interesting that many fruits have burst, ejecting some of their contents in the same way as do ripe gooseberries in water (Thomas 1925, pl. 11, fig. 8).

In each of the Yorkshire species we know of small fruits, usually without any seeds, or with half formed ones. These fruits have been called young, but it is more accurate to call them abortive. Their epidermis is thickly cutinised and it would be impossible for them to expand to full size without there being obvious signs of this growth in the epidermis. No such growth has occurred in large fruits, for the cells are of even size and of uniform arrangement and must have formed and grown while the epidermis was still soft. These abortive fruits seem to have

been arrested at different stages of growth and the series suggests some of the stages of fruit ontogeny. The stalk, mouth and lip are normal but the pouch is small and it is easy to trace cell rows from the stalk over the pouch on to the lip. The form suggests an incurved tip of a flattened organ in which the upper epidermis is enclosed. (See diagram, Text-fig. 10, 1.)

I have argued (Harris 1940a) that by the time of pollination the fruit and seeds had nearly attained their mature form except that there were open canals leading separately from under the lip to the micropyle of each seed. After pollination the inner parts of these canals were obliterated by tissue growth (the micropyles also closed) but the openings of the canals remain as a row of chinks under the lip.

In *C. kendalli* a delicate internal cuticle of the fruit has now been recognised. While not informative, its occurrence here suggests that in some species not yet studied it may be robust enough to show the internal organisation of the fruit. Although the different species agree in all fundamentals each shows some feature particularly favourable for study.

Much still remains to be learnt about *Caytonia*, particularly about how the megasporophylls were grouped on the stem and their position in relation to leaves. Knowledge of the vascular anatomy of the fruit would be most welcome.

The genus *Gristhorpia* was merged into *Caytonia* (Harris 1940a). All additional information supports this, and as will be seen from the table of comparison, the species form a very uniform group with small distinguishing characters, and almost every character of a particular species, taken separately, is found in at least one other. The species are indeed so similar that the less favourably preserved specimens are scarcely to be distinguished.

*Caytonia* dates from 1925, when Thomas published the name with a diagnosis and figures. He published *Gristhorpia* at the same time. Now that these two are united I have retained the name *Caytonia* in accordance with Thomas' implied preference. Thomas mentioned *Caytonia* in 1912 but *Gristhorpia* first in 1922. He did publish some early descriptive notes, but without figures or diagnoses and until 1925 both names remained *nomina nuda*. In 1920 Krasser published his *Laconiella* and gave a diagnosis but no figure; hence this was not valid publication, since the rule requires a figure. In fact, no one recognised that he had dealt with the same fossil as Thomas until Edwards (1929) examined his labelled specimen and published Krasser's previously unused photograph (the specimen having deteriorated). *Laconiella* is strictly a *nomen nudum*.

### *Caytonia seawardi* Thomas

Pl. 1, figs. 2, 3, 8, 9; Pl. 2, figs. 1, 4; Text-fig. 9

- 1925 *Caytonia seawardi* Thomas, p. 315, pl. 12, figs. 14-24; pl. 13, figs. 25-32; pl. 15, fig. 48; Text-figs. 5-9. (Details of fruit and seed.)
- 1933 *Caytonia seawardi* Thomas: Harris, p. 111. (Comparison with *C. thomasi*.)
- 1934 *Caytonia seawardi* Thomas: Thomas, p. 193, text-fig. 15. (Lip structure, angiospermy reaffirmed.)
- 1940a *Caytonia seawardi* Thomas: Harris, p. 714, pl. 7, figs. 1, 2, 4, 6, 9-11. (Emended diagnosis, fruit and seed details.)
- 1958 *Caytonia seawardi* Thomas: Harris, p. 93, pl. 1; pl. 2, figs. 7, 8, 10; text-figs. 1, 4, 8. (Seed.)

EMENDED DIAGNOSIS. Rachis without prominent longitudinal ribs, cuticle showing cells with jagged thickenings on their lateral walls, trichomes numerous but small, simple and sac-like or composed of a chain of up to three short cutinised cells, not glandular. Fruit

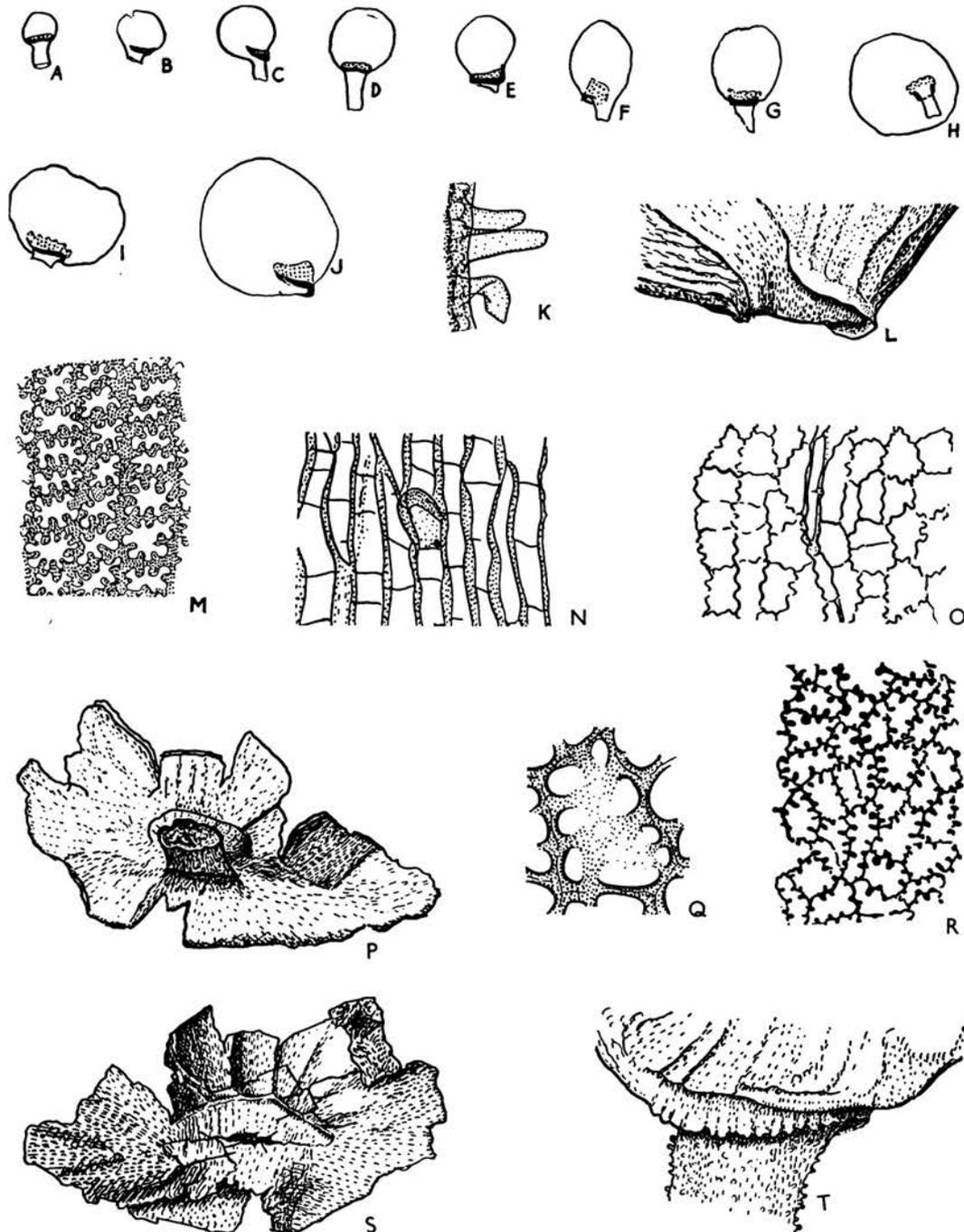


Fig. 9. *Caytonia sewardi* Thomas

A-G is a series of small, abortive fruits without seeds. H-J are normal fruits. The projecting lip is shown in black, the cuticle of the mouth is stippled. All  $\times 5$ . K, trichomes on fruit stalk, V.26640,  $\times 250$ . L, details (lit from above) of fruit shown in J,  $\times 20$ . M, cuticle of fruit wall (heavily thickened form), V.26650,  $\times 250$ . N, upper cuticle of fruit stalk; O, lower cuticle of fruit stalk, both V.26648,  $\times 250$ . P, S, fragments of fruit wall; P, from the outside showing the lip and stalk; S, from the inside, both V.26647,  $\times 20$ . Q, cell of fruit wall, V.26649,  $\times 800$ . R, thin form of cuticle of fruit wall, V.26649,  $\times 250$ . T, details (lit from above) of fruit shown in G,  $\times 40$ .

A-J are V.26637-46 respectively. All the specimens are from the Gristhorpe Bed and all the figures are from Harris (1940a) by permission of the publishers of *Annals of Botany*.

rounded, up to 4.0 mm. wide; pedicel narrow, mouth of fruit barely 1 mm. wide and curved round the pedicel and appearing less than 1 mm. wide. Cuticle of fruit thick, cells with sinuous walls or with broad walls with strong, jagged thickenings; up to eight seeds maturing; lip of fruit showing about eight transverse dark bars. Flesh of fruit showing numerous large stone cells. Seed ovate, typically 1.5 × 1.0 mm., substance often 0.2 mm. thick in compressed state and seed estimated to have been originally 0.6 mm. thick. Surface cells nearly isodiametric, sunken, forming honeycomb-like pits. Stone of integument (testa) with one outer layer of isodiametric stone cells and several layers of elongated fibre-like stone cells; interior of cells often filled with resistant matter. Micropylar canal with isodiametric and bulging cells at its mouth but no extensive tracts of specialised bulging cells occurring at edges of seed. Deep membrane of integument ('spotted layer'), if preserved, showing large solid blocks of resistant matter.

LECTOTYPE. V.18589, specimen figured by Thomas (1925, pl. 12, figs. 14, 15).

OCCURRENCE. The fruit of *C. seawardi* has been found only in the Gristhorpe Bed, where it is local. Seeds agreeing with *C. seawardi* also occur in this bed and in many of the Middle Deltaic coals in the moorland coal pits. They were only obtained by macerating the coal in bulk with nitric acid when the delicate cuticles of the integument and micropylar canal are lost and the nucellus, which remains, though robust is hard to distinguish from that of *C. nathorsti* and *C. kendalli*.

The following localities are merely those which gave seeds with a 'spotted layer' like that of *C. seawardi*, but even these are scarcely reliable determinations.

Middle Deltaic Gristhorpe Series.	12 localities
Middle Deltaic Sycarham Series . . . . .	1 locality
Lower Deltaic . . . . .	1 locality

There are specimens in the Manchester Museum (No. 215) called 'sporangia?' by Seward.

DISCUSSION. This species has been discussed at length by Thomas (1925) and by Harris (1940a, 1958) and only the diagnostic features are given here. For comparison see p. 27.

### *Caytonia nathorsti* (Thomas) Harris

Pl. 1, figs. 1, 4-7; Pl. 2, fig. 6; Text-fig. 10

- 1920 *Laconiella sardensis* Krasser, p. 16. (Diagnosis but no figure. Here regarded as *nomen nudum*. Jurassic, Sardinia.)
- 1925 *Gristhorpia nathorsti* Thomas, p. 305, pl. 11, figs. 1-13; pl. 14, figs. 41, 42; pl. 15, figs. 43-47; text-figs. 1-4. (Sporophyll, fruit, seeds, diagnosis, discussion.)
- 1929 *Gristhorpia nathorsti* Thomas: Edwards, p. 386, pl. 4, figs. 1, 2. (Krasser's specimen of *Laconiella* reinterpreted and his photos published. Middle Jurassic, Sardinia.)
- 1933 *Gristhorpia nathorsti* Thomas: Harris, p. 111. (Comparison with other species.)
- 1940a *Caytonia nathorsti* (Thomas): Harris, p. 718, pl. 7, figs. 3, 5, 7, 8; text-figs. 2 G-M, 3. (Structure of fruit and seed.)
- 1951 *Caytonia nathorsti* (Thomas): Harris, p. 34, text-figs. 3. (Restorations.)
- 1958 *Caytonia nathorsti* (Thomas): Harris, p. 93, pl. 2, figs. 6, 9; text-figs. 2, 3, 5-7. (Seed.)

EMENDED DIAGNOSIS. Rachis showing about five strong longitudinal ribs below and two separated by a broad median groove above. Cuticle showing rows of cells with thick, straight walls. Trichomes frequent along margins, consisting of a simple hair of up to three cells. Fruit rounded, up to 4 mm. wide; pedicel broad above; mouth of fruit typically 1.2 mm.

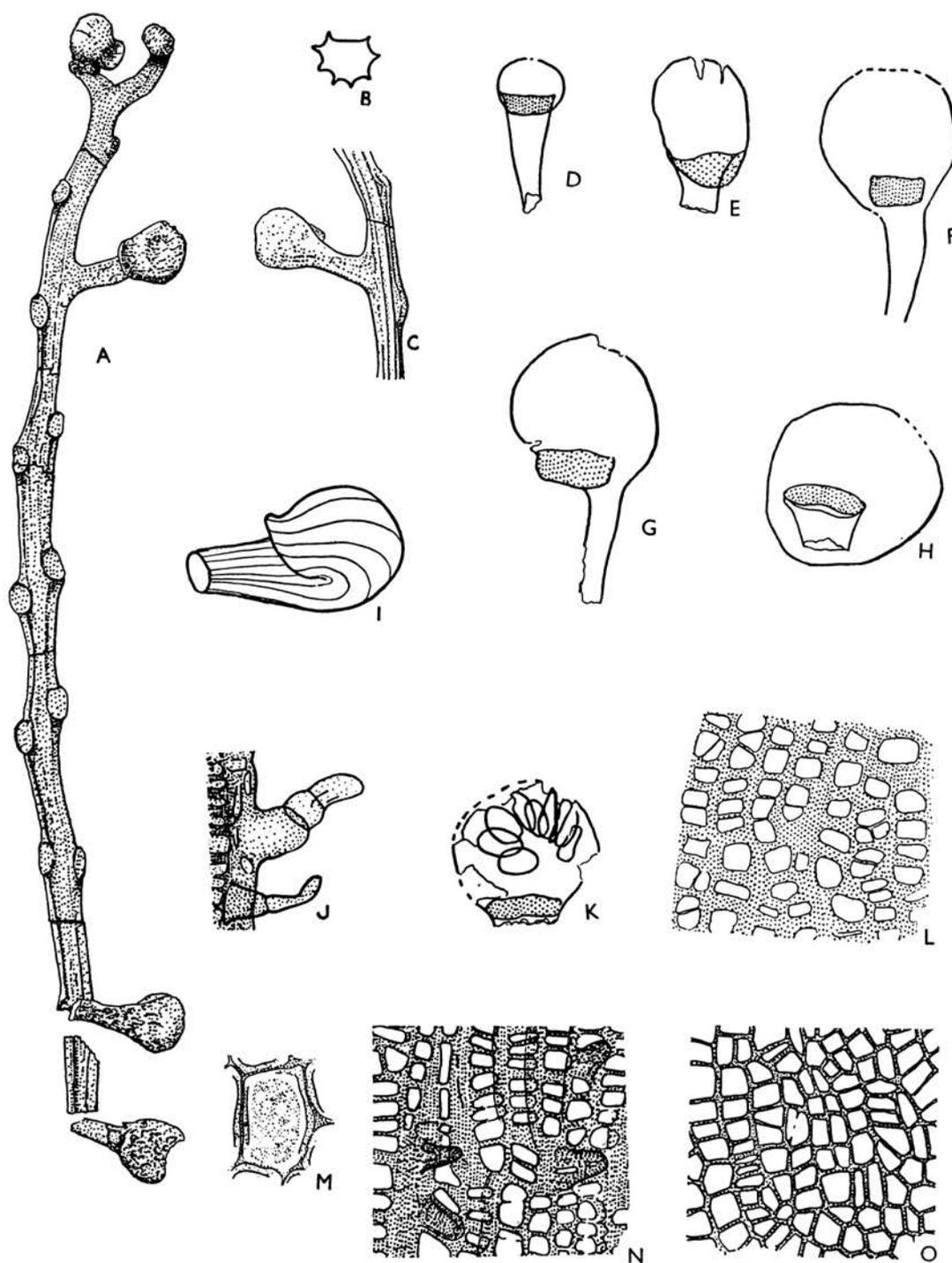


Fig. 10. *Caytonia nathorsti* (Thomas)

A, upper surface of megasporophyll (balsam transfer). B, restoration of section through A. C, part of A before being transferred, showing ridges on lower side. A, C, V.26661,  $\times 5$ . D, abortive fruit, V.26659,  $\times 5$ . E-H, fruits of various sizes, V.26662, V.26658, V.26667, V.26668, all  $\times 5$ . I, generalised diagram of small fruit indicating the direction of cell rows. J, hairs on fruit stalk, V.26659,  $\times 250$ . K, macerated fruit, nine seeds still in position, three others have been removed, V.26664,  $\times 5$ . L, fruit cuticle, V.26658,  $\times 250$ . M, details of a cell from a thin region (? lenticel) in fruit wall, V.26658,  $\times 800$ . N, O, upper and lower sides of fruit stalk, V.26660,  $\times 250$ .

All the specimens are from the Gristhorpe Bed. All the figures are from Harris (1940a) by permission of the publishers of *Annals of Botany*.

wide, lip prominent forming a straight flange across the flat pedicel. Cuticle of fruit thick, cells with broadly marked lateral walls and without sinuous thickenings. Lip typically showing about 15 transverse bars. Seed typically elliptical,  $1.7 \times 1.1$  mm., both ends rounded, substance thin (as compressed), often 0.05 mm. thick. Surface cells of testa slightly elongated, interior scarcely sunken and testa appearing smooth. Cells near micropyle bulging and bulging cells extending for some distance back along the edges of the seed. Stone of testa thin, rarely showing cells, and cells not impregnated with resistant matter. Fibres probably absent. Micropylar canal with somewhat elongated cells. Deep membrane of integument ('spotted layer') if preserved usually showing rings of resinous matter.

LECTOTYPE. V.18580, specimen figured by Thomas (1925, pl. 11, fig. 1).

OCCURRENCE. The fruit of *C. nathorsti* is locally common in the Gristhorpe Bed. Fragments of fruit cuticles agreeing with *C. nathorsti* are known from Farndale, Swinacle Coal pit and from Bilsdale, Ladhill Coal pit (both Gristhorpe Series); Lockwood Hissing Scar (base of Upper Deltaic) and Scalby, probably the drifted plant bed (Upper Deltaic).

Isolated seeds resembling *C. nathorsti* occur widely in bulk macerations of the Middle and Lower Deltaic rocks, but having lost all parts outside the nucellus are hard to determine and are not listed here.

DISCUSSION. *C. nathorsti* has been discussed at length by Thomas (1925) and by Harris (1940a) and the seed in particular by Harris (1958). Only the diagnostic features are given here. For comparisons see p. 27.

### *Caytonia kendalli* sp. nov.

Pl. 2, figs. 5, 7; Pl. 5, fig. 14; Text-fig. 11

DIAGNOSIS. Megasporophyll rachis longitudinally ribbed below (details of cuticle unknown). Fruit rounded, up to 4 mm. wide, pedicel broadened above, mouth of fruit typically 2 mm. wide, somewhat curved round the pedicel, lip showing about 30 obscure transverse bars. Pedicel with numerous short sac-like trichomes along its margins. Cuticle of fruit thick, cells with broad, straight walls with a few slight jagged extensions. Flesh of fruit not resinous, containing numerous stone cells. Seed ovate, typically  $1.4 \times 1.0$  mm., thickness in compressed state 0.1 mm., originally rather flat. Surface cells isodiametric or slightly elongated, somewhat sunken, forming a shallow honeycomb. Stone of integument (possibly without an outer palisade layer) but with a few internal layers of slightly elongated stone cells. Contents of stone cells not resistant to maceration. Micropylar canal short, with elongated cells, specialised cells near micropyle not forming extensive tracts along the edges of the seed. Nucellar beak short and wide.

HOLOTYPE. V.45571 (Text-fig. 11 A).

OCCURRENCE.

Lower Deltaic:

Ryston Nab.

Roseberry Topping.

Hasty Bank.

There are old specimens in the Manchester Museum labelled 'Berries or seeds'.

DESCRIPTION. The material of *C. kendalli* is from three Lower Deltaic localities where

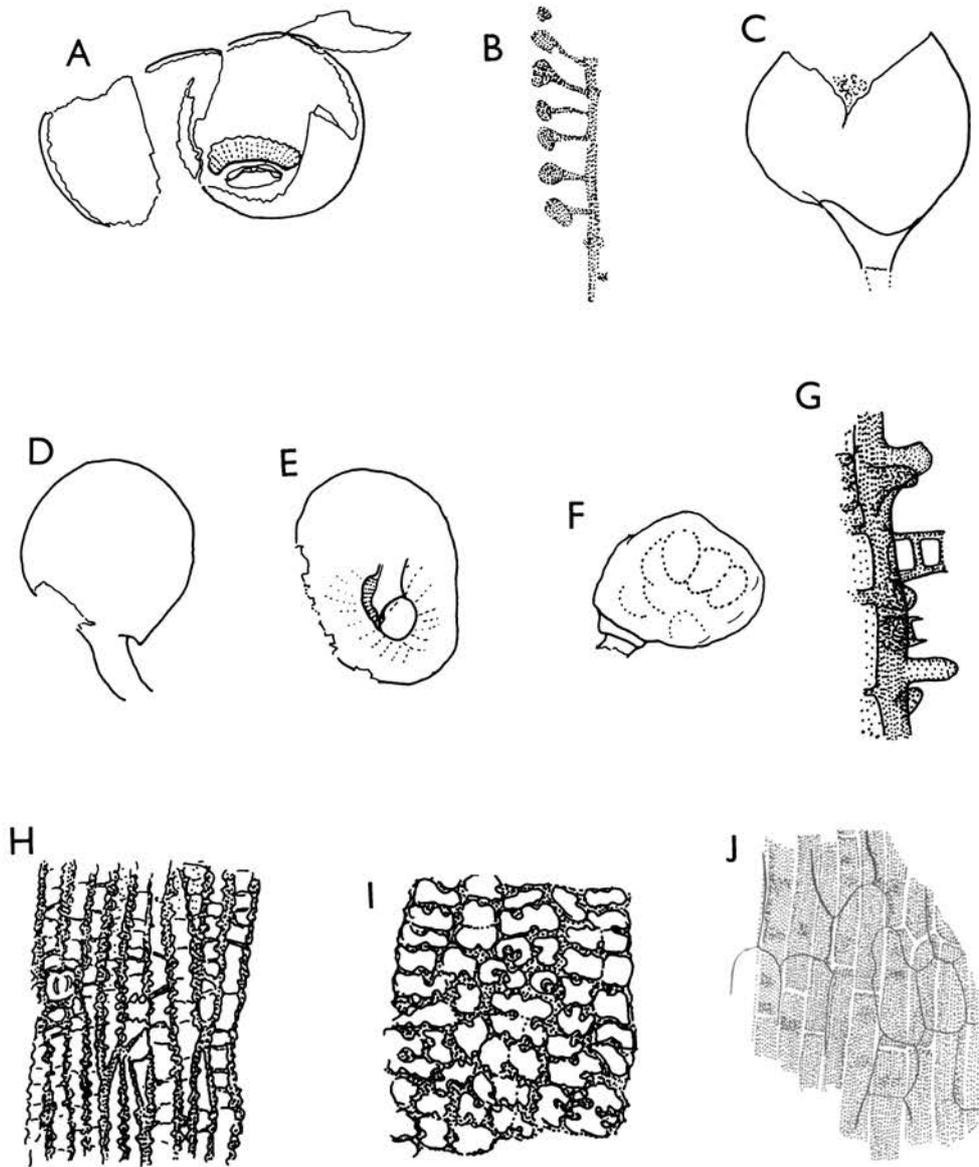


Fig. 11. *Caytonia kendalli* sp. nov.

A, holotype (cuticle preparation of whole fruit, the lip is shown striated and the broken stalk is just below, V.45571,  $\times 5$ . B, poorly preserved megasporophyll, V.42416,  $\times 1$ . C, naturally burst fruit with some extruded sclerids, V.42417,  $\times 5$ . D, fruit cuticle, V.42418,  $\times 5$ . E, isolated fruit, the compressed stalk is in the middle and the lip on its left, V.45576,  $\times 5$ . F, isolated fruit (lip and stalk bottom left); seeds are seen through the fruit coat, V.45576,  $\times 5$ . G, trichomes on edge of fruit stalk, V.45577,  $\times 200$ . H, I, cuticle of fruit, H of side with lip (front) and I of back, V.45572,  $\times 200$ . J, fragment of inner delicate cuticle of fruit, the cells with curved black walls possibly belong to the seed integument but are unusually large, V.45573,  $\times 200$ .

Specimens A, C, D, H-J are from Ryston Nab. B from Hasty Bank. E-G from Roseberry Topping.

the shale contains much *Sagenopteris colpodes* (the large form) but no other species of the genus and at Ryston the particular layer gave no other species of leaf. At Ryston isolated fruits are common, and pollen sacs of *Caytonanthus* sp. A were obtained by macerating the fruit-bearing shale. At Roseberry Topping fruits and seeds were again frequent, but only in a very thin layer. At Hasty Bank isolated fruits are occasional, and a single megasporophyll was found, but unfortunately it had deteriorated through weathering. As will be seen from the table of comparison (p. 27), *C. kendalli* is intermediate in several respects between *C. sewardi* and *C. nathorsti* and the possibility was considered that the material might be a mixture of these two.

On maceration, fruits of *C. kendalli* yield good seed cuticles, one moderate sized fruit gave fifteen recognisable nucellar cuticles, but some were small and some folded together as though they were abortive seeds that had never developed a thick integument. A few stomata were noted in the fruit wall and also a very few short trichomes. The cuticle of the fruit looks more like that of *C. nathorsti* than *C. sewardi* as the jagged extensions of the wall are only small and inconspicuous. Some of the fruits were macerated rather gently (using HNO<sub>3</sub> alone and in cold weather) and yielded, possibly because of this treatment, fragments of a delicate internal cuticle of a kind not previously noted. It appears to be the cuticle of the inner epidermis of the fruit.

The seeds are of nearly uniform size (length 1.2–1.6 mm.; width 0.9–1.1 mm.; thickness in compressed state about 0.1 mm., except where the epidermis is missing when most of the integument may be missing, too.) Where the epidermis is missing there is no suggestion of isodiametric stone cells but only of slightly elongated ones. In a few seeds folding or other distortion suggests that the seed was originally rather flat. The epidermal cells are usually short and distinctly sunken as in *C. sewardi*, but may be slightly elongated and only slightly sunken. The cuticle is very delicate and shows cell outlines so finely as to be nearly invisible. It is unsculptured. Near the micropyle the epidermal cells bulge, but they soon become flat or sunken.

The stone is thin in all specimens. A few were macerated with special care, and after a short treatment first with nitric acid alone and afterwards with ammonia, the stone was crushed and fixed with calcium chloride; in all it showed fibrous stone cells like those of *C. sewardi*, but forming a thinner layer and apparently composed of shorter cells. In no seed did the interior of these stone cells last longer than the walls, though it was sometimes distinguished by its dark colour. There is no sign of palisade-like stone cells on the outside.

The micropylar canal is short in every specimen and is composed of cells about twice as long as broad and with very conspicuous walls. The cells of the integument near the micropyle have a strongly bulging surface but at a short distance become flat. At the other end there is often a plug of partly preserved tissue connecting the chalaza to the hilum, but in no specimen is there any cellular tissue preserved round the micropyle as there sometimes is in *C. nathorsti*.

No specimen showed a well developed 'spotted layer'. Most seeds do show scattered solid spots outside the nucellus, but the spots are smaller than in the other two Yorkshire species and are scattered at random rather than regularly spaced. They look like small, loose, oil drops rather than solidified cell contents and may be of different nature from the 'spots' of the other two.

The broad, inner cells of the integument are just like those of the other two species and so are the cells of the nucellus, but the beak is always very short and broad, while in *C. nathorsti* it may be rather long. All the isolated seeds show pollen grains, possibly all *Caytonanthus*, in

their micropyles or nucellar beaks but they could not be seen clearly. The broad cells of the inner epidermis of the integument are exactly as in the other two Yorkshire species and so are the cells of the nucellus and the cells of aleurone which are occasionally well preserved. After rough maceration, when the micropylar canals are lost, the inner cuticles of the seeds of the different species are scarcely to be distinguished.

The species is named after Miss M. W. Kendall who collected much of the material.

#### Comparison of species of *Caytonia*

<i>C. thomasi</i>	<i>C. sewardi</i>	<i>C. nathorsti</i>	<i>C. kendalli</i>
Fruit broader than long	fruit round	fruit round	fruit round
Mouth 2.5 mm.	mouth under 1 mm.	mouth over 1 mm.	mouth nearly 2 mm.
Epidermal cells of fruit straight-walled	cell walls strongly jagged	walls straight	walls weakly jagged
(Rachis unknown)	rachis smooth	rachis ribbed	rachis ribbed
Micropylar cells long	cells round	cells long	cells long
Integument strongly fibrous	strongly fibrous	not fibrous	weakly fibrous
(Spotted layer of integument not studied)	spots large, evenly crowded	spots ring-like, sparse	spots small and solid, scattered

In *C. thomasi* alone the hairs on the peduncle are sometimes glandular.

#### Coprolites of Caytonialean Fragments

Small coprolites of Caytonialean remains were described by Thomas in a lecture in Cambridge, but not published, and many years later some were described by Harris (1946, 1956). These latter are on a slab in the Yorkshire Museum and though imperfectly localised are probably from the Gristhorpe Bed. The slab shows two groups of round pellets about 4 mm. wide, the larger group has about 70 pellets. Each pellet contains a vast number of beautifully preserved *Caytonanthus arberi* pollen grains (and a few immature tetrads and abnormal grains); a good deal of indeterminable delicate cuticle largely perhaps *Caytonanthus arberi*, a few bits of *Sagenopteris phillipsi* and one minute piece of *Ginkgo digitata*. There are no robust leaf cuticles.

Later a coprolite of about the same size was obtained from the Gristhorpe Bed which on maceration proved to consist largely of *Caytonia* with fragments of the fruits of both species and well preserved seeds of both; again no robust leaf cuticles occur. No pollen occurs in this specimen apart from a very few grains of *Caytonanthus* in the nucellar beaks of the seeds.

A third specimen of what looked like the same coprolite was found in the Beast Cliff *Otozamites* Bed. No Caytonialean material is known in this bed and no fragments were recognised in the coprolite but only delicate characterless cuticles and a minute and delicate piece of Bennettitalean cuticle.

It is interesting that there is a specimen from the Gristhorpe Bed collected by Mr. J. F. Jackson and preserved in the Cardiff Museum which shows a group of coprolites just like the groups on the Yorkshire Museum specimen. Their contents are different for they showed many kinds of cuticle, nearly all delicate, and a lot of pollen grains resembling those of *Androstrobilus prisma*. No Caytonialean remains were recognised with certainty.

From this slender evidence it might be argued that the small unknown animal was rather fastidious in its feeding, avoiding harsh leaves and preferring *Caytonia* flowers and fruits when

available, and further that it had not the powerful digestion of some herbivores (e.g. the goat) which as I was able to show experimentally, digests delicate cuticles of leaves and pollen completely. It further looks as though the *Caytonia* plant produced its microsporophylls at one season and its ripe fruits at another. The two species *C. seawardi* and *C. nathorsti* however, ripen their small, berry-like fruits at the same time.

### Genus AMPHORISPERMUM Harris 1932a : 14

EMENDED DIAGNOSIS. Small, oval, originally flattened orthotropous seed; micropyle not projecting, hilum small, round. Integument single; outer cuticle thin. Micropylar canal short, wide, cutinised. Inner cuticles invested by a single layer of small cells with thickened interior and thin walls, the 'spotted layer'. Nucellar cuticle robust, chalaza small, micropylar opening minute; cells of micropylar canal elongated. Megaspore not cutinised.

TYPE SPECIES. *Amphorispermum ellipticum* Harris.

DISCUSSION. The genus *Amphorispermum* was intended for isolated seeds like those of *Caytonia* in cutinised membranes, but specifically distinct from any known species of *Caytonia*. The diagnosis has been emended but chiefly in terminology because the seed cuticles of *Caytonia* are better understood, and the new features recognised in them were readily seen in the seed described here. These new features are the 'spotted layer', a striking layer of cells of unknown morphological nature; the nucellus cuticle itself and the complete absence of any megaspore membrane. Previously, these inner cuticles, together, were called the 'nucellus' and the outlines of the cells of the spotted layer alone were taken into account.

Apart from differences taken to be of specific value, the only differences between *A. pullum* and the species of *Caytonia* are:

- (1) Pollen grains are not normally seen in the micropyle.
- (2) The epidermis is the main thickened layer of the integument; in *Caytonia* one or more deeper layers are thickened as well.
- (3) The outer cuticle of the integument is a little thicker than in *Caytonia*.

As has been noted earlier, a good many seeds of the three Greenland species were searched for pollen and only one showed them; (winged *Caytonanthus*-like grains). None has been seen in the Yorkshire specimens studied. As pollen is rare it is possible that one find was in a mistakenly determined seed and that there is a real difference from *Caytonia* in pollination. The points of structural agreement on the other hand are impressive and that is why it is provisionally included with the Caytoniales.

There is no evidence to suggest that *Amphorispermum* belongs to the same plant as any known leaf; on the contrary, the distribution of all four species is against it. They are scattered thinly in the rocks of many localities and nowhere locally abundant and this suggests the seeds of some inland plant which had been carried far by water.

### *Amphorispermum pullum* Harris

Pl. 4, figs. 1, 2, 4, 5; Text-fig. 12

1943a *Amphorispermum pullum* Harris, p. 850, text-figs. 5, 6. (Figures reproduced here.)

EMENDED DIAGNOSIS. Seed oval, typically 2.0 × 1.4 mm., probably less than 1 mm. thick originally (substance in fossil state very thin). Micropyle not quite opposite hilum.

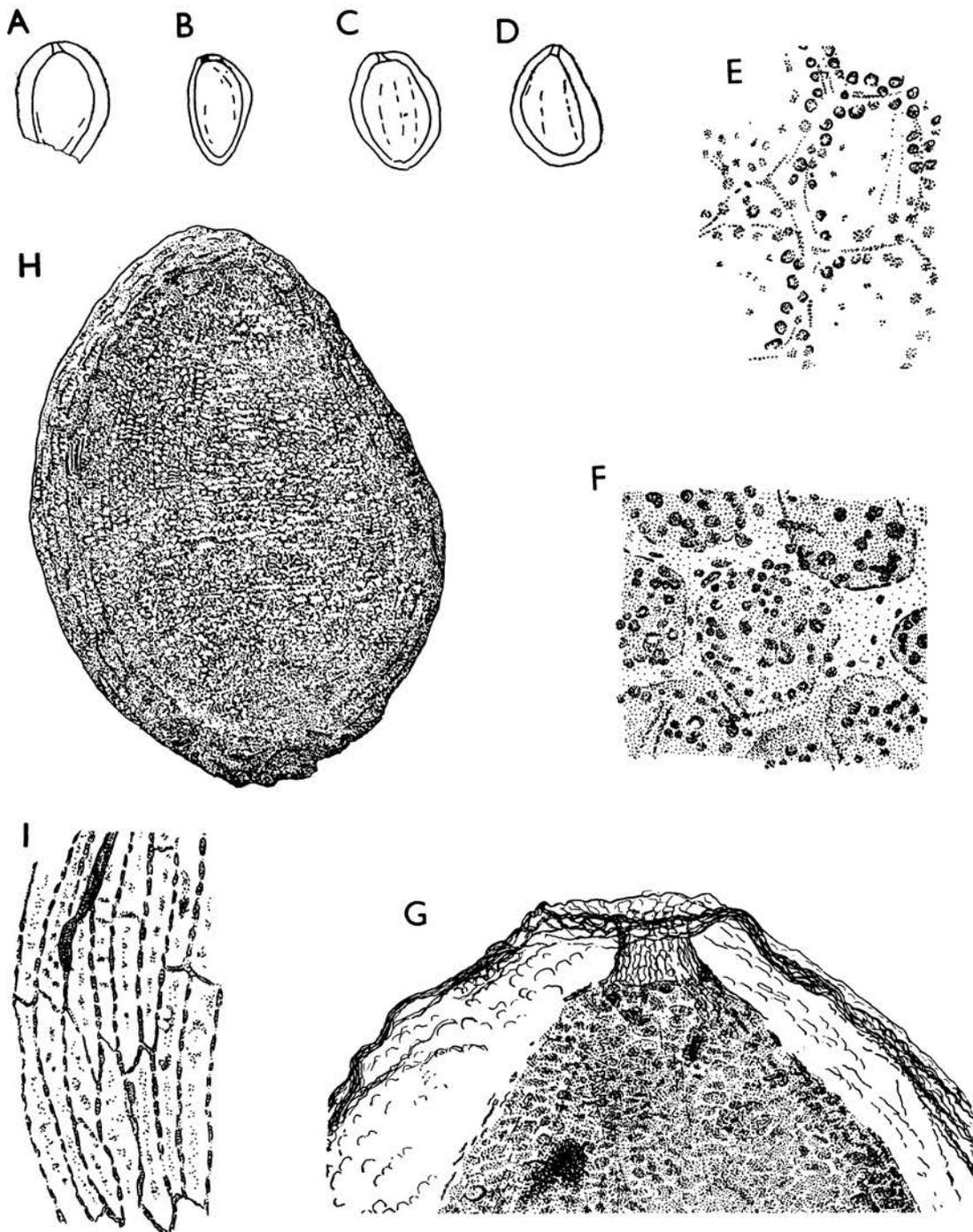


Fig. 12. *Amphispermum pullum* Harris

A-D, outline drawings of macerated specimens showing integument, micropyle and nucellus, V.26874-77,  $\times 10$ . E, outer cuticle of integument showing projections, V.26874,  $\times 800$ . F, surface of spotted layer, V.26874,  $\times 800$ . G, apex of macerated seed, V.26876,  $\times 100$ . H, holotype, V.26873,  $\times 40$ . I, cells of nucellus, V.45518,  $\times 150$ .

All the specimens are from the Gristhorpe Bed and all the figures except I are from Harris (1943a).

Surface strongly pitted, cells over most of surface isodiametric but slightly elongated towards edges of flattened seed and there forming longitudinal rows. Cells with minute projections near their walls giving the surface a dull lustre, outer cuticle barely  $1\mu$  thick, but coherent, cell outlines often obscure but indicated by cutinised pegs near the walls. Lateral walls and interior basal walls of surface cells strongly thickened (but uncutinised) and forming the sole robust layer of integument.

Micropylar canal opening on to a slight depression; neighbouring integument cells not specialised. Canal short, slightly constricted in the middle; cells slightly elongated, with conspicuous walls. Spotted layer usually conspicuous; cells small, typically isodiametric, often 6-sided. Walls thin but cell interiors thickened, raised and marked with conspicuous outwardly projecting granules. Nucellar cuticle robust, often nearly  $10\mu$  thick; cells with straight, not very conspicuous walls. Apex of nucellus nearly flat, not projecting far up into micropyle.

HOLOTYPE. V.26873, figured Harris (1943a, text-fig. 5); Text-fig. 12 H.

OCCURRENCE. *Amphorispermum pullum* is known from 16 localities as follows:

Middle Deltaic Gristhorpe Series	3 localities
Middle Deltaic Sycarham Series	3 localities
Lower Deltaic	10 localities

Most of the specimens are from the Gristhorpe Bed (from which far more shale has been macerated than anywhere else).

DISCUSSION. Some thirty additional specimens of *A. pullum* have now been found, usually as a single specimen in a maceration. Some of these show features additional to those previously given, but the main differences in the diagnosis result from fresh interpretation.

Some of the new specimens were naturally clear enough to show the thickened cells of the integument by transmitted light. These cells are shown by careful maceration to correspond to the cells seen in the cuticle. A few obliquely compressed seeds give some evidence of the original shape and indicate that the seed was flat. Most specimens when macerated show their 'spotted layer' very clearly and this effectively hides the cells of the nucellus underneath. In a few, however, the spotted layer is poorly developed and then the nucellar cells are plain. The spotted layer can be seen to overlap the nucellus at its compressed sides and also the base of the micropylar canal; this last fact that it does not form the micropylar canal proves that it is not the inner cuticle of the integument.

No seed showed any recognisable trace corresponding to the inner cuticle of the integument (seen in favourable seeds of *Caytonia*), nor of any endosperm cells (seen clearly in certain seeds of *Caytonia* and as a disorganised relic in many). There is a trace of coaly matter within the nucellus, but this dissolves and the cuticles of the two sides separate readily.

COMPARISON. Of the three species of the Greenland Rhaeto-Liassic, *A. ellipticum* and *A. rotundum* differ in their smaller size as well as in other respects but *A. major* is very similar. *A. pullum* is usually longer, wider and with a slightly longer micropyle. The cells of the spotted layer are usually isodiametric instead of broader than long. Both species are variable and some specimens attributed to each species are indistinguishable from the other. *A. pullum* is younger (Bajocian of Yorkshire) while *A. major* is from the basal Lias (*Thaumatopteris* Zone of East Greenland).

# Cycadales and Pteridosperms

The fossils described under this heading are isolated leaves and a few fructifications linked with certain of these leaves. The characters the leaves have in common are:

(1) They have an essentially pinnate architecture, shown by the veins and usually by the segmentation of the lamina as well.

(2) Their epidermis is cutinised and their stomata are of the Gymnosperm type and with haplocheilic subsidiary cells.

It is the second character which separates the Bennettitales from the leaves under consideration. This division of Cycadophyte foliage was only recognised gradually. In the early years of this century most of the Mesozoic Pteridosperm leaves were regarded as ferns while the leaves of Cycads, Bennettitales and some others were all called Cycads. Nathorst's more cautious term 'Cycadophyte' recognised this confusion and he made a start with the study of their cuticles but the first division of the whole series was made by Thomas & Bancroft (1913). They recognised the characteristic Bennettitalean arrangement of subsidiary cells (which we now call syndetocheilic). Florin and others made the division more precise by a better understanding of the stomata, but the division they made still stands. They called the non-Bennettitalean Cycadophytes the Nilssoniales but this class is not used here and I think the period of its usefulness has passed. In the main it is an alternative name for a fossil of the Cycadales, but as proposed it included *Ptilozamites* which is better regarded as a Pteridosperm.

The division of the non-Bennettitalean Cycadophyte leaves into Cycadales and Pteridospermae is difficult since we have no simple character to mark the two classes off from one another. Their cuticles are very similar and we can only use general leaf architecture. The idea of this division has also developed gradually and I think it still premature to consider it as sharp. In 1932 I divided the leaves in question into two 'series' one of which was called the *Ctenis* series and the other the *Thinnfeldia* series; I would now go further and say most of the *Ctenis* series are Cycads and most of the *Thinnfeldia* series are Pteridosperms. Since then we have learnt about the reproductive organs of a number of both series and one can feel more confident that these two groups are natural divisions, even though certain genera are left unplaced.

The characters of the fossil Cycad leaves are:

The rachis is never forked. The branching shown by the veins is simply pinnate and the veins themselves are nearly parallel.

The characters of the Pteridosperms are:

The rachis may be simple or forked. The branching shown by the veins is two or more times pinnate and the veins diverge in a Pecopterid or Odontopterid manner. There is a tendency for the lamina of a pinna to be strongly decurrent on to the rachis, or in a more divided leaf for there to be *Zwischenfieder* on the rachis.

These characters are merely a guide; there are doubtless exceptions, as for instance the bipinnate *Bowenia* among the living Cycads.

The fossil Cycad genera whose reproductive organs are known (with microscopic detail) are *Nilssonia* (male and female), *Pseudoctenis* (male) and *Bjuvia* (female). The Pteridosperms

with reproductive organs are *Lepidopteris* (male and female) and *Dicroidium*, including *Xylopteris* (male and female), *Ptilozamites* (male) and *Pachypteris* (male). Several genera remain with none, for instance *Ctenis* and *Paracycas* which belong to the Cycad series and *Thinnfeldia*, *Cycadopteris* and *Stenopteris* of the Pteridosperms. These genera may perhaps be linked mentally with those supported by reproductive organs, for instance *Thinnfeldia* and *Cycadopteris* with *Pachypteris* or *Dicroidium*, but we need facts firmer than such a link for classification. With *Ctenozamites*, in particular, I have reservations: this leaf may be linked with *Ptilozamites* with some confidence and *Ptilozamites* with *Harrisothea* but the organisation of *Harrisothea* is not that of a normal Pteridosperm microsporophyll. It is, however, even more different from a Cycad. Because of such uncertainty I have refrained from making the division, but I suggest that of the genera treated here *Nilssonina*, *Ctenis*, *Pseudoctenis* and *Paracycas* are Cycadalean while *Ctenozamites*, *Stenopteris* and *Pachypteris* are Pteridosperms.

### Genus NILSSONIA Brongniart 1825 : 200

The main facts known about *Nilssonina* are:

Leaf as a whole linear or oblanceolate, lamina gradually increasing in width from the base. Lamina attached to upper edge of rachis and entirely concealing it from above, lamina entire or cut transversely into segments. Veins simple, numerous, equal and ending at its distal margin; resin bodies often present between veins. Stomata confined to lower side, scattered between veins, guard cells lightly cutinised, exposed or sunken and surrounded and more or less protected by a more or less regular ring of subsidiary cells; subsidiary cells unspecialised or each bearing a papilla projecting over the aperture. Unicellular trichome bases occurring on the under side, at least on veins. Petiole base expanded, cut off by an absciss layer showing a curved group or ring of vascular strands (Halle 1913 and p. 35 below). Vascular bundles of lamina showing centripetal xylem (Stopes 1910); vernation of leaves circinate (Nathorst 1909).

The stem is unknown but the scale leaf (*Deltolepis*), the male cone (*Androstrobus*), and the female cone (*Beania*) including details of the seed are known.

Work done on *Nilssonina* since 1825 (especially by Nathorst 1909, Florin 1920) has sharpened its distinction from other genera but a large number of species have been described which cannot be distinguished on published characters, and the identification of a *Nilssonina* is becoming very difficult even where there is abundant good material (fortunately *Nilssonina* often does occur in abundance). Its distribution suggests that it grew in the deltas, perhaps on the river banks. Leaves of fairly similar form recur throughout the Mesozoic and species based on form alone have little stratigraphic value, no doubt the species are composite. Whether the addition of the characters of presence or absence of resin and of various microscopic features in the cuticle will fully differentiate species remains to be shown, as too few have yet been studied, but it does give hope. Because of this difficulty some of the less fully known species of the Yorkshire flora are left imperfectly determined.

#### Key to typical specimens of the Yorkshire species of *Nilssonina*

(1)	Lamina almost entire . . . . .	2
	Lamina much segmented . . . . .	5
(2)	Lamina over 4 cm. wide . . . . .	<i>N. thomasi</i>
	Lamina under 4 cm. wide . . . . .	3

(3)	Lamina over 1 cm. wide . . . . .	. . . . . 4
	Lamina under 1 cm. wide . . . . .	<i>N. revoluta</i>
(4)	Lamina linear . . . . .	<i>N. tenuinervis</i>
	Lamina narrowly obovate . . . . .	<i>Nilssonia</i> sp. A
(5)	Length of segment at least 4 times width . . . . .	. . . . . 6
	Length of segment less than 4 times width . . . . .	. . . . . 7
(6)	Segments curving forwards, margins depressed . . . . .	<i>N. syllis</i>
	Segments straight, margins flat . . . . .	<i>N. tenuicaulis</i>
(7)	Leaf usually large, veins about 15 per cm. near rachis . . . . .	<i>N. compta</i>
	Leaf usually small, veins about 35 per cm. . . . .	. . . . . 8
(8)	Cuticle delicate . . . . .	<i>N. kendalli</i>
	Cuticle thick . . . . .	<i>Nilssonia</i> sp. B

*Nilssonia tenuinervis* Seward

Pl. 1, fig. 10; Text-figs. 13, 14

All the following specimens are from Yorkshire:

- 1880 *Nilssonia tenuinervis* Nathorst, pp. 35, 83. (*Nomen nudum*.)  
 1900 *Nilssonia tenuinervis* Seward, p. 230, text-fig. 41. (Brief description and figure; mention of Nathorst's specimens.)  
 1900a *Nilssonia tenuinervis* Seward: Seward, p. 4. (Mention of occurrence.)  
 1909 *Nilssoniopteris tenuinervis* Nathorst (in part), pp. 27–29, pl. 6, fig. 24. (Not pl. 6, figs. 23, 25; pl. 7, fig. 21 which represent *Taeniopteris vittata*, and most of the text refers to that species.)  
 1910 *Nilssonia schaubergensis* (Dunk.): Bartholin, p. 264, pl. 1. (Leaf from Marske.)  
 1913 *Nilssonia orientalis* Heer: Thomas, p. 240, pl. 23, fig. 7; pl. 25, fig. 1. (Leaf fragments, discussion of *Nilssoniopteris*.)  
 1913 *Nilssonia orientalis* Heer: Thomas & Bancroft, p. 192, pl. 20, fig. 11. (Cuticle, discussion of *Nilssoniopteris*.)  
 1933 *Nilssonia orientalis* Heer: Florin, p. 12, footnote. (Discussion of *Nilssoniopteris*.)  
 1943a *Nilssonia tenuinervis* Seward: Harris, p. 838, text-figs. 1, 2. (Emended diagnosis; gross features and cuticle.)  
 1961 *Nilssonia tenuinervis* Seward: Harris, text-fig. 2. (Restoration.)

A list of foreign specimens of similar appearance is given on pp. 36, 37 but none is definitely determined as *N. tenuinervis*.

DIAGNOSIS (slightly expanded from Harris 1943a). Leaf linear; length estimated at about 80 cm., width in middle region typically 2–3 cm., rarely 4 cm., occasionally only 1 cm. wide. Apex typically acute, lamina tapering below, petiole short or absent but rachis base expanded at its attachment. Lamina typically entire but sometimes irregularly divided to the midrib. Surface of lamina not undulating, margins and midrib both depressed. Veins fine, typically 35–40 per cm., rarely less than 30 or more than 50; typically arising from the midrib at an angle of 85° but curving forwards to meet the margin at 70°. Veins only projecting slightly, lamina thin, containing a series of resin bodies 100μ wide between pairs of veins. Surfaces glabrous in mature leaf.

Upper cuticle very delicate, composed of elongated straight-walled cells. Cell outlines forming fine ridges but often appearing as a thin strip flanked by thicker borders; surface wall finely mottled. Trichomes and stomata absent; cells along veins slightly narrower than cells between veins. Lower cuticle very delicate, cells along veins elongated, cells between veins isodiametric or irregular, outlines often indistinct. Oval thickened cells (trichome bases) frequent along veins, occasional between veins. Stomata scattered in relatively broad strips between veins. Guard cells only slightly sunken, subsidiary cells forming an irregular group,

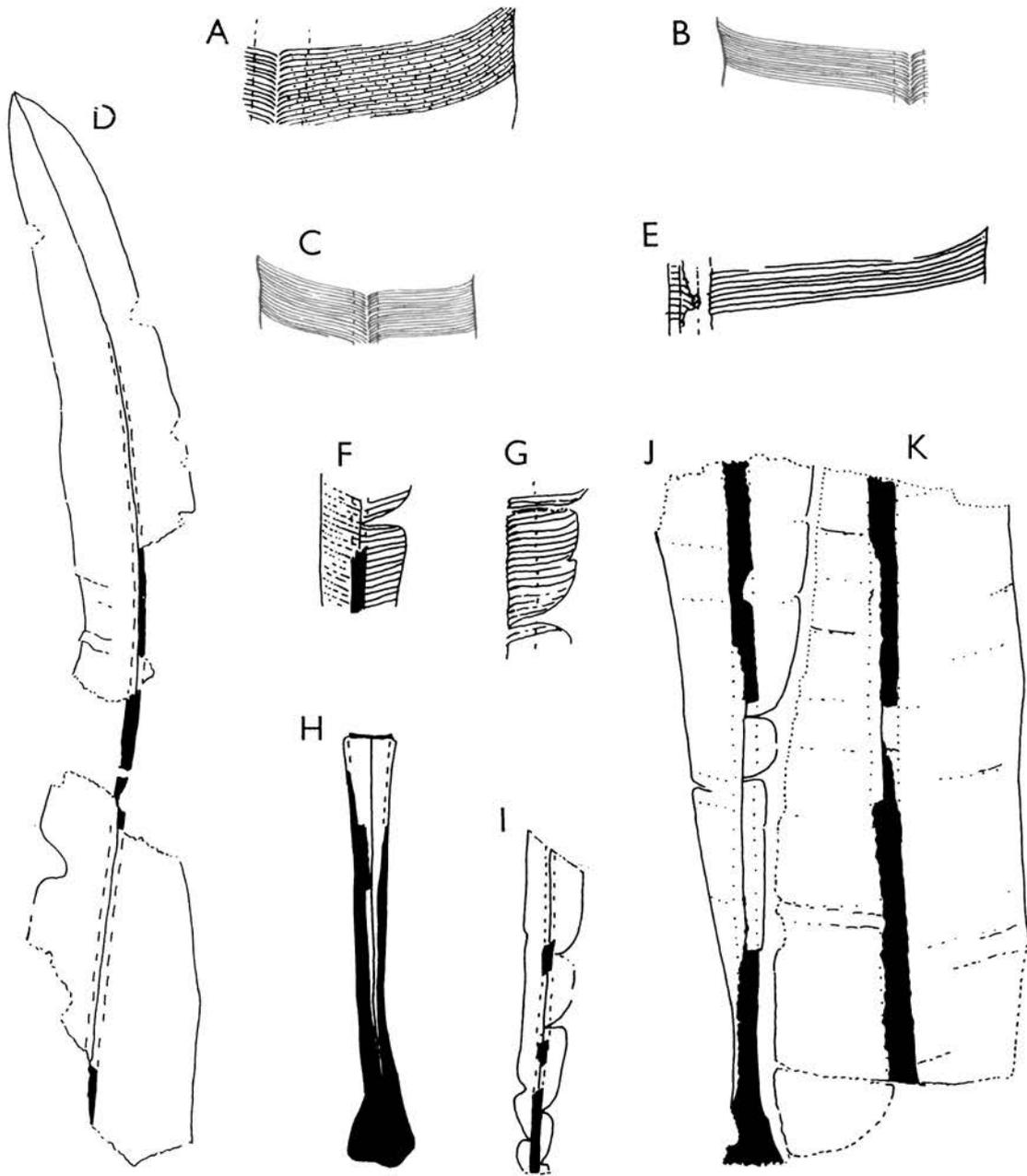


Fig. 13. *Nilssonia tenuinervis* Seward

A, veins and resin bodies from wide leaf, V.26870,  $\times 2$ . B, veins of typical leaf, resin omitted, V.25896,  $\times 2$ . C, veins from V.26869,  $\times 2$ . D, fragment from top of normal leaf, V.26869,  $\times 1$ . E, veins from leaf in K,  $\times 2$ . F, veins from leaf in I,  $\times 2$ . G, veins from leaf in J,  $\times 2$ . H, base of leaf showing lamina diminishing on the surface of the petiole, V.25906,  $\times 1$ . I, lower part of small leaf, V.41106,  $\times 1$ . J, K, adjacent fragments of two large leaves, V.41119,  $\times 1$ .

E, G, J, K are from the Cloughton *Nilssonia* Bed. F, I from Farndale Hillhouse Plant Bed. The rest are from the Gristhorpe Bed. A-C, D, H are from Harris (1943a, text-fig. 1).

unspecialised or one or more bearing a thickened area forming a rather flat papilla, or projecting to form a hollow papilla.

HOLOTYPE. 13502, figured by Seward (1900, text-fig. 41).

OCCURRENCE. *N. tenuinervis* is found throughout the Yorkshire Deltaic Series. It is abundant at a few points and here the reproductive organs occur. Specimens from all the localities given below have yielded cuticles, a few others, without cuticles, have been rejected as indeterminable.

Upper Deltaic:

Burniston *Zamites* Bed.

Middle Deltaic Gristhorpe Series:

Gristhorpe Bed.

Cloughton *Solenites* Bed.

Fryup Dale Head, Coalpits.

Farndale Low Quarter, Coalpits.

Middle Deltaic Sycarham Series:

Cloughton *Nilssonina* Bed.

Lower Deltaic:

Roseberry Topping.

Hasty Bank.

Whitby Long Bight Plant Bed, and in coaly shale above this bed.

Hawsker Cliffs, fallen blocks near Gnipe Howe.

Hawsker Cliffs, Jackass Trod.

Beast Cliff *Otozamites* Bed.

DISCUSSION. Although *N. tenuinervis* is abundant, no complete full sized leaf has yet been seen. The great majority of specimens conform fully with the diagnosis, but a few were noted in which the veins arose at an angle as low as  $70^\circ$ . Resin bodies may be easily visible or may require maceration to show them. The cuticle is constant in so far as it was seen satisfactorily.

The leaf base in Pl. 1, fig. 10 shows its attachment area. There is a series of small lumps, or perhaps an uneven ridge forming a flattened oval (it is hardly seen on the left even when this side is well illuminated). This ridge may represent the vascular strands, but it is possible that it is of other nature. If it is a flattened ring of vascular tissue it is different from what Halle (1913, text-fig. 11) noted in the leaf base of *N. taeniopteroides* where there is a single arc of separate bundles. The margins of the leaf base form a delicate wing at the sides of the massive central tissue.

*N. tenuinervis* was formerly confused with *Taeniopteris vittata* and *Nilssoniopteris tenuinervis* Nathorst (1909) was based on a mixture of the two species. Florin (1933) has used *Nilssoniopteris* in the restricted sense for the Bennettitalean leaves alone (including the former *Taeniopteris vittata*) and there should be no more confusion. This error is easy to make. The two species occur mixed at both the Gristhorpe Bed and the Cloughton *Solenites* Bed, and although most specimens of each are easily distinguished, some are so similar that I could only settle their

identity by preparing their cuticles. Usually the leaf of *N. vittata* is distinguished by the incomplete concealment of the upper surface of the rachis and also by the forking of some of the lateral veins, but in some specimens neither of these characters is plain.

*N. tenuinervis* has acquired new interest from its association with reproductive organs appropriate to a *Nilssonia*. (See *Androstrobus wonnacotti* and *Beania mamayi*.)

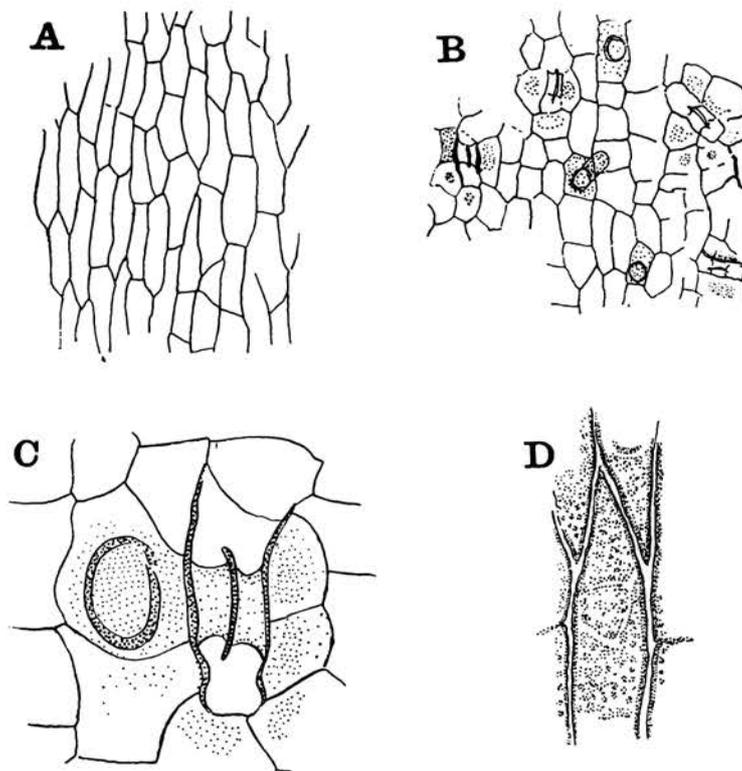


Fig. 14. *Nilssonia tenuinervis* Seward

A, upper cuticle, a vein lies on the left, V.26870,  $\times 200$ . B, lower cuticle, a vein occupies the middle of the fragment, V.26871,  $\times 200$ . C, stoma and trichome base, V.26871,  $\times 800$ . D, cell of upper epidermis, V.26870,  $\times 800$ .

All the specimens are from the Gristhorpe Bed and all the figures are from Harris (1943a, text-fig. 2).

COMPARISON. *N. tenuinervis* has not been identified outside Yorkshire but some of the leaves described under the name *N. orientalis* resemble it in the characters they are known to show. These specimens are listed below; in making this comparison only the typical form of *N. tenuinervis* is considered, if abnormal leaves were taken the list of similar specimens would be longer. Most of the specimens of the *orientalis* group differ in one or more of the following features: the leaf is shorter, or broader (over 3 cm.) or has less than 30 veins per cm., or the veins are at a smaller angle, or the lamina is transversely waved.

The following specimens look similar (in some cases the specimen cited is the most similar of a series in which the rest are different).

*N. ozoama* Yokoyama 1889, pl. 10, figs. 26, 11-14. (Upper Jurassic of Japan.)

*N. schaumbergensis* Nathorst 1890, pl. 1, figs. 4-5 only. (Cretaceous of Japan.)

*N. parvula* (Heer) Fontaine in Ward 1905, pl. 17, figs. 1-7 (like smallest forms of *N. tenuinervis*.)

*N. orientalis* Heer: Thomas 1911, pl. 7, fig. 1. (Jurassic of Russia.)

*N. orientalis* Heer: Seward 1911, pl. 4, figs. 63, 65; pl. 9, figs. 34, 42 (but excluding other specimens). Upper Jurassic of Scotland.

*N. orientalis* Heer: Seward 1912, pl. 3, fig. 46 (Jurassic of Afghanistan.)

*N. orientalis* Heer: Makarewiczowna 1928, pl. 10, fig. 1. (Lower Lias of Poland.)

*N. orientalis* Heer: Frentzen 1932, pl. 2, fig. 4. (Rhaetic of Germany.)

*N. orientalis* Heer: Baranova, Burakova & Bekasova 1963, pl. 52, fig. 1; pl. 53, figs. 1-3; text-fig. 81. (Jurassic, Central Asia.)

As will be seen these specimens range from Rhaetic to Cretaceous and since I have refused to identify such of my own specimens as show no microscopic structure, I have refrained from identifying any of these. Should any be shown to agree in resin bodies and in cuticle it should be identified with *N. tenuinervis* even if their ages differ.

Oishi (1940 : 307) gives a useful list of other specimens of *N. orientalis*. *Nilssonia obtusa* (Nathorst) Harris (1932) from the basal Lias of East Greenland, is very similar in form, resin bodies and in cuticle but the veins are less crowded (about 25 per cm.). In *N. obtusa* trichome bases are apparently absent from the lower cuticle.

*Nilssonia thomasi* sp. nov.

Pl. 5, fig. 6; Text-fig. 15

DIAGNOSIS. Leaf large (length unknown), width typically 5.0-6.5 cm., margins entire or slightly and irregularly incised. Apex retuse (base not known). Midrib up to 7 mm. broad, veins arising at right angles to it below but at about 70° above; veins curving forwards. Veins prominent below, sunk above, rather fine; traversing the lamina at 20-32 per cm. Leaf substance moderately thick, lamina surface flat apart from fine ridges due to veins.

Upper cuticle moderately thick, showing elongated cells; cells over veins rather narrower and thicker walled than those between veins. Cell outlines rather broad and ill defined, especially between veins, but under phase-contrast light appearing nodular and interrupted. Surface wall smooth. Lower cuticle rather thin. Veins marked by narrow strips of elongated cells. Intervals between veins with short and irregular cells and numerous scattered stomata. Cell outlines rather obscurely marked, especially in cells between veins; under phase-contrast light cell surface often showing one or two slightly thickened areas and nodular thickening of lateral walls. Stomata only slightly sunken, mostly longitudinal, surrounded by an irregular ring of subsidiary cells, each cell tending to bulge as a large hollow papilla which may point outwards and leave the guard cells exposed or overhang the surface.

Trichomes rather few and feebly thickened, occurring both on and between veins, consisting of an oval cell bearing a thickened ring on its surface.

Resin bodies (both large and small) absent.

HOLOTYPE. V.41118 (Text-fig. 15 A).

OCCURRENCE. *Nilssonia thomasi* is known from three localities in the Lower Deltaic (Roseberry Topping, Hasty Bank and Haiburn Wyke).

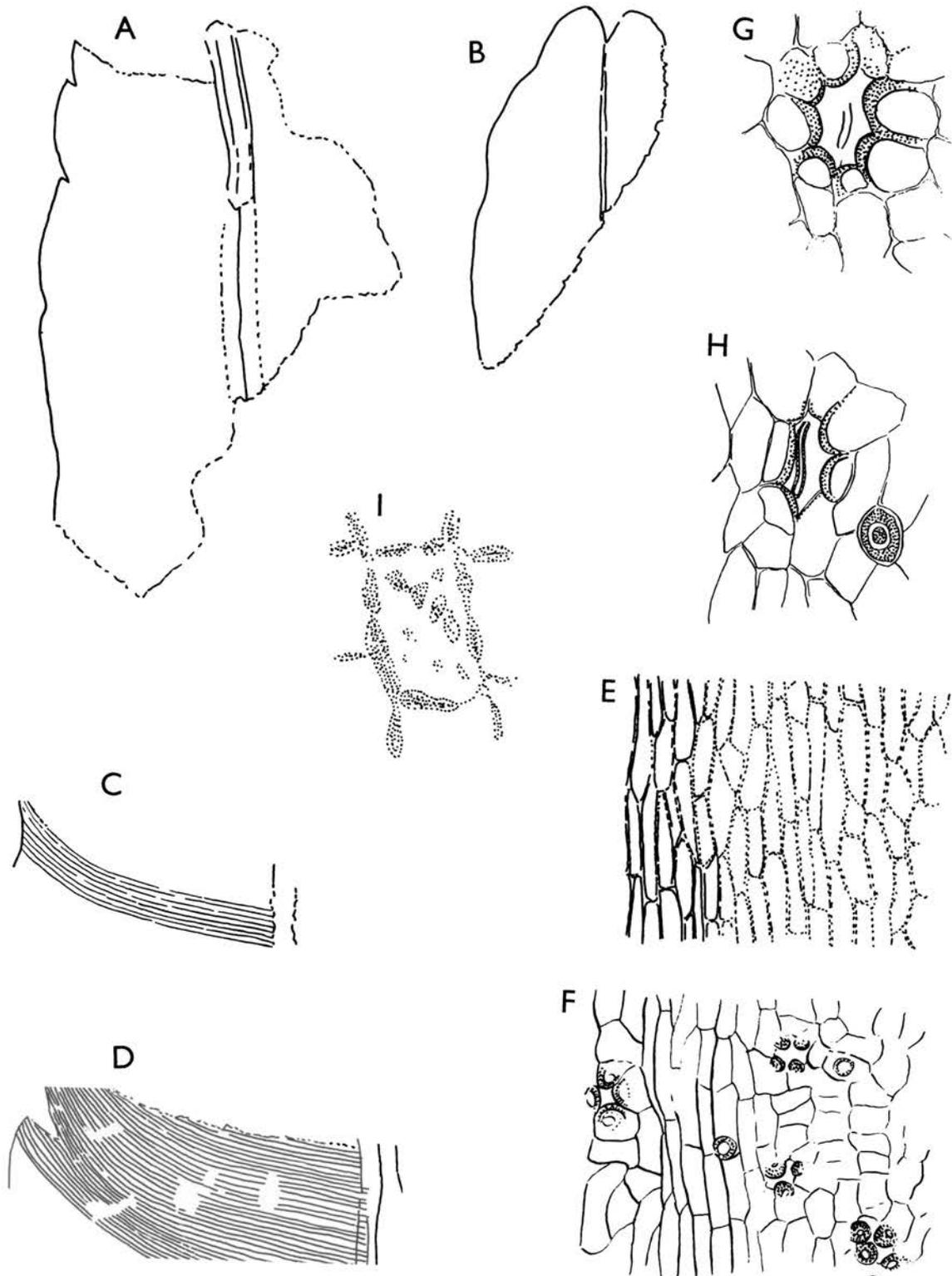


Fig. 15. *Nilssonia thomasi* sp. nov.

A, holotype, the largest fragment, V.41118,  $\times 1$ . B, apical fragment, V.41151,  $\times 1$ . C, veins of B,  $\times 2$ . D, veins of A,  $\times 2$ . E, upper and F, lower cuticle from A,  $\times 200$ . G, H, two stomata from V.45552,  $\times 400$ . I, upper epidermal cell as seen under phase-contrast illumination, V.45552,  $\times 800$ .

All from Roseberry Topping.

DISCUSSION. *Nilssonia thomasi* is rare. It is represented by several large fragments at Roseberry Topping collected by Hamshaw Thomas, by Miss M. W. Kendall and myself; and a single old specimen (V.1008) from Haiburn Wyke. All these are rather poorly preserved but gave fragments of cuticle which could just be used to confirm that the specimens belonged to one species. A better preserved fragment was later found at Hasty Bank which gave good cuticles.

*N. thomasi* is distinguished from both *N. tenuinervis* and *Nilssonia* sp. A of Yorkshire by having no resin, as well as by its much larger size. *N. undulata* from East Greenland is rather similar but differs in its undulating surface and numerous minute resin bodies.

Leaves as broad as this have been included in *N. orientalis*. See for example Oishi (1940, pl. 24, figs. 1, 5) and Semaka (1962, pl. 5, fig. 4; pl. 6, fig. 1). The veins of Oishi's leaves are similar or rather denser, but we have no information about resin or cuticle. I regard *N. orientalis* as a useful aggregate name for a good many *Nilssonia* species where microscopic information is lacking.

The species is named after Dr. Hamshaw Thomas who collected some of the specimens.

### *Nilssonia* sp. A

#### Text-fig. 16

Lamina narrowly obovate, entire, flat, 5–9 cm. long, up to 2.5 cm. wide near to apex, base tapering, apex rounded but with midrib forming a small mucro. Veins fine, variable, traversing the lamina at a concentration of about 12–30 per cm., rounded resin bodies occurring between veins.

Upper cuticle (V.41117a) thin, showing cells of irregular shapes and a few thickenings on their surfaces.

Lower cuticle (Yorkshire Museum specimen) moderately thin, showing elongated cells along veins, isodiametric cells and scattered stomata between veins. Cell walls straight, finely marked but fairly distinct, cell surface smooth. Trichomes present both on veins and between veins, consisting of a small, thickened basal cell bearing a ring. Stomata rather sunken, surrounded by an irregular ring of thickened subsidiary cells.

The specimen shown in Text-fig. 16 A must originally have been perfect, but it has no locality label and has been disfigured with a varnish which could not be removed and which has destroyed the upper cuticle and conceals the veins and resin bodies at many points.

The veins are irregular, some are 0.25 mm., others 0.5 mm. apart. One vein was seen to end in the lamina and merely continue by a disconnected series of dark cells, another (in the drawing) has this form throughout. A few cases were noted where two veins anastomose and cases where two arise so close together as to constitute a single forking vein.

The only other specimen, V.41117, was collected by Dr. Hamshaw Thomas from Roseberry Topping. It shows less crowded veins and a rather thicker but very crumbly leaf structure. Resin bodies cannot be seen but maceration yielded what were taken to be fragments of normal resin bodies. It is not certain that these two specimens are of the same species, and one or both might be a very abnormal form of *N. tenuinervis*, but although *N. tenuinervis* occurs in both localities no specimen approaching this short leaf has yet been seen.

The following leaves resemble *Nilssonia* sp. A macroscopically:

*Nilssonia orientalis* Heer: Yokoyama (1889, pl. 14, figs. 4-9).

*Nilssonia orientalis* Heer: Oishi (1940, pl. 26, figs. 2-4).

*Nilssonia* cf. *orientalis* Heer: Kimura (1958, pl. 9, figs. 1-4, 7).

*Nilssonia tanakai* Kimura (1959, pl. 1, figs. 5-7).

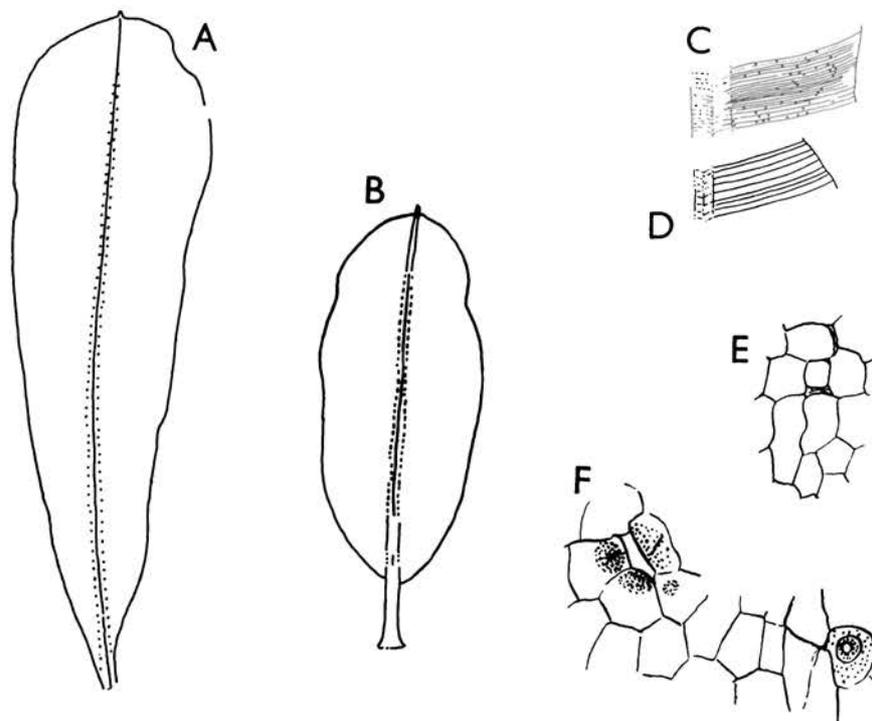


Fig. 16. *Nilssonia* sp. A

A, Yorkshire Museum specimen (unlocalised),  $\times 1$ . B, leaf from Roseberry Topping, V.41117,  $\times 1$ . C, veins and resin bodies of A (partly obscured by varnish),  $\times 2$ . D, veins from B,  $\times 2$ . E, cells of upper cuticle from V.41117,  $\times 200$ . F, stoma, trichome and other cells of lower cuticle from A,  $\times 200$ .

*Nilssonia revoluta* sp. nov.

Pl. 1, figs. 13, 20; Text-fig. 17

**DIAGNOSIS.** Leaf entire, very narrow (typically 3-5 mm.) margins of lamina curved downward and revolute. Veins nearly transverse, running at a concentration of 25-30 per cm. Upper surface of lamina glabrous; veins only slightly prominent above, but more prominent below. Substance of lamina fairly thick. Upper cuticle moderately thick, cells uniform, veins scarcely shown. Cells isodiametric or elongated and mostly orientated parallel with the veins. Cell outlines conspicuous, walls straight or gently curved, often with nodular thickenings and occasionally interrupted. Surface of cell often showing two or three well defined thickened areas. Reflexed part of upper surface similar, but cells variably orientated. Lower cuticle very delicate. Veins strongly indicated by elongated cells and by the absence of stomata; moderately broad, showing slight crushing along their margins. Cells between veins small, isodiametric,

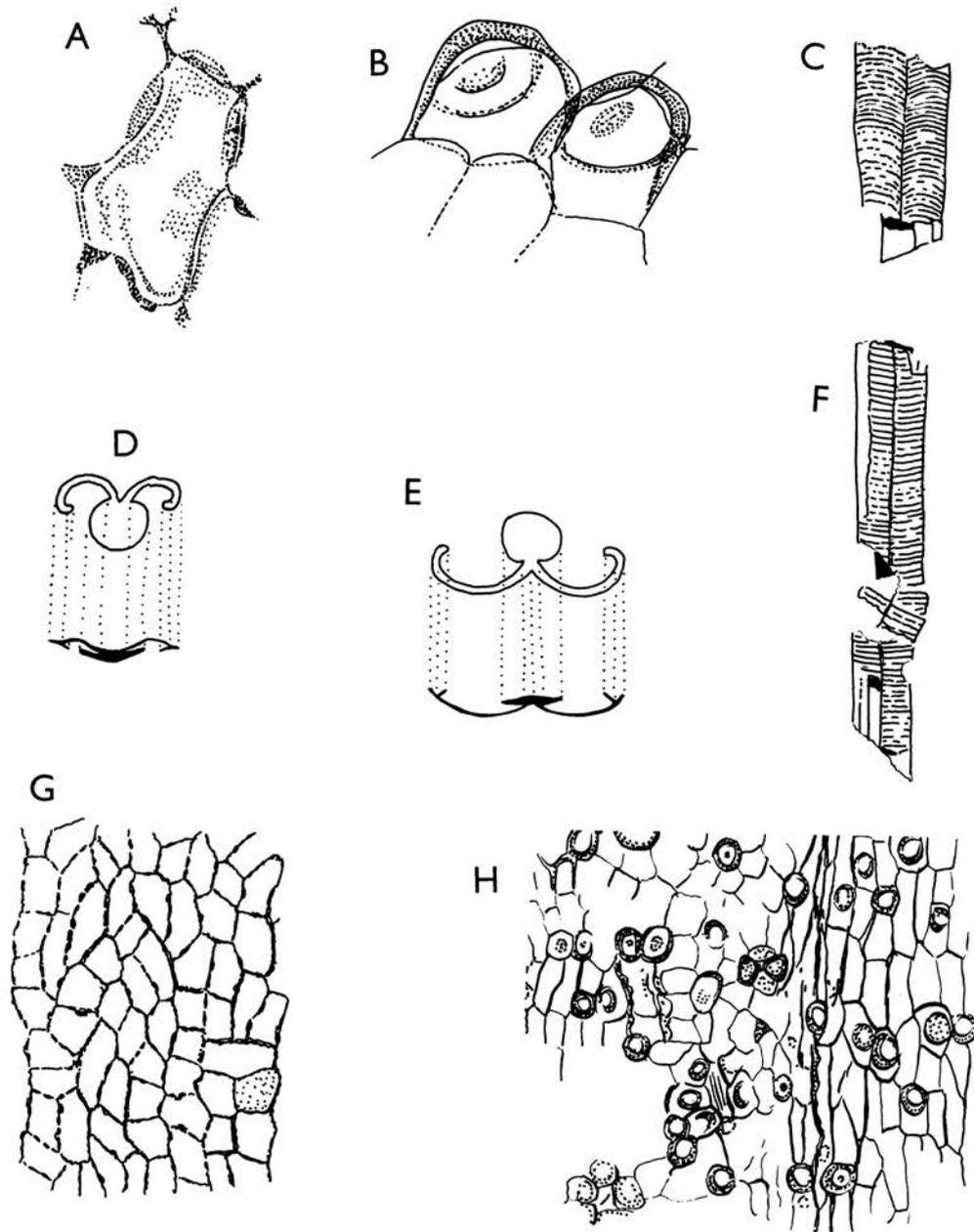


Fig. 17. *Nilssonia revoluta* sp. nov.

A, cell from upper epidermis of holotype, V.23967,  $\times 800$ . B, two bulging cells of lower epidermis of holotype, compressed obliquely,  $\times 800$ . C, holotype,  $\times 2$ . D, diagram of V.23968 in its imaginary original form and as compressed. E, diagram of V.23967 in its original form and compressed. In both D and E the vertical and horizontal scales are both  $\times 4$ ; the plane of cleavage has exposed the morphologically upper surface in each. F, V.23968,  $\times 2$ . On the left the substance has broken away, exposing the impression of the border. G, upper epidermis, V.23967,  $\times 200$ . H, lower epidermis, V.23967,  $\times 200$ . Where the cells are obscure they are left blank. Both specimens are from South Cliff, Scarborough.

with thin, straight walls, walls often very inconspicuous. Stomata scattered in areas between veins, surrounded by an irregular ring of about six more or less equal-sized subsidiary cells. Surface of subsidiary cells usually thickened and bulging and projecting over the aperture. Trichomes or bulging cells numerous both on veins and between them. Trichomes on veins consisting of a small, thickened cell with a ring of thickening in the interior (? trichome base only). Trichomes between veins consisting of a rounded cell with a thickened surface, surface bulging as a hemisphere, base with a thickened area.

Resin bodies absent, so far as is known.

HOLOTYPE. V.23967 (Pl. 1, fig. 20).

OCCURRENCE. Upper Deltaic. South Cliff, Scarborough.

DISCUSSION. The only two specimens are figured. They are small but well preserved in a typical Upper Deltaic clay. Their surface contour is slightly different and the difference is fully accountable on Walton's theory of compression (by which the surface at first lying downwards largely determines the final form of the compression). The holotype is presumed to have had its upper surface facing down and V.23968 its upper surface facing upwards, but both show the upper surface exposed, as usual in *Nilssonia*. The margin shows a compression border 0.3–0.4 mm. thick, the original thickness of the lamina, and from this a flange points inwards for nearly half a millimetre, and this represents the extent of the revolute part of the lamina. This flange is shown both in the original fossil and in cuticle preparations.

COMPARISON. Very few *Nilssonia* leaves have been described that are less than 1 cm. wide, and none has a revolute margin, though this point might be missed. It is also exceptional in the bulging cells among the stomata, both features are xeromorphic.

Although it is only known from two small specimens, these characters are extreme enough to justify making a new species for it. The only fossils known which look similar are:

*Jacutiella amurensis* (Novopokrovski) Samylina (1956, 1963) which has a broader leaf, and agrees with *N. revoluta* in its strongly depressed margins and almost concealed and sunken midrib, though the rock may break to expose the whole midrib. In some of the specimens the veins are simple as in *Nilssonia*, but in others (Samylina 1956, text-fig. 4) a good many are forked. In a diagram the margins in *Jacutiella* are shown as distinctly curved.

*Taenopteris gracilis* Kimura 1959 from the Liassic of Japan looks similar but as the lamina is described as attached laterally, and the veins are occasionally forked, it is presumably entirely different.

*Nilssonia schaubergensis* var. *parvula* Yabe. See Oishi (1940, pl. 26, fig. 9). A leaf of similar width and with a convex upper surface.

*Nilssonia parvula* Fontaine in Ward (1905, pl. 17, fig. 17).

### *Nilssonia syllis* sp. nov.

Pl. 1, fig. 15; Text-figs. 18, 19

1913 *Nilssonia mediana* Leckenby: Thomas, p. 239. (No figure, but figure given by Thomas & Bancroft 1913.)

1913 *Nilssonia mediana* Leckenby: Thomas & Bancroft, p. 191, pl. 19, fig. 15; pl. 20, fig. 10. (Cuticle of specimen from Marske.)

1949 *Nilssonia* cf. *pterophylloides* Nathorst: Sze, p. 10, pl. 6, fig. 1. (Good leaf. West Hupeh, China.)

DIAGNOSIS. Leaf as a whole long, oblanceolate, lamina tapering gradually below but apex more or less obtuse; length probably exceeding 100 cm., width in middle and upper parts

about 10 cm. Rachis typically up to 7 mm. wide, showing longitudinal ridges. (Petiole and petiole base unknown.) Lamina segments in middle and upper parts of leaf typically 5 cm. long  $\times$  5 mm. wide at the base but tapering distally to about 2 mm. Apex of segment obtuse or acute; at base segments in contact with neighbouring segments. Segments typically making an angle of  $70^\circ$  to the rachis but curving forwards to about  $55^\circ$ – $65^\circ$  to the rachis. In lower parts

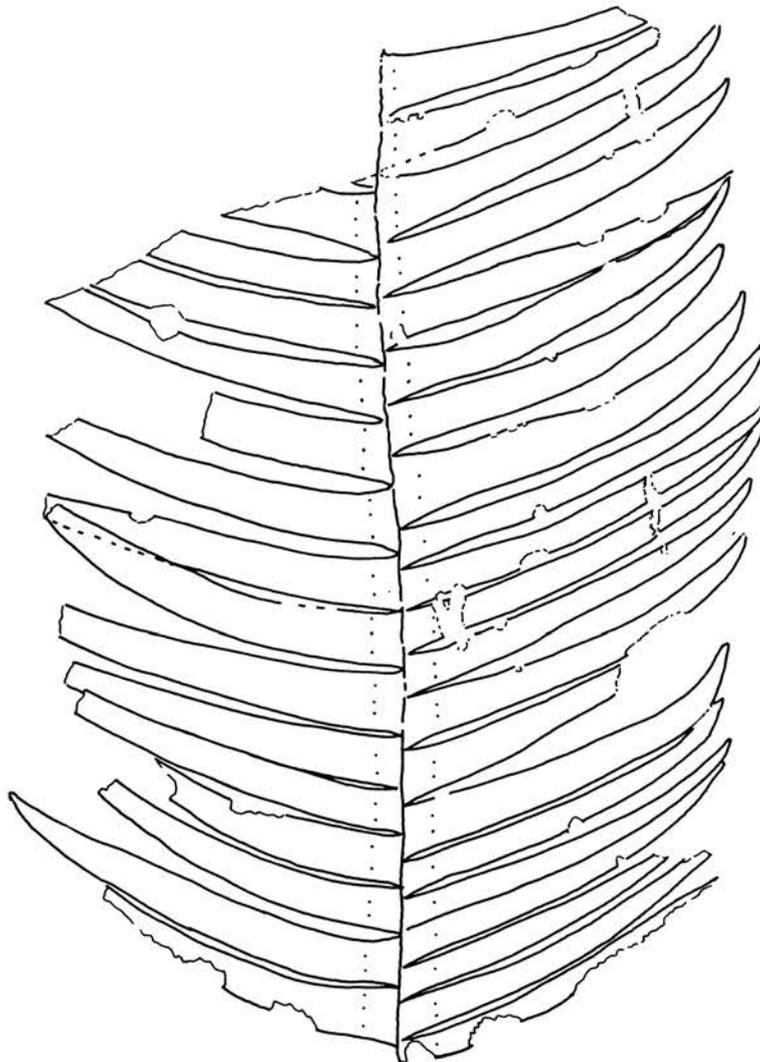


Fig. 18. *Nilssoniasyllis* sp. nov.

Holotype, V.41811,  $\times 1$ . Beast Cliff *Otozamites* Bed.

of leaf and also at leaf apex segments shorter and narrower. Margins of segments depressed, especially in the distal parts of the segments but scarcely revolute. Upper surface of segments showing ill-defined grooves between veins. Lamina either without longitudinal sunken folds or with a single roughly median one. Veins fairly distinct, in typical segment about 22 per cm. near rachis but more crowded (25 per cm.) in narrow basal and apical segments and less crowded (13 per cm.) in largest segments. Veins converging towards apex of segment and concentration increasing about three-fold; all veins reaching the apex. Substance of lamina thin; resin bodies absent.

Cuticles thin. Upper scarcely showing the veins. Cells typically elongated and straight-walled, but in some specimens irregular. Cell outlines moderately broad and clearly marked, straight or very slightly sinuous, interrupted by thin places. Cell surface usually showing some ill-defined, slightly thickened areas. Unicellular trichome bases rare or moderately frequent, consisting of a small oval cell with thick anticlinal walls and a thick central papilla. Lower cuticle showing well marked vein and intervenal areas. On veins, cells elongated with finely marked, nearly straight walls. Cell surface almost evenly thick, except at sides of veins where cells are less regular; walls may be interrupted by pits and the cell surface may show some obscurely thickened areas. Unicellular trichome bases frequent, occurring singly or in groups of two or three. Epidermal cells in intervenal areas small, isodiametric, surface originally bulging and giving a rounded outline with apparently thick lateral walls. Surface smooth, unicellular trichome bases occasional. Stomata frequent, scattered but inconspicuous; guard cells thinly cutinised and sunken and enclosed in a small angular pit formed by about six subsidiary cells forming an irregular ring. Subsidiary cells forming hollow papillae projecting over the pit; papillae sometimes equal and meeting over the pit but some often poorly developed and leaving the pit partly open. Encircling cells absent.

The name is from *Syllis*, a marine worm of similar appearance.

HOLOTYPE. V.41811, Text-fig. 18.

OCCURRENCE.

Lower Deltaic:

Beast Cliff *Otozamites* Bed (common).

Roseberry Topping (occasional).

Haiburn Wyke Plant Bed on beach (rare).

Marske Quarry (see Thomas 1913 and Thomas & Bancroft 1913 as *N. mediana*).

DISCUSSION. *Nilssonia syllis* is very common in the Beast Cliff *Otozamites* Bed, a locality which previous workers seem not to have known. It is occasional elsewhere. The leaf must have been very large; the longest fragment (40 cm.) shows a rachis almost exactly 4 mm. wide near both ends. Another fragment, 12 cm. long., shows a rachis 7 mm. wide throughout. Nearly all specimens appear to be fragments of full sized leaves but there are a few from Roseberry Topping which are determined as diminutive leaves of this species. In one from the middle region the segments are only 4 cm. long and up to 6 mm. wide, but otherwise normal; in the other from the lower part of a leaf the pointed segments are about 2 cm.  $\times$  4 mm. and exceptional in standing at right angles to the rachis and in having flat margins. The rachis is only 2.5 mm. wide. Both specimens match *N. syllis* in cuticle but in form they are more like *N. tenuicaulis*. A few abnormally large leaves with a rachis up to 1 cm. wide and segments at least 7 cm.  $\times$  up to 12 mm. broad occur at Roseberry Topping with normal sized leaves.

In several leaves with rather wide segments there is an ill-defined depression running along the middle of the segment from near the base to the apex. Nothing is known about the cuticle of this groove, but it is so shallow that it may well show no differences.

The cuticle is delicate and could only be prepared from the better preserved leaves, but it proved constant in its small bulging cells on the lower epidermis; the upper epidermis often shows more regularly arranged and elongated cells than the specimen figured. On the lower

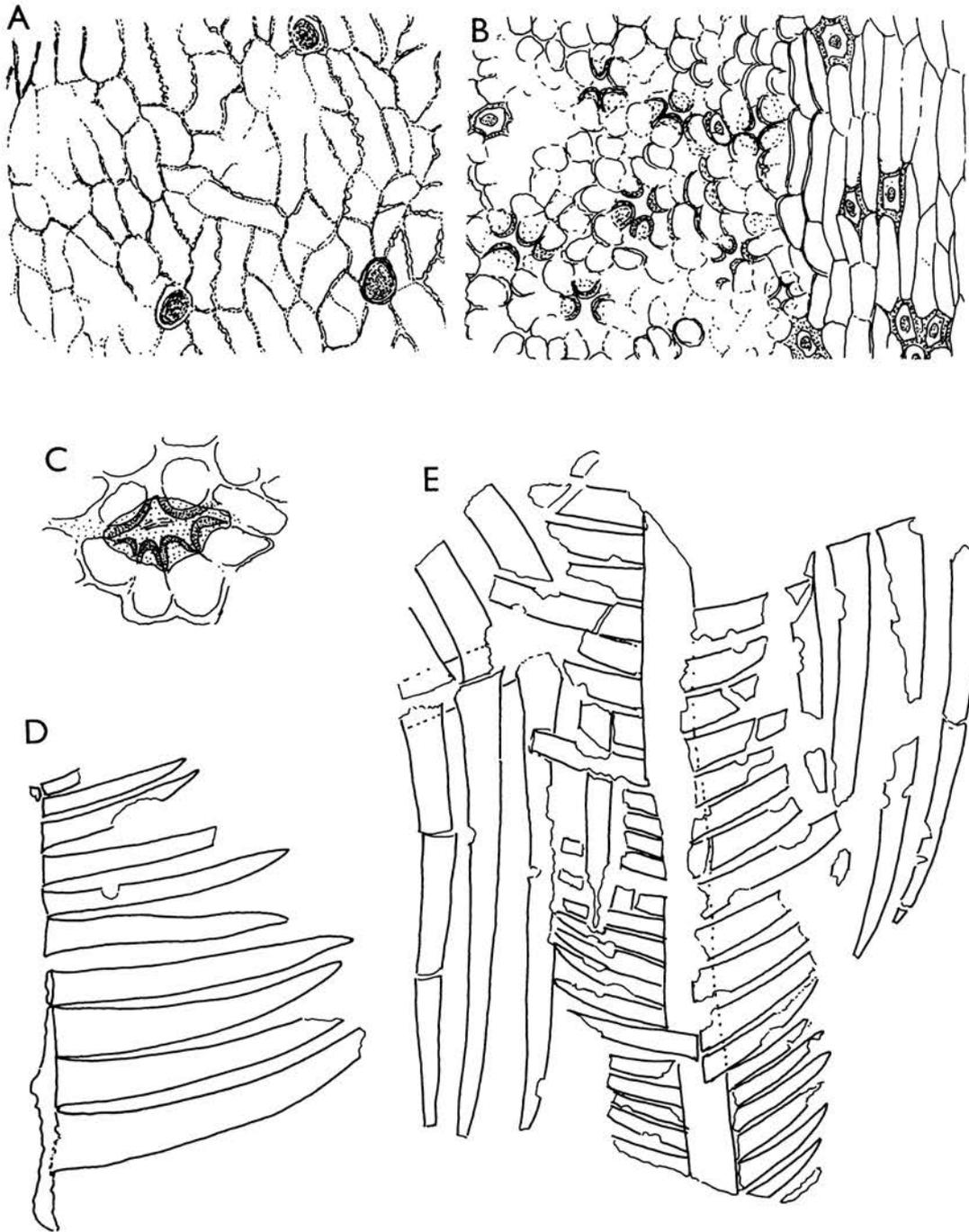


Fig. 19. *Nilssonia syllis* sp. nov.

A, upper cuticle, B, lower cuticle of large leaf, V.45555,  $\times 200$ . C, stoma from V.45555,  $\times 400$ . D, near apex of leaf, V.41813,  $\times 1$ . E, near base of one leaf and middle region of another, V.41812,  $\times 1$ .

The specimen in A-C is from Roseberry Topping. D, E are from Beast Cliff *Otozamites* Bed.

side, near the veins the bulge of the cells tends to point away from the vein and this indicates that the vein originally projected below the interveinal strips, but the absence of any line of crushing indicates that it only projected slightly.

Since no other *Nilssonia* occurs in this part of the Beast Cliff locality, its association there with *Deltolepis mitra* is noteworthy. No *Beania* has yet been found in that bed, however.

IDENTIFICATION. Thomas & Bancroft (1913) give an excellent figure of the lower cuticle of this leaf from Marske Quarry under the name *N. mediana* (= *N. tenuicaulis*) which, however, proves distinct. They refer to the cuticle as being 'well thickened', but the Marske cuticles from which I have made further preparations are rather thin, though thicker than those of *N. tenuicaulis*. The present material is also identified with Sze's (1949) specimen named *N. cf. pterophylloides* although its cuticle is unknown. As Sze pointed out, his specimen has less prominent veins than in *N. pterophylloides*. Moreover, the veins are more crowded, not separated by sharp grooves between them; the segments are narrow, more crowded and seem to have depressed margins. In all these respects it matches *N. syllis* rather than typical *N. pterophylloides*.

COMPARISON. *N. syllis* resembles *N. pterophylloides* Nathorst (1879, 1909) in form and in cuticle. Typical specimens of *N. syllis* differ, however, in their more crowded leaf segments which taper to a sharper point and curve more forwards. In *N. pterophylloides* the veins are less crowded (about 10 per cm. near the rachis, instead of 15-25) and they increase in concentration distally to a less extent. There are accordingly fewer veins per segment. The segment margin in *N. pterophylloides* is shown as flat in Nathorst's figures, and there are distinct sunken folds on the upper side while *N. syllis* has none, or at most one. In *N. pterophylloides* these grooves are represented by strips of broader cells in the upper cuticle, but nothing of the sort is seen in *N. syllis*. The substance of the lamina may be thicker in *N. pterophylloides*, *N. syllis* could not be described as 'fairly thick and strongly coally'.

The Korean leaf described as *N. pterophylloides* by Kawasaki (1925) is smaller than typical *N. syllis*. Further information is needed before it can be compared fully. This applies to *N. pseudopterophylloides* Hollick (1930) from the Cretaceous of Alaska.

The Yorkshire *N. tenuicaulis* (= *N. mediana* Leckenby) is compared with *N. syllis* later.

*N. linearis* Sze (1933), from the Jurassic of China, seems to be distinguished by its narrower and more widely spaced segments. No microscopic details are known.

### *Nilssonia tenuicaulis* (Phillips) Fox-Strangways

Text-figs. 20, 21

The following are all Yorkshire specimens:

- 1829 *Cycadites tenuicaulis* Phillips, pp. 148, 189, pl. 7, fig. 19. (Poor figure without description; specimen in Yorkshire Museum drawn at  $\times \frac{2}{3}$  and 2 cm. of rachis at base omitted.)
- 1864 *Pterophyllum medianum* Leckenby, p. 77, pl. 8, fig. 3. (Typical leaf.)
- 1864 *Pterophyllum angustifolium* Leckenby, p. 77, pl. 8, fig. 2. (Typical leaf.)
- 1873 *Pterophyllum medianum* Leckenby: Zigno, p. 24, pl. 29, fig. 4. (Good leaf from Yorkshire.)
- 1875 *Pterophyllum medianum* Phillips: Phillips, p. 226, Lign. 55. (Poor figure.)
- 1875 *Pterophyllum tenuicaule* (Phillips) Phillips, p. 227, pl. 7, fig. 19. (Same specimen as Phillips 1829 but redrawn.)
- 1875 *Pterophyllum angustifolium* Leckenby: Phillips, p. 227, Lign. 56. (Poor figure.)
- 1892 *Nilssonia tenuicaulis* (Phillips) Fox-Strangways, p. 219. (Name.)
- 1900 *Nilssonia mediana* (Leckenby) Seward, p. 227, pl. 4, figs. 1-4. (Good leaves.)
- 1943a *Nilssonia tenuicaulis* (Phillips): Harris, p. 844, text-figs. 3, 4. (Leaf and cuticle.)

Specimens from other regions determined as *N. tenuicaulis* or *N. mediana* (Cuticles unknown):

- 1911 *Nilssonia mediana* (Leckenby): Seward, p. 697, pl. 7, fig. 13; Text-fig. 13 c. (Poor specimens, Upper Jurassic, Scotland.)  
 1912a *Nilssonia mediana* (Leckenby): Seward, pp. 12, 28, pl. 2, fig. 13. (Fragment, Jurassic, Amurland.)  
 1912 *Nilssonia mediana* (Leckenby): Seward, p. 29, pl. 3, fig. 35. (Not typical, segments at 70° to rachis, Jurassic, Afghanistan.)  
 1926 cf. *Nilssonia tenuicaulis* (Phillips): Kawasaki, p. 19, pl. 5, fig. 15. (Segments with acute apices, Jurassic, Korea.)  
 1929 *Nilssonia tenuicaulis* (Phillips): Yabe & Oishi, p. 86, pl. 18, fig. 1; pl. 19, fig. 1. (Good leaves, Jurassic, China and Korea.)  
 1933 *Nilssonia mediana* (Leckenby): Prinada, p. 21, pl. 2, fig. 8, ? fig. 9, cf. pp. 21, 38. (Jurassic, Transcaucasia.)  
 1940 cf. *Nilssonia tenuicaulis* (Phillips): Oishi, p. 318, pl. 34, fig. 4. (Pinnae lateral?, Jurassic, Japan.)  
 1961 *Nilssonia mediana* (Leckenby): Vachrameev & Doludenko, p. 94, pl. 42, figs. 1, 2; pl. 43, fig. 4. (Upper Jurassic, Central Siberia.)  
 1963 *Nilssonia mediana* (Leckenby): Basanova, Burakova & Bekasova, p. 196, pl. 50, fig. 1. (Jurassic, Central Asia.)

The following are distinct:

- 1913 *Nilssonia mediana* (Leckenby): Thomas, p. 239. (No figure; see Thomas & Bancroft below.)  
 1913 *Nilssonia mediana* (Leckenby): Thomas & Bancroft, p. 191, pl. 19, fig. 15; pl. 20, fig. 10. (*N. syllis* see p. 46 above.)

EMENDED DIAGNOSIS. Leaf as a whole oblanceolate, lamina tapering more gradually below, but apex obtuse or rounded; length unknown (possibly 20–30 cm.), width typically 5–8 cm., but often less. Rachis rather slender (2–4 mm.) longitudinally ribbed, petiole short, base expanded. Lamina segments in middle region of leaf typically 4 cm. × 10 mm. wide basally, and in contact with adjacent segments, quickly contracting to about 6 mm. but then only diminishing slightly to about 4 mm. near the apex; apex usually obtuse but other shapes occurring; segments with acute apices occasional. Segments typically at right angles to the rachis and almost straight. Segments near leaf base short and truncate but acute near leaf apex. Margins of segments flat (occasionally incurved near apex), upper surface of lamina almost smooth, no longitudinal grooves present on upper surface. Veins fine and not prominent on either side, except near rachis, arising at 11–25 per cm. at the rachis and increasing as the segment narrows to its apex. Veins ending in the truncate end or in blunt apical teeth. Substance of lamina delicate. Resin present in lamina but only visible after maceration, forming round bodies, 150 $\mu$  wide, at intervals of 1–2 mm.

Cuticle of lamina very thin. Upper showing rows of more elongated cells along the veins, less elongated cells between the veins. Cell walls straight, outlines often appearing double as though thin along the middle. Surface of cell flat, finely mottled or faintly striated. Trichomes and stomata absent.

Lower cuticle slightly thinner; cells along veins elongated, cells in wide interveinal areas isodiametric. Trichome bases occasional, chiefly along veins. Cell outlines very faintly marked; cell surface flat, sometimes faintly striated. Stomata scattered, aperture only slightly sunken, subsidiary cells irregularly placed, but often with two larger lateral ones present. Inner edge of subsidiary cell slightly thickened to form a shallow stomatal pit.

LECTOTYPE. Specimen figured by Phillips (1829, pl. 7, fig. 19). Yorkshire Museum.

OCCURRENCE. *N. tenuicaulis* is known only from the Gristhorpe Bed (Middle Deltaic Gristhorpe Series). There are a few specimens from other localities, notably some from Whitby, collected by Dr. Hamshaw Thomas, which match it moderately well in form but are not well enough preserved for their cuticles to confirm the determination.

DISCUSSION. *N. tenuicaulis* proves to be an uncommon leaf and the few new specimens merely confirm the statements given in Seward 1900 and Harris 1943a about the form and cuticle. The diagnosis has been slightly extended. The length of a full sized leaf must be more

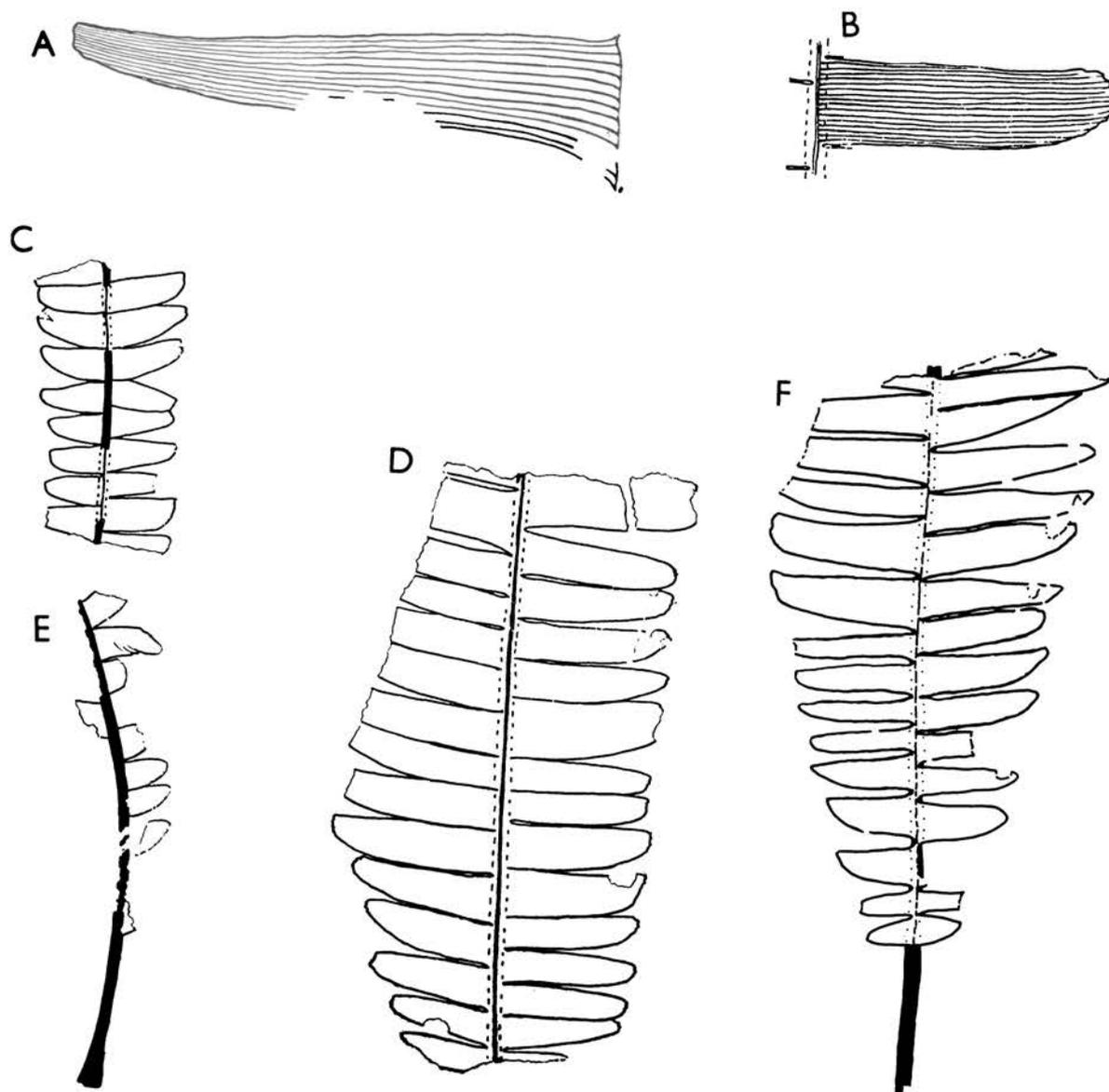


Fig. 20. *Nilssonia tenuicaulis* (Phillips)

A, detached pinna, V.26872,  $\times 2$ . B, one pinna from D,  $\times 2$ . C, D, E, three leaf-fragments, all on V.25866,  $\times 1$ . F, leaf base, K.256, Sedgwick Museum, Cambridge,  $\times 1$ .

A-E are from the Gristhorpe Bed. F, probably from the Gristhorpe Bed. A-E are from Harris (1943a, text-fig. 3).

than the estimate of 20 cm. previously given, since certain fragments of about this length are plainly not complete, but there is nothing to suggest that it is a long leaf. Diminutive leaves of *N. tenuicaulis* are frequent at Gristhorpe.

COMPARISON. *N. tenuicaulis* is rather like *N. sylis* but differs as follows: *N. tenuicaulis* is a smaller leaf with more nearly parallel-sided segments which stand at right angles to the rachis and have a more truncate apex (except near the top of the leaf where they taper and are acute). The segment margins are flat, the veins much less prominent, resin bodies are present. The

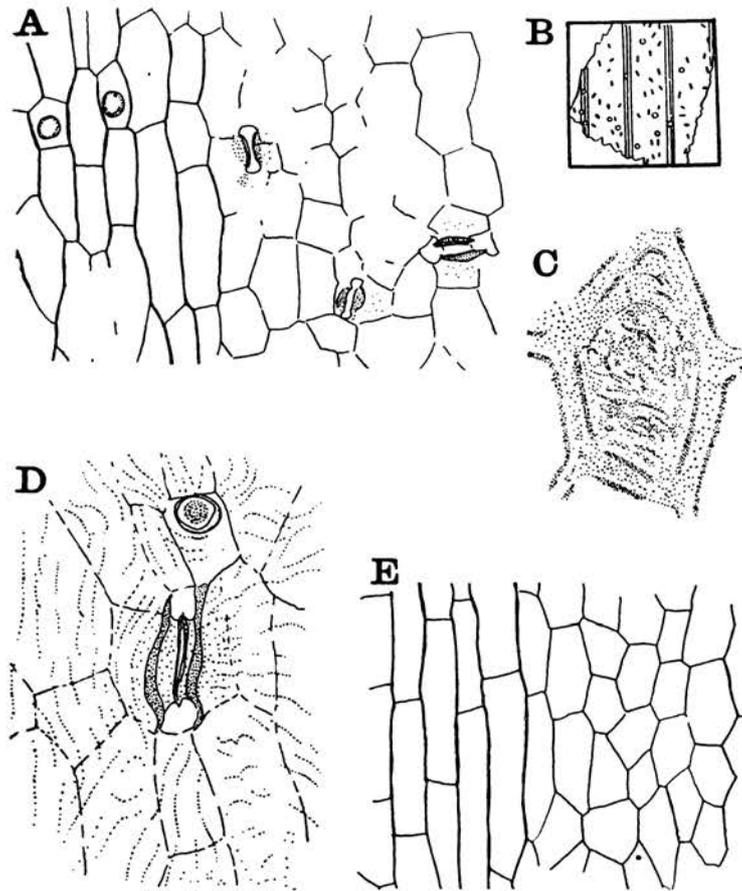


Fig. 21. *Nilssonia tenuicaulis* (Phillips)

A, lower cuticle, V.25866a,  $\times 200$ . B, fragment of lower epidermis, the square is 1 sq. mm.; rulings represent veins, circles trichomes, black ovals stomatal apertures; some of the stomata and trichomes have probably been missed, V.25866b. C, one cell of upper epidermis, V.25866b,  $\times 800$ . D, stoma and trichome, V.25866b,  $\times 400$ . E, upper cuticle, a vein is on the left, V.25866b  $\times 200$ .

The specimens are from the Gristhorpe Bed. The figures are from Harris (1943a, text-fig. 4).

cuticles are thinner, the upper cuticle shows the veins more distinctly and no trichomes occur; the lower cuticle shows flat instead of bulging cells in the interveinal areas and the stomata are more exposed.

There is no reason to attribute any reproductive organ to *N. tenuicaulis*.

*Nilssonia compta* (Phillips) Bronn

Text-figs. 22, 23

## 1. Yorkshire specimens:

- 1822 'Fern in Sandstone', Young & Bird, p. 184, pl. 3, fig. 2.  
 1828a *Pterophyllum williamsonis* Brongniart, p. 95. (*Nomen nudum*.)  
 1829 *Cycadites comptus* Phillips, p. 148, pl. 7, fig. 20. (Poor drawing.)  
 1833 *Pterophyllum comptum* (Phillips) Lindley & Hutton, pl. 66. (Moderately good drawings.)  
 1848 *Nilssonia compta* (Phillips) Bronn, p. 812. (Name.)  
 1864 *Pterophyllum comptum* (Phillips): Leckenby, p. 77, pl. 9, fig. 1. (Specimen κ. 250 in Leckenby Collection, Sedgwick Museum, Cambridge.)  
 1875 *Pterophyllum comptum* (Phillips): Phillips, p. 227, pl. 7, fig. 20. (As Phillips 1829.)  
 1900 *Nilssonia compta* (Phillips): Seward, p. 223, pl. 4, fig. 5; text-figs. 39, 40. (Good leaves.)  
 1913 *Nilssonia compta* (Phillips): Thomas & Bancroft, p. 190. (Description of cuticle. Figures possibly not of this species.)  
 1914 *Nilssonia compta* (Phillips): Gothan, p. 125. (Notes on Yorkshire material and comparison with *N. acuminata*.)  
 1917 *Nilssonia compta* (Phillips): Seward, p. 573, text-fig. 622. (Portion of a large leaf.)  
 1942 *Nilssonia compta* (Phillips): Harris, p. 578, text-figs. 5, 6. (Form and cuticle.)

2. Specimens determined as *Nilssonia compta* from other regions (in no case confirmed by cuticle):

- 1883 *Nilssonia compta* (Phillips): Schenk, p. 262, pl. 54, fig. 2. (Jurassic, China.)  
 1905 *Nilssonia compta* (Phillips): Ward, p. 94, pl. 17, figs. 11-14. (Jurassic, Oregon, U.S.A.)  
 1911 *Nilssonia* cf. *compta* (Phillips): Seward, p. 697, pl. 5, figs. 78, 81. (Fragments, Upper Jurassic, Scotland.)  
 1911 *Nilssonia compta* (Phillips): Thomas, pp. 39, 85, pl. 6, fig. 3. (Fragment, Kamenka, Russia.)  
 1912 *Nilssonia compta* (Phillips): Seward, p. 28, pl. 7, fig. 84. (Good leaf, Jurassic, Afghanistan.)  
 1917 *Nilssonia compta*? (Phillips): Arber, p. 51, pl. 8, figs. 2, 3, 9. (Jurassic, New Zealand.)  
 1929 *Nilssonia* cf. *compta* (Phillips): Yabe & Oishi, p. 87, pl. 19, fig. 2; pl. 20, fig. 1, 1 A. (Jurassic, China.)  
 1934 *Nilssonia compta* (Phillips): Edwards, p. 98, pl. 5, fig. 1. (Jurassic, New Zealand.)  
 1949 *Nilssonia* cf. *compta* (Phillips): Sze, p. 10, pl. 6, fig. 2; pl. 8, fig. 89. (Jurassic, West Hupeh, China.)  
 1957 *Nilssonia compta* (Phillips): Stanislavski, p. 58, pl. 6, figs. 2, 3; pl. 7, figs. 4, 5.  
 1963 *Nilssonia compta* (Phillips): Baranova, Burakova & Bekasova, p. 198, pl. 51, fig. 8. (Jurassic, Central Asia.)

3. Specimens of unknown structure, determined under other names but more or less resembling forms of *Nilssonia compta* or *N. kendalli*:

- 1876 *Anomozamites acutilobus* Heer, p. 102, pl. 23, fig. 1 A; pl. 24, figs. 1-3; pl. 25, fig. 9; pl. 28, fig. 3 B. (Jurassic, Amurland.)  
 1876 *Anomozamites angulatus* Heer, p. 103, pl. 25, fig. 1. (Jurassic, Amurland.)  
 1876 *Anomozamites schmidtii* Heer, p. 100, pl. 23, figs. 2, 3; pl. 24, figs. 4-7. (Jurassic, Amurland.)  
 1876 *Pterophyllum helmersenianum* Heer, p. 104, pl. 25, figs. 2-6; pl. 29, fig. 1 D. (Jurassic, Amurland.)  
 1876 *Pterophyllum lancilobium* Heer, p. 104, pl. 25, figs. 7, 8. (Jurassic, Amurland.)  
 (These five names may represent a single species of *Nilssonia*.)  
 1907 *Nilssonia* sp. cf. *polymorpha* Schenk: Salfeld, p. 175, pl. 15, fig. 7. (Fragment, no details, Rhaetic, Germany.)  
 1909 *Nilssonia* (*Williamsonia*) *polymorpha* Schenk: Salfeld, p. 23, pl. 2, figs. 15-20. (Lower Lias, N. Germany.)  
 1912a *Nilssonia schmidtii* (Heer) Seward, pp. 11, 27, pl. 2, figs. 11, 12, 14. (Jurassic, Amurland.)  
 1930 *Nilssonia serotina* Heer: Hollick, p. 43, pl. 4, figs. 1-7; pl. 5, figs. 1-5 A; pl. 7, figs. 6 A, 6 B, 10 A; pl. 29, figs. 3 B, 5 A; pl. 30, figs. 2 A, 3 B. (Upper Cretaceous, Alaska.)  
 1930 *Nilssonia comptula* Heer var. *approximata* Hollick, p. 44, pl. 6, fig. 1. (Cretaceous, Alaska.)  
 1931 *Nilssonia acuminata* (Presl): Prinada, p. 27, pl. 3, fig. 32; pl. 4, figs. 34, 35, 39; pl. 6, fig. 64. (Middle Jurassic, Central Asia.)  
 1933 *Nilssonia acuminata* (Presl): Kryshstofovich, pl. 17, fig. 3. (Jurassic, Angaraland.)  
 1933 *Nilssonia acuminata* (Presl): Sze, p. 40, pl. 10, figs. 1-3. (Jurassic, Kiangsi, China) and pl. 5, figs. 1-6 (Jurassic, Hopei, China.)  
 1933 *Nilssonia variabilis* Prinada, p. 22, pl. 2, fig. 10. (Jurassic, Transcaucasia.)

- 1940 *Nilssonia nipponensis* Yokohama: Oishi, p. 306, pl. 27, figs. 1-3. (Jurassic, Japan.)  
 1940 *Nilssonia schaubergensis* (Dunker) Oishi, p. 311, pl. 27, figs. 5-11; pl. 28, fig. 2. (Small leaves, Lower Cretaceous, Japan.)  
 1940 *Nilssonia serotina* Heer: Oishi, p. 315, pl. 2; pl. 5, figs. 1, 3. (Jurassic, Japan.)  
 1940 *Nilssonia yabei* Tateiwa: Oishi, p. 320, pl. 28, fig. 1. (Jurassic, Japan.)  
 1952 *Nilssonia* cf. *acuminata* (Presl): Sze & Lee, p. 7, pl. 4, fig. 1; pl. 5, fig. 6. (Jurassic, Szechuan, China.)  
 1961 *Nilssonia schmidtii* (Heer): Vachrameev & Doludenko, p. 96, pl. 43, figs. 5, 6. (Upper Jurassic, Burenska Basin, Central Siberia.)

EMENDED DIAGNOSIS. Leaf as a whole long, oblanceolate, lamina tapering gradually below but apex more or less obtuse. Length in normal sized leaves possibly 50 cm., width about 4 cm. in middle or upper parts, largest leaves about 6 cm. broad and length probably greater than 50 cm. Diminutive leaves occurring commonly with the normal ones. Petiole typically 3-4 mm. wide and 5 cm. long in normal leaves, base widely expanded.

Lamina divided into segments, but segments often very uneven in width; commonly broader than long in lower part of leaf but soon becoming equal and then longer than broad in the middle and upper parts of leaf. Shape of segments very varied. Commonest form approaching rhomboidal, but with lower lateral margin curving forwards and continuing without a break into the distal margin. Other forms are: segments with margins strictly parallel and thus rhomboidal or lateral margins converging, the segment thus approaching triangular in shape. Unsegmented form exceptional. Distal margin of segment varied, entire or lobed, or irregularly dentate.

Veins broad and projecting below, inconspicuous above, arising from the rachis at an angle of 70°-80°, running nearly parallel to nearest lateral margin and the lower ones at least, thus tending to curve forwards and their concentration to increase distally. In full sized leaf, veins arising at about 14 per cm. near rachis, but often becoming closer near the distal margin; typical concentration at about the middle of a segment 20 per cm. Veins finer and more crowded in small leaves.

Substance of lamina fairly thick but fragile; in most leaves, segments without folds, but in certain leaves, segments showing two or three conspicuous longitudinal depressions. Lamina without interstitial ducts or resin bodies between the veins. Epidermal cells inconspicuous above but rather conspicuous below. Margins of segments flat.

Cuticle moderately thin. Upper showing nearly uniform polygonal cells slightly elongated in the direction of the veins; veins unmarked or obscurely shown by slightly narrower cells. Stomata absent, trichomes absent except near segment margins. Cell walls often inconspicuously marked, walls straight, sometimes appearing as a thin strip between two slightly thickened borders. Surface of cells flat, inconspicuously marked with slightly thickened areas.

Lower cuticle showing elongated cells and no stomata along veins, shorter cells and stomata between veins. Width of vein bands about equalling interveinal bands. Cell outlines usually clearly marked along veins, trichome bases numerous; cells at sides of veins adjoining interveinal bands often crushed. In interveinal bands cells only slightly elongated or isodiametric, cell outlines very prominent; cell surface raised as a hemispherical dome but with only inconspicuous ornamentation. Trichome bases usually absent.

Trichome bases consisting of a small, thickly cutinised cell with a ring-shaped scar on the surface; outlines of ordinary cells sometimes traceable underneath trichome base. Trichomes usually shed; free part uncutinised, tapering, those on veins 300 $\mu$  long, those on rachis up to 500 $\mu$ .

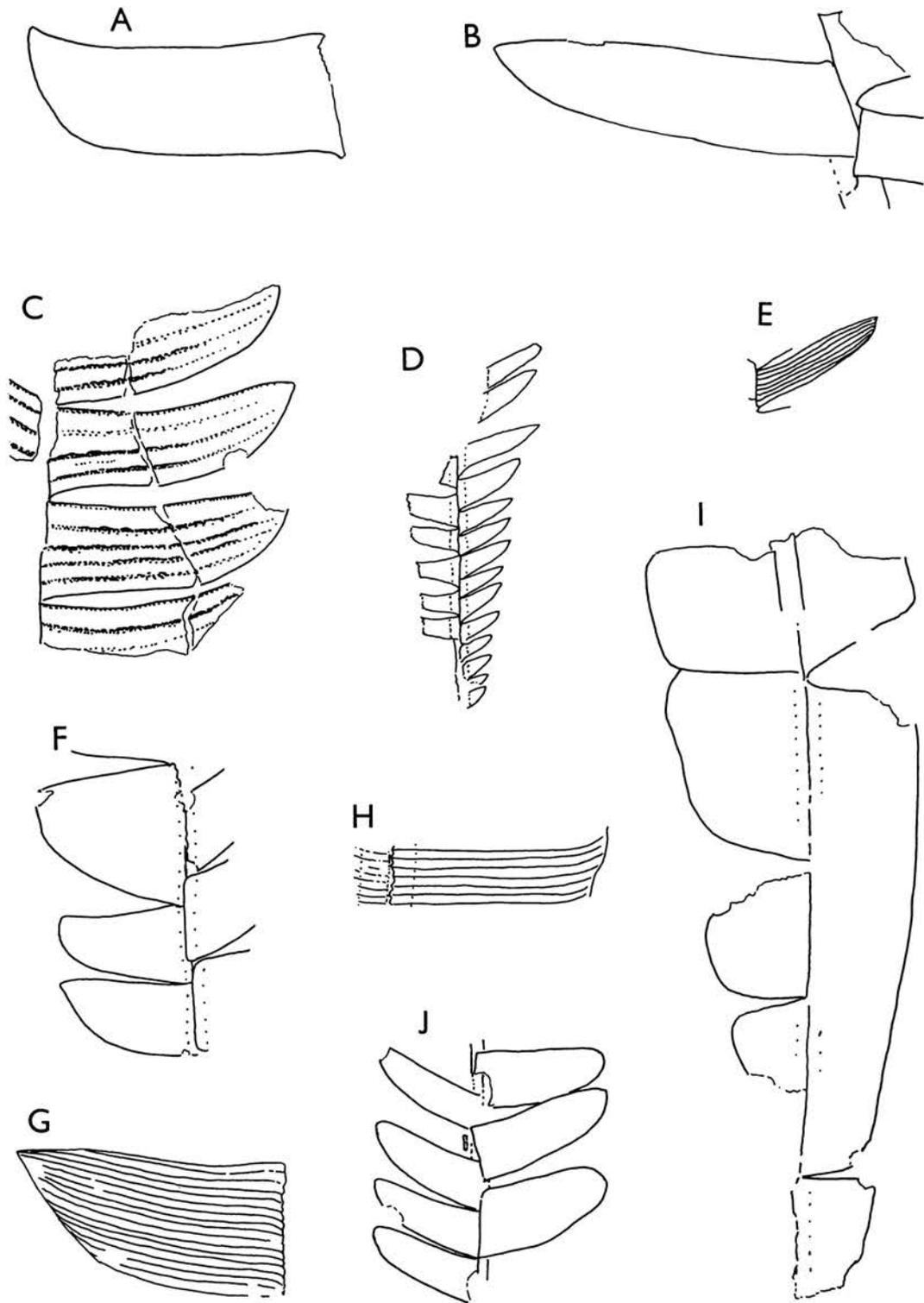


Fig. 22. *Nilssonina compta* (Phillips)

A, V.41819,  $\times 1$ . B, portion only of V.27626,  $\times 1$ . C, leaf with grooves along upper side of segments, V.41818,  $\times 1$ . D, V.41817,  $\times 1$ . E, a segment of D,  $\times 2$ . F, portion only of leaf, V.41814,  $\times 1$ . G, a segment from F,  $\times 2$ . H, veins from I,  $\times 2$ . I, V.41815,  $\times 1$ . J, V.41816,  $\times 1$ .

A, Thimbleby Bank. B, fallen block, Beast Cliff. C, Farndale, Harland Coalpit. D, E, Beast Cliff *Otozamites* Bed. F-J, Roseberry Topping.

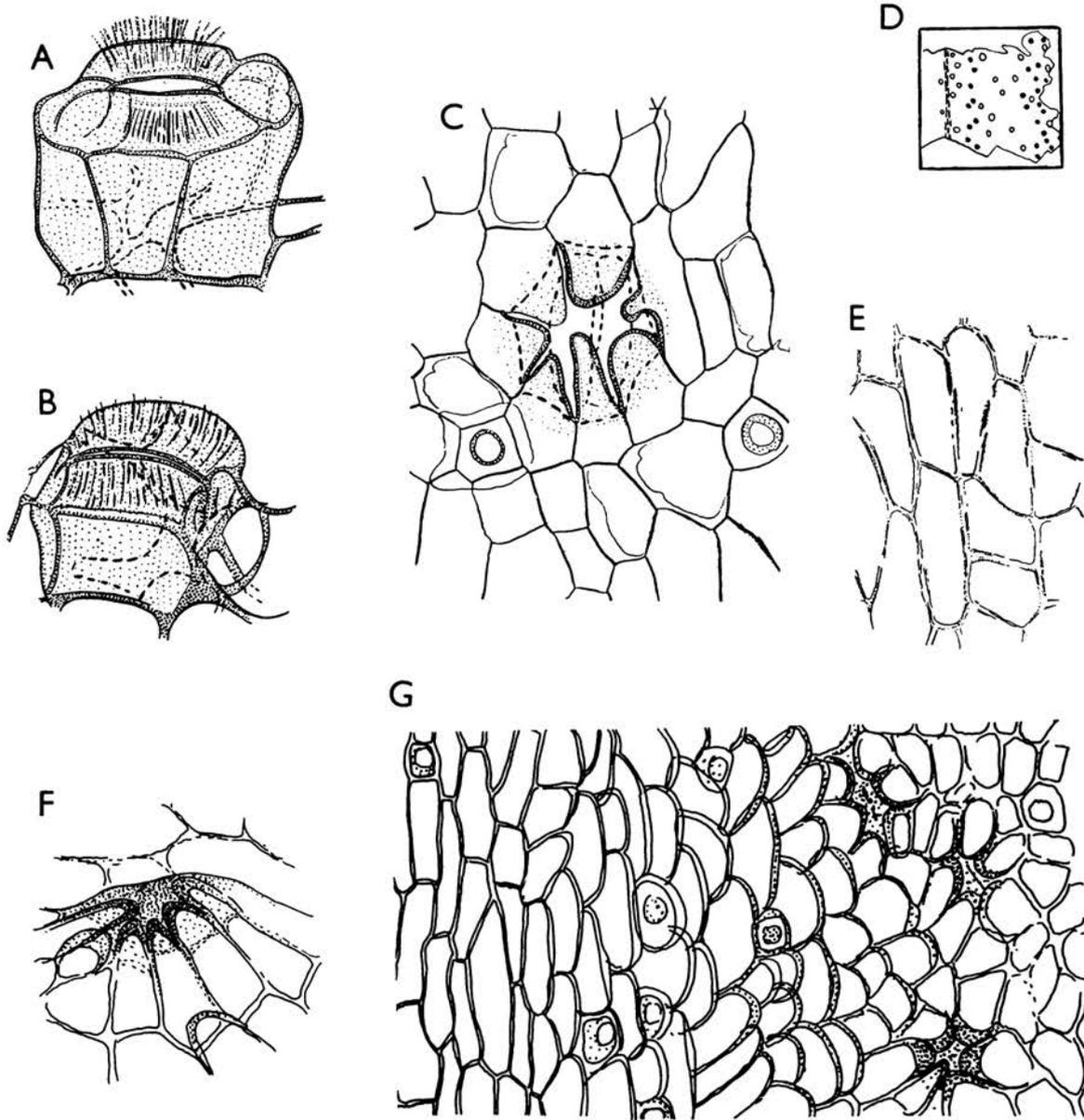


Fig. 23. *Nilssonia compta* (Phillips). Cuticle

A, distorted stomatal pit from the inside; the guard cell fibrils are separate from the main cutinised layer,  $\times 800$ . B, similar stomatal pit; the arched surface of the guard cell is seen. In A and B the papillae are shown by broken lines. C, stomata and trichome bases from the outside; the stomatal pit and guard cells are represented by broken lines,  $\times 400$ . D, fragment of cuticle, lower surface to the right; stomata represented by black dots, trichomes by open circles; the square is 1 mm.,  $\times 20$ . E, upper cuticle,  $\times 400$ . All from V.26835. F, obliquely compressed stoma from outside, V.45554,  $\times 400$ . G, vein (to the left) and intervenal strip showing obliquely compressed, bulging cells at side of vein, V.45554,  $\times 100$ .

All the specimens are from the Gristhorpe Bed. A-E are from Harris (1942, text-fig. 6).

Stomata scattered in intervenal bands, guard cells at the bottom of a wide and deep pit. Six to eight subsidiary cells present, forming an irregular ring, cuticle of surface of subsidiary cells usually projecting horizontally over one edge of the pit as large, wedge-shaped, hollow papillae; cuticle of papillae only slightly thicker than general surface. Occasional epidermal cells bearing a short, upward-pointing, hollow papilla.

LECTOTYPE. Specimen figured by Phillips (1829, pl. 7, fig. 20).

OCCURRENCE.

Middle Deltaic Gristhorpe Series:

Gristhorpe Bed (abundant).

Farndale, shale from Harland old Coal pits

Lower Deltaic:

Roseberry Topping.

Thimbleby Bank Plant Bed.

Whitby Long Bight Plant Bed.

Beast Cliff *Otozamites* Bed.

Haiburn Wyke, just below Iron Scar.

DISCUSSION. *Nilssonia compta* is abundant and widespread in the Gristhorpe Bed (from where nearly all the specimens seen in Museums came) and it is abundant in certain layers at Roseberry Topping. Although fairly widespread it is uncommon elsewhere. It is nearly as polymorphic as *N. polymorpha*, except that completely entire forms are lacking. The commonest form of leaf lies between the limits of specimens shown in Text-fig. 22 F and Text-fig. 22 J, and only about a tenth of the specimens are outside these limits. Longitudinal grooves or folds (which I stated in 1942 did not occur) are seen more or less strongly in about one specimen in five and they are particularly strong in Text-fig. 22 C. Some of these aberrant forms approach more typical specimens of other species, for instance, Text-fig. 22 A approaches *N. princeps*, Text-fig. 22 B approaches *N. tenuicaulis*, Text-fig. 22 C, *N. brevis*, Text-fig. 22 D, *N. muensteri*, Text-fig. 22 I approaches *N. orientalis* and the smaller leaves of all forms approach *N. minor* and *N. kendalli*. However, the cuticles of all these figured specimens, and indeed all specimens I have accepted as *N. compta*, agree with the normal form of *N. compta*.

The fibrils in the walls of the guard-cells in Text-fig. 23 A, B are only seen in exceptionally well-preserved leaves and it is possible they may result from *post-mortem* impregnation of pit canals with a substance subsequently changed to a stable resin. The reproductive organs, *Beania gracilis*, *Androstrobis manis* and the scale leaf, *Deltolepis crepidota*, are attributed to the same plant as *Nilssonia compta*.

COMPARISON. 1. Yorkshire Jurassic. *N. compta* has broader segments than *N. syllis* and the cells of its lower epidermis seldom bulge as much. *N. tenuicaulis* has longer and parallel-sided segments, a thinner cuticle, more exposed stomata and resin bodies in the lamina. '*Nilssonia* sp. B' which is only known from fragments has narrow and more protected stomatal bands where the cells are developed as papillae. The most similar is *N. kendalli* which is compared later.

2. Other regions. Many specimens figured from other floras look more or less like *N. compta* and *N. kendalli*, but where fine details have been described there are differences. The question whether such specimens, whether determined as *N. compta* or given other names, are identical with Yorkshire *N. compta* must be left until they are re-examined.

*Nilssonia kendalli* sp. nov.

Text-figs. 24, 25

DIAGNOSIS. Leaf as a whole long-oval, often obtuse apically. Length seldom exceeding 15 cm. and often less than 10 cm.; width typically about 2 cm., but often less; widest leaves 4 cm. Rachis up to 2 mm. wide, obscurely grooved below, petiole very short, leaf base only slightly expanded. Lamina segments in middle region of leaf very varied but most often triangular and about 1 cm. long  $\times$  8 mm. wide; other shapes including long rectangles, short rectangles, rhomboids and two lobed forms. Segments typically pointing slightly forwards and making an angle of  $80^\circ$  with the rachis, but a smaller angle near the leaf apex. Margins of segments flat, unthickened, apex entire or with rounded lobes, never toothed. Surface of segments flat and nearly smooth.

Veins fine, faintly marked, not prominent on either side, typically about 35 per cm. near the base of a segment but increasing towards the apex. Range noted in middle and upper parts of leaf 25–60 per cm.; towards base of leaf occasionally less than 20 per cm. Substance of lamina thin, resin bodies absent. Cuticles very delicate. Upper showing almost uniform, somewhat elongated cells, slightly narrower and longer over veins. Cell walls straight, marked by a very fine line, or scarcely marked at all. Cell surface flat and almost without local thickenings. Stomata absent, trichome bases usually absent. Lower cuticle showing polygonal or slightly elongated cells along veins almost the same as cells between veins. Cell outlines often invisible, or very finely and faintly marked, cell surface without local thickenings. Veins (distinguished by absence of stomata) a third or half as wide as interveinal strips, no crushing occurring at sides of veins. Stomata scattered in interveinal strips, mostly longitudinal. Poles of guard cells at surface level, aperture only slightly sunken. Subsidiary cells unspecialised and without papillae, forming an indefinite group, but lateral ones thickened along their inner borders, perhaps marking a slight depression of the guard cell surface opposite the stomatal aperture. Trichome bases numerous both on veins and between veins, consisting of a small cell with a slightly thickened surface round a circular gap; free part lost before preservation.

HOLOTYPE. V.41094 (Text-fig. 24 F).

## OCCURRENCE.

Lower Deltaic (all near the base):

Marske Quarry—in the clay above the massive sandstone.  
 Roseberry Topping (abundant throughout most of the section).  
 Ryston Nab Quarry, Roseberry.  
 Hasty Bank (abundant throughout most of the section).  
 Ravenscar, Peak Alum Quarry.

Small fragments of similar sized *Nilssonia* leaves with equally crowded veins and delicate and featureless cuticles occur in the Middle Deltaic Gristhorpe Series at Cloughton (at several points) and in the Sycharham Series (at Goathland). It is possible they belong to *N. kendalli* but they are not identified as the information is insufficient.

DISCUSSION. *Nilssonia kendalli* is abundant at Roseberry Topping and at Hasty Bank and the material available for study was large. It proves polymorphic but the various forms intergrade perfectly and the cuticle is constant in structure, though so delicate as to be difficult to prepare.

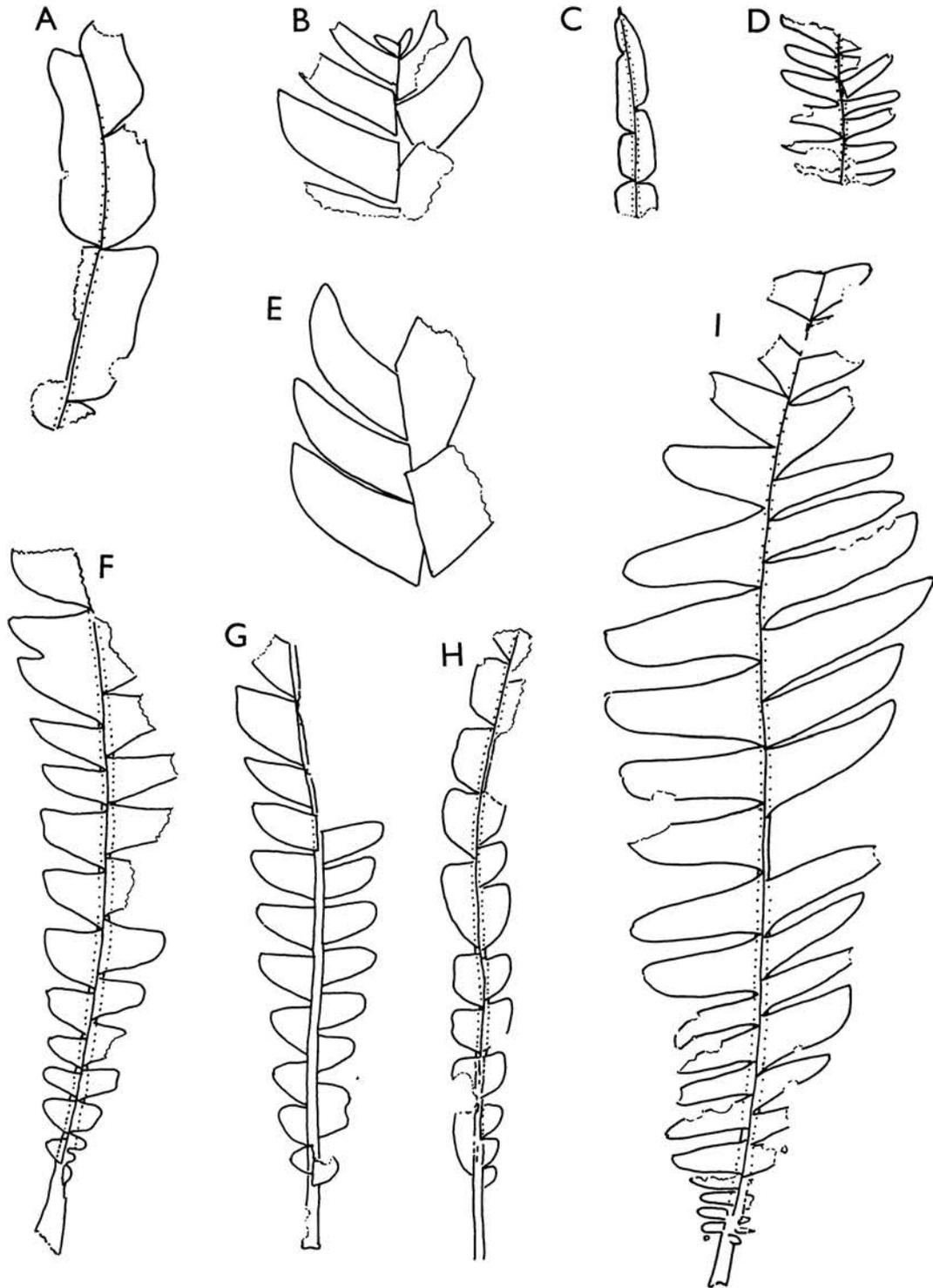


Fig. 24. *Nilssonia kendalli* sp. nov.

Leaves, all natural size

A, apex with broad segments, V.41096. B, apex of large leaf, V.41095. C, apex of very small leaf, V.41093. D, leaf with narrow segments, V.41102. E, apex of large leaf, V.41093. F, lower part of normal leaf, holotype, V.41094. G, lower part of leaf, V.41101. H, lower part of narrow leaf, V.41093. I, almost complete large leaf, V.41097. A-C, E-I, Roseberry Topping. D, Marske Quarry.

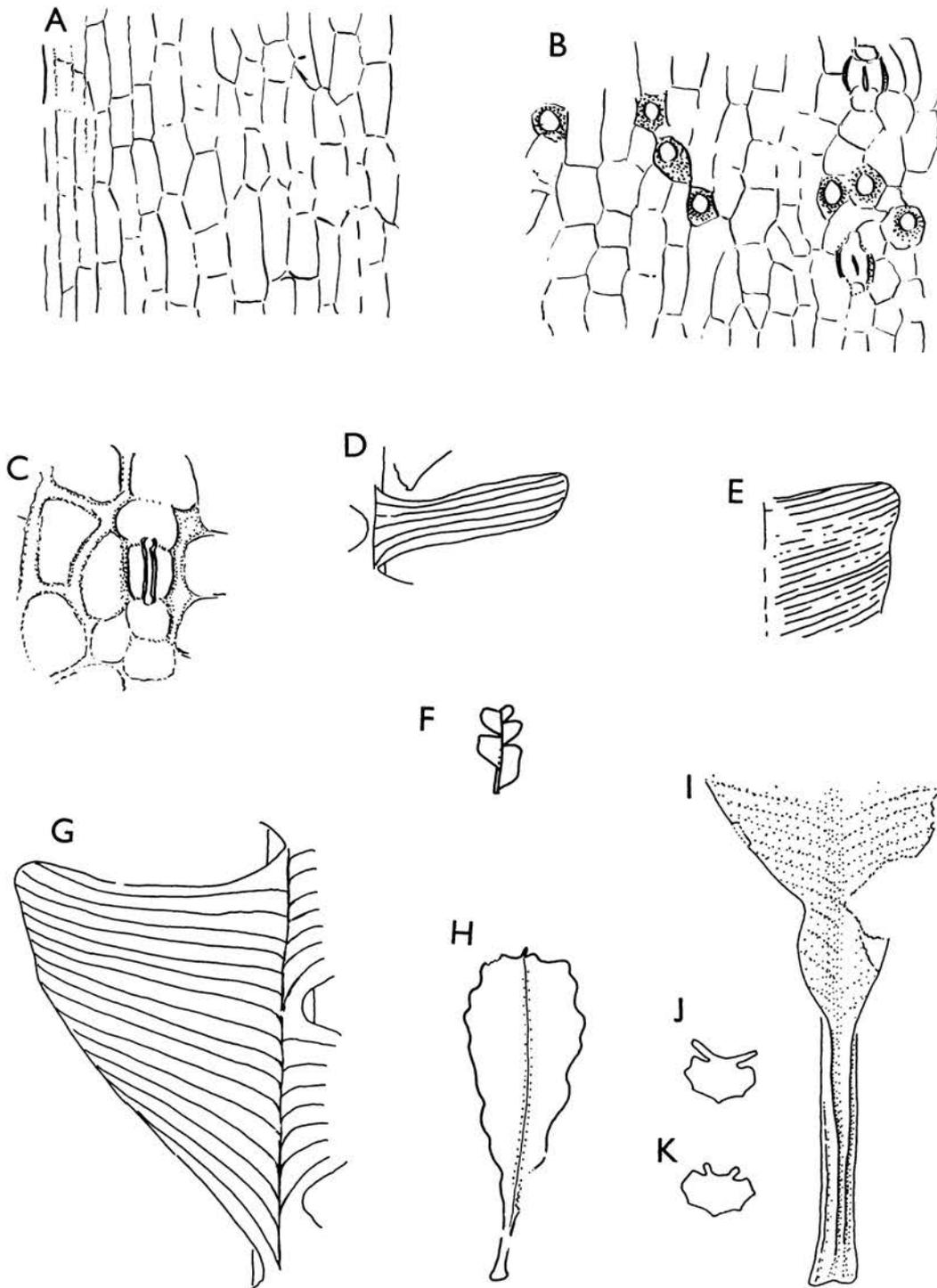


Fig. 25. *Nilssonia kendalli* sp. nov.

A, upper cuticle, vein to left, V.41103,  $\times 200$ . B, lower cuticle of same leaf, vein along middle,  $\times 200$ . C, stoma of same leaf,  $\times 400$ . D, segment of leaf shown in Fig. 24 D, V.41102,  $\times 4$ . E, part of a segment of leaf shown in Fig. 24 A, V.41096,  $\times 4$ . F, apex of small leaf, V.41099,  $\times 1$ . G, triangular segment from lower part of a leaf, V.41100,  $\times 4$ . H, abnormal leaf, V.41098,  $\times 1$ . I, lower part of H showing the lamina continuing on to the petiole,  $\times 4$ . J, K, imaginary sections through the upper and lower parts of petiole of I before compression,  $\times$  about 8.

A-D are from Marske Quarry. E, H-K, Roseberry Topping. F, G, Hasty Bank.

The most exceptional specimen is the entire leaf shown in Text-fig. 25 H, where the veins are unusually widely spaced. Its cuticle is, however, normal and the veins become crowded above. It shows the way the lamina dies away on the surface of the petiole, only disappearing finally at the expanded leaf base. The restored transverse sections are based largely on the ridges shown on the exposed surface. The ridges on the under parts of the petiole (here concealed) are taken from other specimens. There seem to be about seven angles apart from the two ridges formed above by the lamina.

COMPARISON. Although *N. kendalli* has a series of forms matching most forms of *N. compta*, the two are easily distinguished. The leaf in *N. kendalli* is on an average barely half as wide and considerably less than half as long. The substance of the lamina is more delicate; the veins are not prominent below and are more crowded (typically 40 per cm. instead of 15 per cm. near the rachis). The cuticle is very different, being much thinner, the cell walls almost invisible, the stomata exposed and the subsidiary cells not papillate. The two species seem to have been confused earlier, but the confusion ends when one examines their cuticles. Nearly all leaves of the two species can be separated on the concentration of the veins. The only exceptions are very small leaves of *N. compta*, which may have crowded veins (but the normal cuticle of the species) and the lower parts of rather large leaves of *N. kendalli* where the veins may be rather sparse. Again the cuticle is as is normal in *N. kendalli*.

Outside Yorkshire, *N. minor* Harris (1932), from the Greenland Rhaetic, is one of the most similar species. *N. kendalli* differs in its more variable segments (nearly always rhomboidal in *N. minor*) and has more numerous veins (less than 30 per cm. in *N. minor*). Its cuticle is similar but thinner and with even less prominent cell walls and less sunken stomata. *N. kendalli* has the least protected stomata of all species so far studied. Many of the leaves listed previously as resembling *N. compta* are equally like *N. kendalli*, for instance, *N. serotina* as interpreted by Hollick (1930) and *N. schaubergensis* as interpreted by Oishi (1940), but we know nothing of their cuticles. It is certainly possible that, with further knowledge of other floras, *N. kendalli* will prove to be identical with something already described.

The name is after Miss M. W. Kendall who collected most of the specimens described here. She recognised it as a distinct species but previously it seems to have been passed over as small *N. compta*.

### *Nilssonia* sp. B

Text-fig. 26

The cuticle fragments described below are distinct, but the species is not designated as new because the form of the whole leaf is unknown.

DESCRIPTION. Leaf segments 2–4 mm. broad, lower margin meeting free edge at right angles, or curving forwards to meet the upper margin at a point; edges of segment flat and entire; length of segment probably small. Both cuticles thick; upper showing almost uniform, slightly elongated epidermal cells; veins not shown. Cell walls straight, broad, projecting strongly inwards, sometimes slightly nodular, cell surface flat, finely granular. Stomata absent, unicellular trichome bases frequent, scattered, consisting of a small thickened cell with a round scar. Lower cuticle divided into broad strips along veins and narrow stomatal strips between veins; stomatal strips sunken, often deeply sunken and occasionally enclosed by the strips

along the veins meeting over them; stomatal strips often extending under the margin to form a small pouch. Epidermal cells along veins irregularly elongated, walls prominent, nodular, surface wall finely granular. Unicellular trichome bases frequent. Cells of stomatal strips often small and isodiametric, walls specially prominent and sometimes projecting inwards as a peg or flange at a corner of a cell up to  $15\mu$  long. Surface of cells often bulging and thickened to form a hollow papilla. Stomata irregularly crowded, each surrounded by 6–8 subsidiary cells.

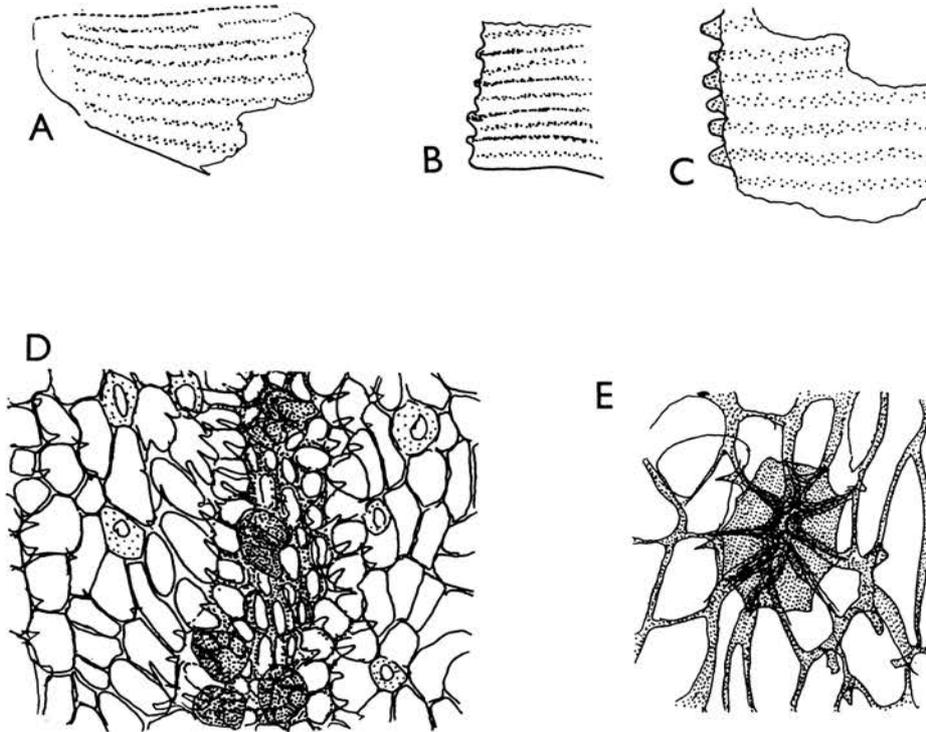


Fig. 26. *Nilssonia* sp. B

A-C, fragments of lower cuticle, all  $\times 8$ . The stomatal grooves are indicated by stippling but the dots do not represent individual stomata accurately. A, apex of pointed pinna, the upper edge is partly restored. B, lower edge of square ended segment, pouches are developed on alternate grooves. C, stomatal grooves wide but pouches strongly developed. D, details of a stomatal groove from B,  $\times 200$ . E, vertically compressed stoma from B,  $\times 400$ . A is V.45545, from Haiburn Wyke 'Gorse Bed'; B is V.45546, from Ladhill Beck, West Coalpit; C is V.45547, from R. Rye Coalpit.

Subsidiary cells of irregular size and shape; each bearing a large, very thick-walled but hollow papilla; papillae pressed together over the stomatal pit. Stomatal pit forming a strongly cutinised cylinder about  $60\mu$  deep and  $40\mu$  wide.

**OCCURRENCE.** *Nilssonia* sp. B has only been seen as cuticle fragments obtained by macerating certain coals and shales, but is occasionally abundant in these macerations. It occurs as follows:

Middle Deltaic Gristhorpe Series:

Hawnby, Ladhill Beck, West Coal pit (abundant).  
Snilesworth, R. Rye Coal pit.

Middle Deltaic Sycarham Series:

Haiburn Cliff 'Gorse' Bed (abundant).

Lower Deltaic:

Sandsend Alum Pit, A.

Raisdale, Great Gill Mells.

DISCUSSION. *Nilssonia* sp. B is interesting for its strong xeromorphy, this consisting in the thickness of its cuticle, the protection of stomata individually and their further protection by the deepness and occasionally the constriction of the stomatal grooves, though it varies in this last character. The other xeromorphic Yorkshire species (*N. revoluta*) has its stomata protected in a different way.

A strange feature of the cuticle of *Nilssonia* sp. B is that the stomatal grooves often extend a short distance as little pouches under the leaf margin and occasionally these pouches are 0.5 mm. long, but usually they are less and are often not formed at all. The upper epidermis bends over and forms an entire margin so that although the lower epidermis forms pouches, these must be buried in the thickness of the lamina.

Although no fragment shows the full length of the segment, the frequency with which apices were met suggests that the length is 1–2 cm. The most similar Yorkshire species is *N. compta*, where, however, the cuticle is far thinner, the veins fewer and the stomatal grooves much less deep.

### Genus DELTOLEPIS Harris 1942: 573

DIAGNOSIS (from Harris 1942). Scale leaf of large size, shape broadly triangular; outer surface convex; attachment scar very wide, situated just above the base on the concave side. Vascular tissue of numerous nearly parallel bundles ending in the margins and apex. Substance thick, but becoming thin towards the margins.

Cuticle well developed; epidermal cell walls nearly straight, guard cells of stomata sunken, surrounded by a single irregular ring of subsidiary cells.

TYPE SPECIES. *Deltolepis crepidota* Harris.

REMARKS. This diagnosis would include the scale leaves of the Recent Cycads. We do not yet know whether the broad scale leaves from the Cretaceous called *Eurycycadolepis* have Cycad-like or Bennettitalean stomata. *Deltolepis* is distinguished from *Cycadolepis* by its stomata which have a ring of haplocheilic subsidiary cells instead of two syndetocheilic cells.

#### *Deltolepis crepidota* Harris

Text-fig. 27

1942 *Deltolepis crepidota* Harris, p. 573, text-figs. 3, 4. (Form and cuticle, figures repeated here.)

DIAGNOSIS (from Harris 1942). Width of scale-leaf at base typically 15 mm., length typically 18 mm. Apex pointed or mucronate, base straight or somewhat rounded. Both surfaces thickly marked with short longitudinal ridges. Resin-bodies absent.

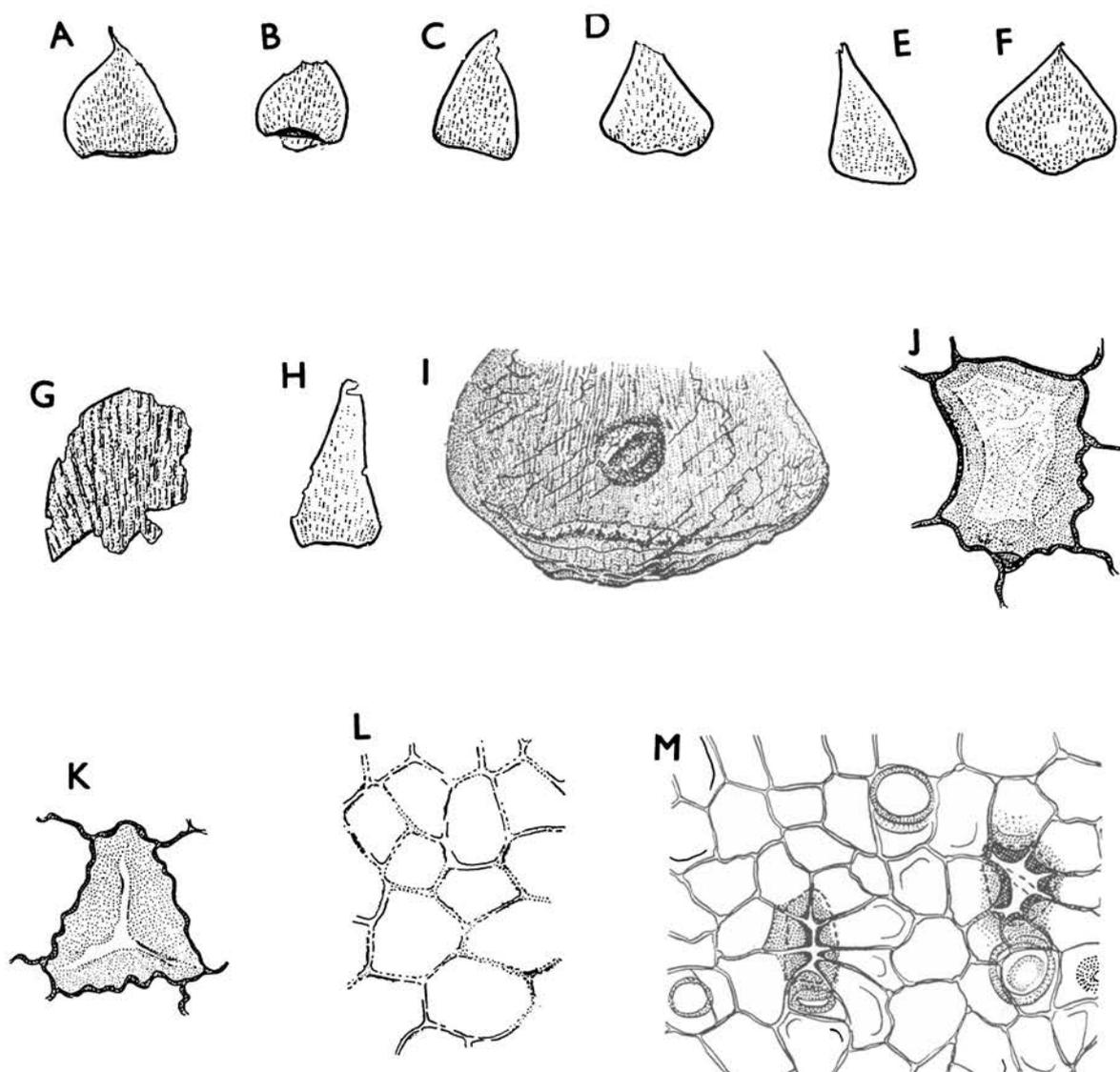


Fig. 27. *Deltolepis crepidota* Harris

In A-F and H, which are natural size, the stippling merely represents the direction of the surface ridges; individual ridges are not shown. Individual ridges are shown to some extent in G, and more distinctly in I. A, V.23935. B, V.25839, showing concave surface and attachment scar. C, V.23952. D, V.21417. E, V.21418. F, holotype, V.21416. G, V.24681, fragment showing veins,  $\times 2$ . H, V.24706. I, transfer of F, holotype, showing the concave surface and attachment scar; the round body in the middle is a pyrites concretion which has nothing to do with the original specimen, V.21416,  $\times 3$ . J, bordered epidermal cell from near lower angle (convex surface), holotype, V.21416,  $\times 800$ . K, broadly bordered epidermal cell from lower part of scale-leaf (convex surface), V.26834,  $\times 800$ . L, cells from near apex of scale (concave surface). V.21416,  $\times 400$ . M, cells of convex side, opposite the part shown in L, V.21416,  $\times 400$ .

All the specimens are from the Gristhorpe Bed. All the figures are from Harris (1942, text-figs. 3, 4).

Cuticle moderately thick; cuticle of convex (i.e. lower) side the thicker, showing frequent stomata in the middle and upper region, but none at the base or lower part or the margins. In upper part of scale cells not in obvious rows; cell-outlines straight, rather strongly marked, surface of cells obscurely mottled. In lower part of scale, cells forming distinct longitudinal rows; lateral walls strongly marked by a fine, inward-pointing lamella of cuticle, the inner margin of which is waved, cell-surface marked by a more or less broad border of slightly thicker cuticle, border occasionally extending to the middle of the cell, but usually leaving an inner mottled area. Stomata scattered, positions not related to vascular supply, subsidiary cells forming a wide and deep cutinised pit, mouth of pit more or less closed by horizontal papillae of subsidiary cells. Guard cells thinly cutinised and wholly immersed. Trichomes frequent in the upper part of the scale-leaf, each consisting of a thick-walled but uncutinised hair over  $200\mu$  long,  $30-40\mu$  broad, borne on a rounded cutinised cell with margins extending over cuticles of the ordinary epidermal cells. Concave side with neither stomata nor trichomes, cell-outlines obscurely marked in the upper part, more distinct below, but never as distinct as on the convex side. Cells isodiametric, polygonal, surface mottled. Cell-outlines often appearing double (i.e. with a median thin strip flanked by thicker bands).

HOLOTYPE. V.21416, figured Harris (1942, text-figs. 3, 4).

OCCURRENCE. Middle Deltaic Gristhorpe Series, Gristhorpe Bed with *Nilssonia compta*.

DISCUSSION. Further collecting has made the close association of *D. crepidota* with *Nilssonia compta* obvious; it is confined to those parts of the Gristhorpe Bed where *N. compta* is abundant. It is, however, less common than *N. compta* and the numerous specimens in the Edwards and Wonnacott collections must have been selected. No forms were seen among new specimens outside the range of those figured. The furrows on the surface of the thicker parts of the scale are thought to be caused by collapse of soft tissues around large sclerotic cells; the veins are rarely seen; Text-fig. 27 G where they are seen represents a naturally cleared specimen.

The evidence of agreement in structure depends on the agreement between the cuticles of the lamina of *N. compta*, and the distal, more leaf-like part of *D. crepidota*. The upper cuticle shows similarly shaped cells with indistinct outlines, commonly looking like a thin strip and two broad borders. Similar sculpture occurs on the cell surface in the two organs. The lower cuticle in *D. crepidota* shows very characteristic stomata, the subsidiary cells having long, conical papillae and also forming a well cutinised pit. Similar trichomes occur.

An intermediate specimen was seen. It is a leaf with a small irregular lamina, but typical *N. compta* cuticle. The petiole is short and expands below into a large base which is triangular and concave. Its surface is wrinkled as in *D. crepidota* and its cuticle is typical in its thin marginal parts but in the middle where the substance is thick it is more like that of a normal *N. compta* leaf base.

It is further to be noted that there is full agreement in cuticle between the lower and rather less leaf-like part of *Deltolepis crepidota* and the free end of the microsporophyll of *Androstrobus manis* and of the megasporophyll of *Beania gracilis*. *Deltolepis* is thus of some help in linking the leaf and reproductive organs.

The specific name refers to the characteristic thickened margin of the epidermal cells.

COMPARISON. See *Deltolepis mitra* and *D. calyptra* (pp. 63, 64).

*Deltolepis mitra* sp. nov.

Pl. 1, fig. 14; Text-fig. 28 A-D

DIAGNOSIS. Shape ovate-deltoid, base up to 2 cm. wide, slightly cordate; scale widening above to 3 cm., length up to 4 cm., apex obtuse. Surfaces thickly marked with short, longitudinal or diverging ridges. Convex side showing uniform, small bulging cells; concave side showing more irregular cells. Cuticles moderately thick. Concave side showing no stomata except near top and edges where a few are present, convex side showing none in lower and middle parts, but numerous stomata near top and edges. Cuticle often slightly thicker on concave side; cells more strongly marked by a broader wall. In lower and middle parts of scale, wall particularly broad but becoming rather finer and still more prominent in upper parts. Cell surface mottled, or occasionally showing one or two parallel lines. Mottling obscure in lower and middle parts of scale but clearer in upper parts. Trichome bases occurring rarely. On convex side cells rather smaller, often isodiametric and in fairly clear longitudinal rows. Cell outlines finely but clearly marked, cell surface bulging but without a thickened papilla; often showing an ill-defined ring (caused by collapse?). Cell surface otherwise unmarked. Stomata where numerous, evenly scattered, guard cells sunken in a cutinised pit; subsidiary cells small, irregular, each with a hollow conical papilla directed over the stoma. Trichomes rare or absent.

Resin bodies about  $300\mu$  wide present in interior.

HOLOTYPE. V.42424 (Pl. 1, fig. 14; Text-fig. 28 A).

OCCURRENCE. Lower Deltaic. Beast Cliff *Otozamites* Bed.

DISCUSSION. The only two specimens are figured. They are imperfectly preserved in a sandy shale and the cuticle, although moderately thick, was only prepared in small pieces and with difficulty. The veins have not been seen, the elongated marks on the surface seem to be isolated sclerids as in *D. crepidota*. Although the stomata are given in the diagnosis as mainly on the convex side, this has not been proved with certainty. No details could be made out in the attachment scar.

The name is from *μιτρα*, a woman's hat, shaped somewhat like this fossil.

COMPARISON. *D. mitra* is very like *D. crepidota* except that *D. mitra* is more than twice as large; the base is rather concave in both specimens but flat as a rule in *D. crepidota*. Their cuticles are rather similar but the epidermal cells among the stomata are more convex in *D. mitra*.

ATTRIBUTION. *D. mitra* is known only from one point in the Beast Cliff *Otozamites* Bed where *Nilssonia syllis* is abundant. The parts of *D. mitra* where stomata occur have cells like those of *N. syllis* but like no other species in this locality. No other *Nilssonia* occurs in this bed and the scale leaf is attributed with some confidence to the same plant as the foliage leaf.

*Deltolepis calyptra* sp. nov.

Text-fig. 28 E-G

DIAGNOSIS. Shape broadly cordate-deltoid, base nearly 1 cm. wide, length about 8-10 mm., apex mucronate. Inner surface strongly and thickly marked with short ridges caused by isolated fibres.

Cuticles rather thin; one side showing polygonal cells with broad, rather ill-marked outlines, occasionally appearing double. Other side showing polygonal cells with walls projecting

inwards as a sharp ridge; cell surface flat. Smaller or narrower cells with thicker walls occurring in groups. Stomata and trichome bases not observed. Round resin bodies,  $100\mu$  wide, frequent in middle part of scale.

HOLOTYPE. V.42425 (Text-fig. 28 E-G).

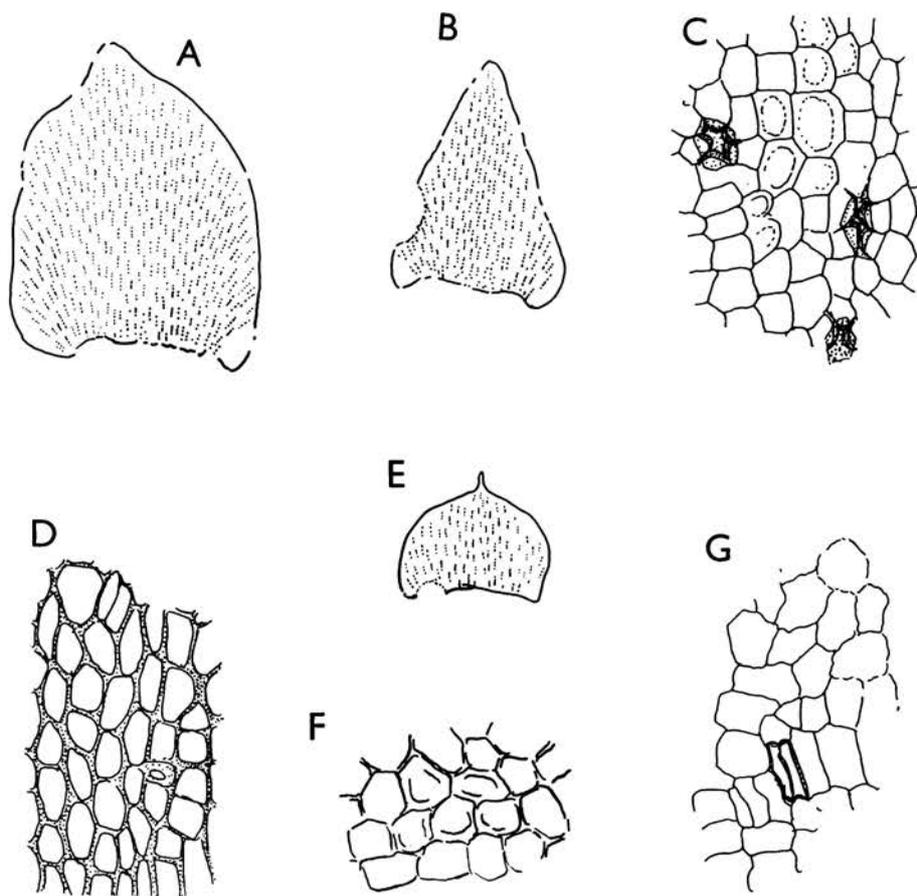


Fig. 28. *Deltolepis mitra* sp. nov., *D. calyptra* sp. nov.

A-D, *Deltolepis mitra*. A, holotype. The stipling represents the direction of surface ridges, not individual marks, V.42424,  $\times 1$ . B, smaller specimen, stippled as A, V.42426,  $\times 1$ . C, cuticle of lower (?) side, from near apex, V.42424a,  $\times 200$ . D, cuticle of upper (?) side below middle, V.42424b,  $\times 200$ . Both specimens from Beast Cliff *Otozamites* Bed.

E-G, *Deltolepis calyptra*. Holotype, V.42425. E, whole specimen, stippling as in A, but magnification is  $\times 2$ . F, G, two fragments of cuticle,  $\times 200$ . The specimen is from Cloughton Wyke *Nilssonina* Bed.

DISCUSSION. *D. calyptra* was only discovered as a result of a deliberate search for a *Deltolepis* by breaking up duplicate specimens from the Cloughton Wyke *Nilssonina* Bed. It is presumed to belong to *Nilssonina tenuinervis*, with which it is associated and with which it shows agreement in resin bodies and in epidermal structure. Unfortunately the cuticle is ill-preserved as the matrix is coarse and the preparations were minute. It is not certain that what appears to be a stoma is of that nature. The Cloughton *Nilssonina* Bed belongs to the Sycarham Series of the

Middle Deltaic. It has a small flora in which *N. tenuinervis* is abundant (but no other *Nilssonia* occurs).

At the end of this investigation a specimen (V.45461) was received which had been collected by Hamshaw Thomas. It showed more or less good specimens of five scales of the same general size and shape as the holotype of *D. calyptra*, and with a similar cuticle; but there is no sign of internal fibres, nor was resin detected in the minute fragments macerated. The dimensions which show a certain range are included in the diagnosis above. The specimens are preserved in a piece of shale full of small fragments including *Nilssonia tenuinervis* and *Androstrobos wonnacotti* (fairly complete). There are no other Cycadales but two Bennettitales, *Nilssoniopteris vittata* and *Ptilophyllum pectinoides*. The shale is localised as Whitby and it resembles a black shale situated about 2 m. above the main plant bed. This association supports the attribution of *D. calyptra* to *N. tenuinervis*.

The name is from *καλυπτρα*, a pointed hat.

### Genus PARACYCAS nov.

*Paracycas* is a more natural group picked out of the old form-genus *Cycadites*. It has segments with a single median vein and the cuticle shows haplocheilic stomata, both characters as in *Cycas*.

*Cycadites* Sternberg 1825 was at first not even a form-genus but an assemblage of fossils which the author hoped were allied to one or another genus of the Cycadales. Gradually it became restricted to leaves with at least a superficial resemblance to *Cycas* and thus became virtually a form-genus. The large and well characterised genus *Pseudocycas* has been removed, leaving the residue which, as inspection of the following list shows, is heterogeneous. I now remove a small group consisting of *P. cteis* and probably of *C. blomqvisti*, and possibly other species. It is interesting that Seward (1917) gave a possible definition of *Cycadites* which would have served for *Paracycas* but made it plain that it was at that time the definition of an imaginary group.

DIAGNOSIS. Leaf simply pinnate; rachis bearing pinnae laterally; pinnae linear, entire, flat, attached by their whole bases to the rachis. Pinnae each with a single, thickened midrib and no other veins. Cuticle present but thin, stomata confined to lower side, scattered, variably orientated, forming a broad, undivided band on either side of the midrib. Epidermal cells straight-walled, stomata haplocheilic, sunken, surrounded by a ring of approximately equal subsidiary cells.

TYPE SPECIES. *Cycadites cteis* Harris (1952 : 614).

REMARKS. It is reasonable to assume that *P. cteis* (Harris) is a member of the Cycadales, but there is not sufficient evidence to indicate close relationship to *Cycas* itself. Its cuticle is much more delicate than in the species now living.

Its reproductive organs are unknown. *Cycadospadix* has sometimes been attributed to *Cycadites*, but on no evidence. Its morphology is open to question and it has not even been proved to bear seeds (those commonly figured on it being a hopeful restoration). A similar looking organ has been shown to be a Bennettitalean scale leaf (Harris 1932a; Florin 1933: 119).

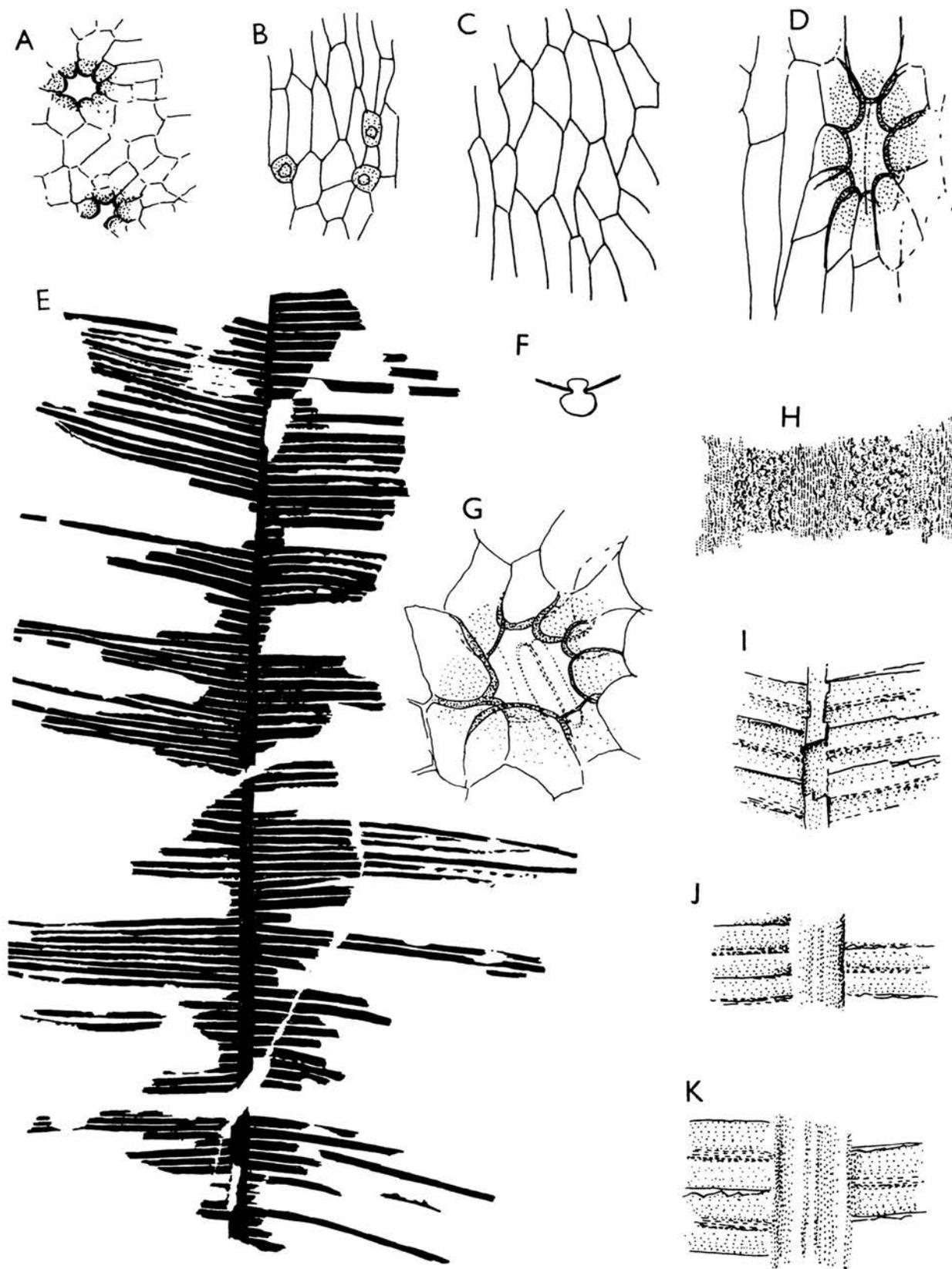


Fig. 29 *see opposite.*

*Paracycas cteis* (Harris) comb. nov.

## Text-fig. 29

1952 *Cycadites cteis* Harris, p. 614, text-figs. 1, 2. (Figures and description repeated here.)

DIAGNOSIS (from Harris 1952). Leaf large, elongated (shape as a whole unknown), width at least 15 cm. Rachis rather slender, smooth, pinnae arising from grooves just above its lateral margins. Pinnae arising almost at right angles to the rachis (angle reduced to 85° near the apex and sometimes increased to about 95° below). Pinnae crowded, in lateral contact below, tapering very gradually from 1.5 or 2.7 mm. at the base to two-thirds of this width at 5–7 cm. from the rachis; apex not known. Surface of pinna flat, but with a slightly thickened midrib, midrib more prominent below; margins flat or very slightly depressed and thickened but never recurved. Substance of lamina, apart from midrib, rather thin; transfusion tissue not observed. Resin bodies absent.

Cuticle thin and fragile (only known from small fragments). Upper surface probably composed of nearly uniform elongated cells with finely, but clearly marked outlines. Lateral walls perfectly straight, cell surface flat, not sculptured.

Lower surface showing two stomatal bands separated by a broad non-stomatal region along the vein and narrower non-stomatal regions along the margin. Epidermal cells along the midrib elongated, straight-walled, interspersed with numerous trichome bases. Trichome base consisting of a small oval cell with a thickened surface, bearing a central ring. Stomatal regions with almost isodiametric cells; cell outlines straight, very finely marked and often faintly shown. Cell surface forming a rounded bulge, but not papillate or sculptured. Stomata fairly numerous, probably irregularly scattered and variably orientated; guard cells rather large, thinly cutinised, sunken at the bottom of a wide, cutinised pit. Margins of pit overhung by hollow ingrowths of subsidiary cells. Subsidiary cells 6–10 more or less equal and forming an imperfect ring, rather small but with strongly thickened cuticle, especially near the stomatal pit.

HOLOTYPE. V.29400, figured Harris (1952; text-figs. 1, 2).

OCCURRENCE. *P. cteis* is rare, only four specimens are known. There is a second fragment associated with the holotype; a smaller fragment from Hasty Bank (V.29401), and an unlocalised fragment in the Stockholm Museum preserved in a matrix which I do not recognise. The specimens, with the possible exception of the last, are of Lower Deltaic age. The cuticle is delicate and poorly preserved in all and was only studied in minute fragments, but the Hasty Bank leaf showed the surface markings well.

COMPARISON. The only Yorkshire leaf resembling *P. cteis* is *Pterophyllum nathorsti* which in extreme forms has just as narrow segments but always with 2–3 veins and a quite different

Fig. 29. *Paracycas cteis* (Harris) comb. nov.

A–D, G, cuticle of holotype. A, lower surface,  $\times 200$ . B, probably midrib,  $\times 200$ . C, upper surface,  $\times 200$ . D, G, stomata,  $\times 400$ . E, holotype, V.29400,  $\times 1$ . F, imaginary section through rachis of I, with thickness restored. H, surface sculpture of under side of pinna, V.29401,  $\times 20$ . I, rachis and pinnae of V.29401,  $\times 4$ . J, rachis and pinnae of holotype,  $\times 4$ . K, rachis and pinna of second leaf on same block as holotype,  $\times 4$ .

A–E, G, J, K from Beast Cliff *Otozamites* Bed. H, I, Hasty Bank. All the figures are from Harris (1952, text-figs. 1, 2).

cuticle. Some of the leaves of other floras determined as species of *Cycadites* may be similar but as will be seen in the long (and doubtless incomplete) list below, very varied fossils have been included.

The most fully comparable leaves are *Cycadites blomqvisti* Antevs (1919) from the Lower Liassic of Sweden and specimens determined as *C. rectangularis* Brauns from the Lower Liassic of England. *C. blomqvisti* is a larger leaf than *P. cteis* (with a rachis about three times as broad), and it has slightly broader segments. Its cuticle is mentioned by Florin (1933: 119) and may be very similar, but no figures or detailed description have been published.

I have re-examined the specimens described by Seward (1904) as *C. rectangularis*. They prove well figured. Specimen V.9009 is preserved in coarse sandstone and shows no fine details, but it may be mentioned that the 10 cm. omitted from Seward's figure agrees with the figured part in both rachis and pinnae. Seward identified it with doubt, but it looks like the others. The other two specimens are in a calcareous shale and must have been good when collected but have been damaged by varnish. In both the pinnae are flat and the midrib is seen as a dark strand about 0.4 mm. broad. The midrib is only slightly thicker in substance than the lamina; it never forms a narrow groove as Seward's fig. 4a might suggest.

The pinnae margins are flat, but in both there is a very narrow dark strand along them: maceration proved that this consists of fibres. In both specimens a few pinnae appear to be complete and to have rounded apices, but I am not quite certain that the true apex is seen. What is certain is that the lamina of one pinna is joined to that of the next along the rachis; this is plain in V.4076 but concealed in 52665 except where the rachis, which overlaps the pinna bases, has broken away. The pinnae in V.4076 are uniformly 1.1 mm. wide, those of 52665 are 2.0 mm. wide near the base and taper to about 1.95 mm.

Their cuticles are very badly preserved, as often happens in plants from the Dorset Lias. Fragments of a delicate cuticle have been seen which show elongated cells with thin straight walls and transverse ends. The surface shows no obvious sculpture; the cells might well be from the midrib. The inner tissues are impregnated with bituminous matter and on maceration cells of the mesophyll are often conspicuous. The midrib yields fibres and some scalariform tracheids and the margins yield a few fibres. No stomata were recognised.

After the varnish (which is water soluble) was removed surface features were recognisable. 52665 shows the upper side of the lamina and this merely shows longitudinally elongated cells more conspicuously elongated along the midrib than elsewhere. V.4076, which exposes the lower side in a typical pinna, showed a zone 430 $\mu$  wide of elongated cells along the midrib flanked by two zones 210 $\mu$  wide with a lumpy surface and these are flanked by two marginal zones 140 $\mu$  wide with a smoother surface. The cells are again elongated but not as conspicuously as on the midrib. The lumpy zone is no doubt stomatal. When the surface of the fossil is moistened with oil the deeper layers are seen, elongated fibres along the midrib and margins and transversely elongated mesophyll cells in the lamina.

These observations suggest that these English Liassic specimens may belong to *Paracycas* but are distinct from *P. cteis*. Those determined as *C. rectangularis* have a broader rachis (9 mm. in 52665) and shorter but broader pinnae (4 cm.  $\times$  2 mm. in 52665) of more nearly uniform width. In *P. cteis* taper is marked. They stand about 0.5 mm. apart near the rachis instead of being in contact.

The form of the pinnae is, however, the same and so are the surface markings of the under

side, and the cuticles do at least agree in being thin and having elongated cells with straight, finely marked walls and a plain surface.

We need more information about the cuticles of this group. Meanwhile, it appears best to leave *C. blomqvisti* and the English specimens of *C. rectangularis* under these present names, rather than to transfer them to *Paracycas*. Seward's identification of the English specimens with *C. rectangularis* Brauns was reasonable but is not supported by any detailed knowledge; on the other hand the figures of some of the specimens determined as *C. rectangularis* suggest that they may be very different.

List of fossils described as species of *Cycadites*, with brief notes on a few resembling *Paracycas cteis*.

- C. acinaciformis* Trautschold, discussed by Seward (1895).  
*C. affinis* Eichwald 1868. Not like *Cycas*.  
*C. alatus* Berger identified with *Nilssonia brevis* by Nathorst (1909).  
*C. althausii* Dunker 1843 is the oldest name of *Matonidium goepperti*, according to several authors.  
*C. apoldensis* Compter 1874 is *Scytophyllum alpodense* (Compter) Linnell (1933).  
*C. blanfordianus* Oldham & Morris identified with *Nilssonia rajmahalensis* by Seward & Sahni (1920).  
*C. blomqvisti* Antevs 1919; Florin (1933) is probably a species of *Paracycas*. See p. 68.  
*C. brongniarti* Mantell is *Nilssonia* or *Dioonites*, Seward (1895).  
*C. bucklandi* Presl is a stem (*Bucklandia*).  
*C. comptus* Phillips 1829 is *Nilssonia compta* (Phillips) Bronn.  
*C. concentricus* Richards 1884 identified with *C. rectangularis* Brauns by Seward (1895).  
*C. conferta* Oldham & Morris and of Feistmantel is identified with *Nilssonia rajmahalensis* by Seward & Sahni (1920).  
*C. constrictus* Feistmantel is *Torreyites constrictus* (Feistmantel) Seward & Sahni (1920).  
*C. contiguus* Eichwald is indeterminable according to Schimper (1870).  
*C. delessei* Saporta 1875; inrolled margins suggest *Pseudocycas*.  
*C. dicksonii* Heer is *Pseudocycas dicksonii* (Heer) Nathorst (1907).  
*C. escheri* Heer is a stem.  
*C. giganteus* Hisinger 1840 identified as *Podozamites distans* Presl by Nathorst (1876).  
*C. gramineus* Phillips 1829 is *Otozamites gramineus* (Phillips) 1875.  
*C. gramineus* Heer is *Taxites gramineus* (Heer) Nathorst (1897). *C. gramineus* of Raciborski is similar.  
*C. gyrosus* Goeppert is indeterminable according to Seward (1917).  
*C. heeri* Schenk discussed by Seward (1895).  
*C. lanceolatus* Phillips 1829 identified as *Otozamites acuminatus* by Seward (1900).  
*C. latifolius* Phillips 1829 identified as *Otozamites acuminatus* by Seward (1900).  
*C. linearis* Sternberg 1825 is a stem.  
*C. longifolius* Nathorst 1876 (indeterminable narrow leaves).  
*C. longifolius* Romanowski 1880 (indeterminable).  
*C. lortetei* Saporta 1875 is *Pseudocycas lortetei* (Saporta) Carpentier (1938).

- C. manchuricus* Oishi 1935 (a Bennettitalean leaf rather like *Pterophyllum fossum*).
- C. morrisianus* Dunker identified as *Pseudocycas dunkerianus* (Goepfert) Florin (1933).
- C. nilssoni* Sternberg 1825 identified as *Nilssonia brevis* by Nathorst (1909).
- C. palmatus* Sternberg identified as *Cordaites* by Seward (1895).
- C. pecten* Phillips 1829 is *Ptilophyllum pecten* (Phillips).
- C. pectinatus* Berger 1832 identified as *C. rectangularis* by Seward (1904).
- C. pinnatilibus* Compter 1894 doubtfully identified as *Scytophyllum bergeri* Bornemann by Linnell (1933).
- C. planicosta* Heer and of Raciborski (indeterminable narrow leaves).
- C. rajmahalensis* Oldham & Morris is *Nilssonia rajmahalensis* (Oldham & Morris), Seward & Sahni (1920).
- C. rectangularis* Brauns 1866 (see also Saporta 1875; Lignier 1895; Seward 1904; Holden 1914; Prinada 1933; Baranova, Burakova & Bekasova 1963). A rather varied series of Liassic or younger leaves, some suggesting *Paracycas* but others more like *Pseudocycas*. Seward's specimen is redescribed on p. 68 above.
- C. renaulti* Lignier 1913 perhaps a *Pseudocycas*.
- C. roemeri* Schenk is *Pseudocycas roemeri* (Schenk) Holden (1914).
- C. rumpfii* Schenk in Compter 1874 and 1894 is doubtfully determined as *Scytophyllum apoldense* by Linnell (1933).
- C. saladini* Zeiller 1903; also of Prinada (1933) has broader and shorter pinnae than *Paracycas cteis*. The 'midrib' appears sunken in some figures so it may be a quite different leaf.
- C. saportae* Seward 1895 is *Pseudocycas saportae* (Seward) Holden (1914).
- C. cf. saportae* Bartholin 1910 is *Pseudocycas bartholini* Florin 1933.
- C. sibiricus* Heer is identified as *Taeniopteris* sp. by Seward (1917).
- Cycadites* n. sp., Nathorst is *Pseudocycas insignis* Nathorst (1907).
- C. spatulata* Konno 1938 (Permian of East Asia) differs from *Paracycas cteis* in its broader and spatulate segments.
- C. steenstrupi* Heer is *Pseudocycas steenstrupi* (Heer) Nathorst (1907).
- C. sulcicaulis* Phillips 1829 is *Ctenis sulcicaulis* (Phillips).
- C. taxodinus* Goepfert is indeterminable according to Seward (1917).
- C. tenuicaulis* Phillips is *Nilssonia tenuicaulis* (Phillips) Fox-Strangways.
- C. tenuilobus* Prinada 1934 (looks like *C. rectangularis* Brauns).
- C. tenuinervis* Fontaine 1883 (Nature obscure).
- C. tenuisectus* Saporta is *Pseudocycas tenuisectus* (Saporta) Florin (1933).
- C. unjuga* Dawson is not a Cycad, Seward (1895).
- C. zamifolius* Sternberg is Coniferous, Seward (1895).
- C. zamioides* Leckenby 1864 is *Thomasiocladus zamioides* (Leckenby) Florin (1958), a conifer.

### Genus PSEUDOCTENIS Seward 1911: 691

EMENDED DIAGNOSIS. Leaf large, elongated, simply pinnate. Pinnae broad or narrow and elongated, lanceolate or parallel-sided, arising laterally on the rachis. Pinna margins entire, apex truncate or contracted, base expanded or contracted. Veins numerous, parallel, simple or forked, not anastomosing. Lamina thick, hypostomatic. Stomata scattered, orientation

variable or longitudinal; haplocheilic; guard cells sunken in a cutinised pit formed by a ring of haplocheilic subsidiary cells. Cell walls straight or nearly straight.

TYPE SPECIES. *Zamites eathiensis* Richards (1884 : 117).

DISCUSSION. *Pseudoctenis* was discussed by Harris (1950 : 1015). Since then there has been some advance in the discovery of the typically Cycadaceous male cone of *P. lanei* (Thomas & Harris 1961) which reinforces the earlier conclusion that the better known species at least are true Cycads. Seward at first had trouble in deciding whether the veins in some of his obscurely preserved specimens did or did not anastomose. In good specimens of *Pseudoctenis* it is easy to see the course of the veins and then it is quite clear that anastomoses are absent. It is true, however, that in *Pseudoctenis*, as in many other leaves with nearly parallel veins, prolonged search does give an example of true anastomosis of two veins, but this is so rare as to be an abnormality. Occasional difficulty with these and other thickly cutinised leaves is that the interior liquefied at an early stage of preservation and the veins shifted laterally to give a false appearance of anastomosis, but the cuticle still indicates their original position.

*Pseudoctenis* as used here forms a useful and presumably natural group, though it would include the leaves of more than one genus of Recent Cycads. It is doubtful if it is valid. In the first place it is perhaps antedated by *Dioonites* Miquel (1851), or by *Ctenophyllum* Schimper (1870), and possibly by other names for *Zamia*-like leaves. So far as I am aware the type-species of none of these genera has yet been studied microscopically, and *Pseudoctenis* must be left until it is shown that an older name is valid. The definition of *Pseudoctenis* was at first vague; Seward named *P. eathiensis* as the type-species but gave no diagnosis. He stated that his new genus differed from *Ctenis* in having few or no vein anastomoses; from *Pterophyllum* in having relatively sparse veins, and from *Zamites* in having decurrent lower margins to the pinnae. The definition was emended by Harris (1932) when facts about the stomata were included. Unfortunately the cuticle of *P. eathiensis* remains unknown so it has not been proved that Harris's species agree with that in cuticle. I have re-examined the specimens of *P. eathiensis* from Eathie; there appears to be no hope that they will yield useful cuticles.

With the emphasis on the characters of the stoma shown by the cuticle, two of the characters given by Seward become unnecessary. The stoma distinguishes it sharply from both *Zamites* and *Pterophyllum* and the rather vague macroscopic characters originally given to distinguish it from those two genera become unnecessary and have been dropped. Thus the genus now includes species which look like a *Pterophyllum* in veins or a *Zamites* in pinna base.

The following species of *Pseudoctenis* have been described with information about their cuticles:

*Pseudoctenis cteniforme* (Nathorst) Harris 1950 = *Pseudopterophyllum cteniforme*. (Nathorst) Florin 1933 (Rhaetic, Sweden).

*Pseudoctenis depressa* Harris 1932 (Lower Lias, Greenland).

*Pseudoctenis florini* Lundblad 1950 (Rhaetic, Sweden).

*Pseudoctenis herriesi* Harris 1950. This work, p. 72.

*Pseudoctenis lanei* Thomas 1913; Harris (1932, 1950). This work, p. 82.

*Pseudoctenis locusta* Harris 1949. This work, p. 76.

*Pseudoctenis oleosa* Harris 1949. This work, p. 78.

*Pseudoctenis spectabilis* Harris 1932 (Rhaeto-Liassic, Greenland).

*Pseudoctenis* sp., Carpentier 1939 (Wealden, N. France).

The following species have been described without microscopic characters:

*Pseudoctenis amurensis* Novopokrovski 1912 (Jurassic, Amurland).

*Pseudoctenis balli* (Feistmantel) Seward 1917 = *Anomozamites balli* Feistmantel (Jurassic, India.)

*Pseudoctenis brevipennis* Oishi 1940; Takahasi 1951 (Jurassic, Japan).

*Pseudoctenis crassinervis* Seward 1911 (Upper Oolite, Scotland).

*Pseudoctenis* cf. *crassinervis* Seward: Sze 1931 (Lias, China).

*Pseudoctenis eathiensis* (Richards) Seward 1911 for *Zamites eathiensis* Richards 1884. Type species of genus (Upper Oolite, Scotland). See also Walkom 1917, 1924 (Upper Trias or Lower Jurassic, Queensland).

*Pseudoctenis ensiformis* Halle 1913 (Jurassic, Graham Land).

*Pseudoctenis* sp., cf. *Ctenophyllum angustum* Fontaine: Kawasaki 1926 (Lias, Korea). Referred to *Pterophyllum* cf. *sinensis* by Kawasaki 1939.

*Pseudoctenis footeana* (Feistmantel) Seward & Sahni 1920 for *Pterophyllum footeanum* Feistmantel and for *Zamites proximus* Feistmantel (Upper Gondwanas, India).

*Pseudoctenis lanei* Thomas: Oishi 1940 (Jurassic, Japan).

*Pseudoctenis* cf. *medlicottiana* (Oldham & Morris) Halle 1913 (Jurassic, Graham Land).

*Pseudoctenis?* *pachyrachis* Carpentier 1947 (Lower Lias, France).

Very possibly some of the leaves which have been described without microscopic details as species of *Dioonites*, *Ctenophyllum*, *Pterophyllum* and *Zamites* will prove to have stomata like those of *Pseudoctenis*.

#### Key to the Yorkshire species of *Pseudoctenis*

(This key deals with the middle region of the leaf)

(1) Lower margin of pinna contracted . . . . .	2
Lower margin not contracted, but more or less decurrent . . . . .	4
(2) Pinna lanceolate, usually over 12 mm. broad . . . . .	3
Pinna strap shaped, under 10 mm. broad . . . . .	<i>P. lanei</i>
(3) Pinna broadly lanceolate, less than 10 veins per cm. . . . .	<i>P. locusta</i>
Pinna long lanceolate, more than 10 veins per cm. . . . .	<i>P. oleosa</i>
(4) Pinna gradually tapering to acute apex . . . . .	<i>P. lanei</i>
Pinna scarcely tapered, apex truncate . . . . .	<i>P. herriesi</i>

*Pseudoctenis* sp. A agrees in the distal part of its pinna with *P. herriesi*. *Pseudoctenis* sp. B is based on cuticle fragments, the form of the pinna being unknown.

#### *Pseudoctenis herriesi* Harris

Text-figs. 30-32

1946a *Pseudoctenis herriesi* Harris, p. 829, text-figs. 4-6. (Figures repeated here.)

DIAGNOSIS (slightly emended). Largest leaves possibly over 1 m. long. Petiole up to 8 mm. wide, but in small leaves only about 4 mm., nearly smooth, hairless. In lower part of leaf, pinnae short (about 12 mm. long) and narrow (1-3 mm. wide); in middle region becoming about 10 cm. long and 6-12 mm. wide; becoming rather shorter and narrower near leaf apex.

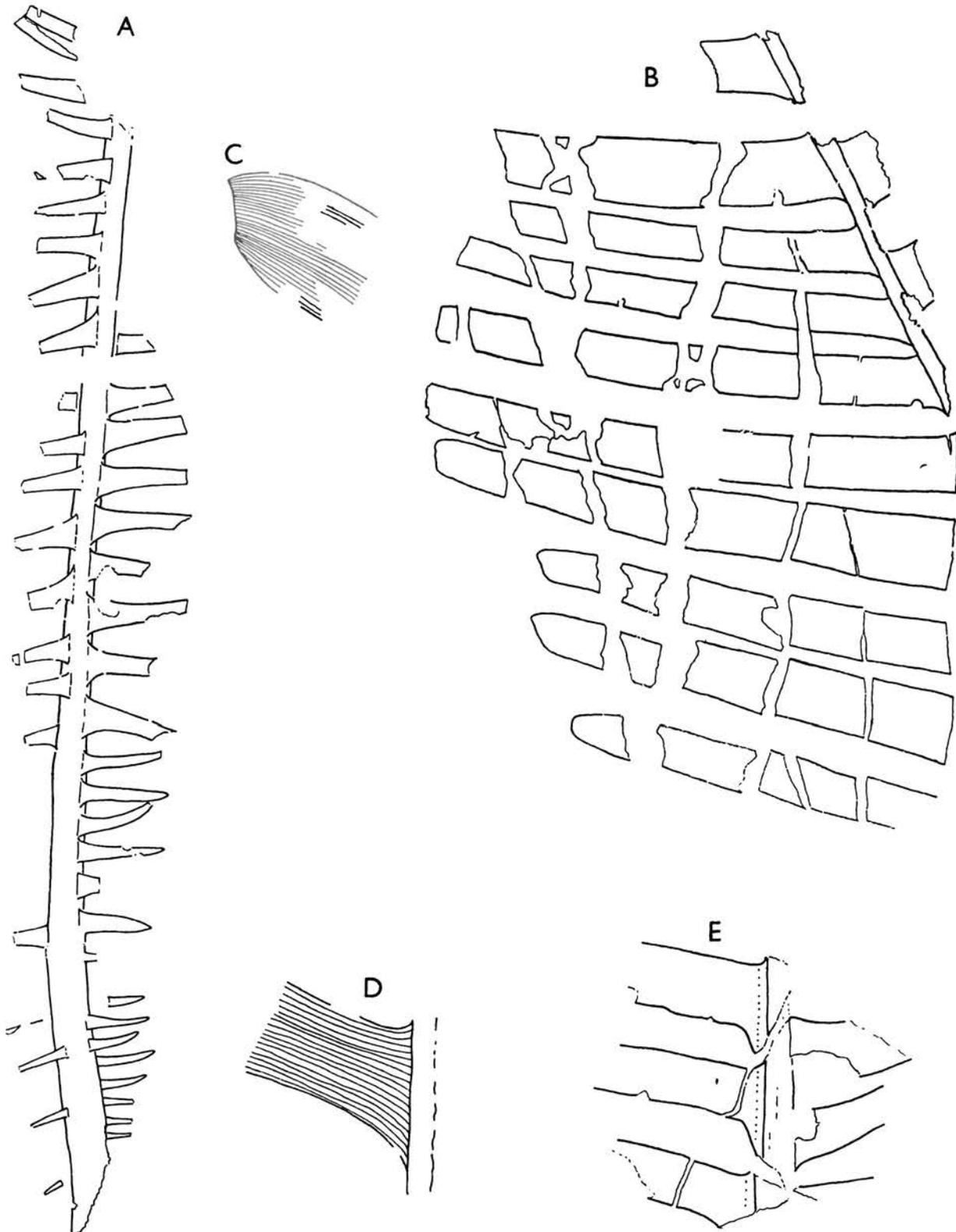


Fig. 30. *Pseudoctenis herriesi* Harris

A, basal part of leaf, V.26909 (drawn from part and counterpart),  $\times 1$ . B, holotype, Yorkshire Museum. The three lowest pinnae have been omitted,  $\times 1$ . C, apex of pinna of holotype showing the veins,  $\times 3$ . D, base of pinna of holotype showing veins,  $\times 3$ . E, part of a specimen showing expanded bases of pinnae (this leaf fragment is about 20 cm. long), V.26910,  $\times 1$ . All the figures are from Harris (1946a, text-fig. 5).

A, E are from Whitby Long Bight. B-D, unlocalised but possibly from Whitby.

In lower part of leaf pinnae arising at  $90^\circ$  to the rachis, tapering to an acute point. In middle region of leaf, pinnae arising at  $60^\circ$ – $80^\circ$  to the rachis, either parallel-sided from near the base or tapering slightly; apex obliquely truncate or slightly contracted and obtuse. At apex of leaf, pinnae at  $50^\circ$  to the rachis, pinnae rather varied, but gaps between pinnae more uniform, often about equal to the width of a pinna. Pinna base expanded in all parts of the leaf; upper margin rising slightly along the rachis, lower more considerably decurrent and often meeting lamina of next pinna.

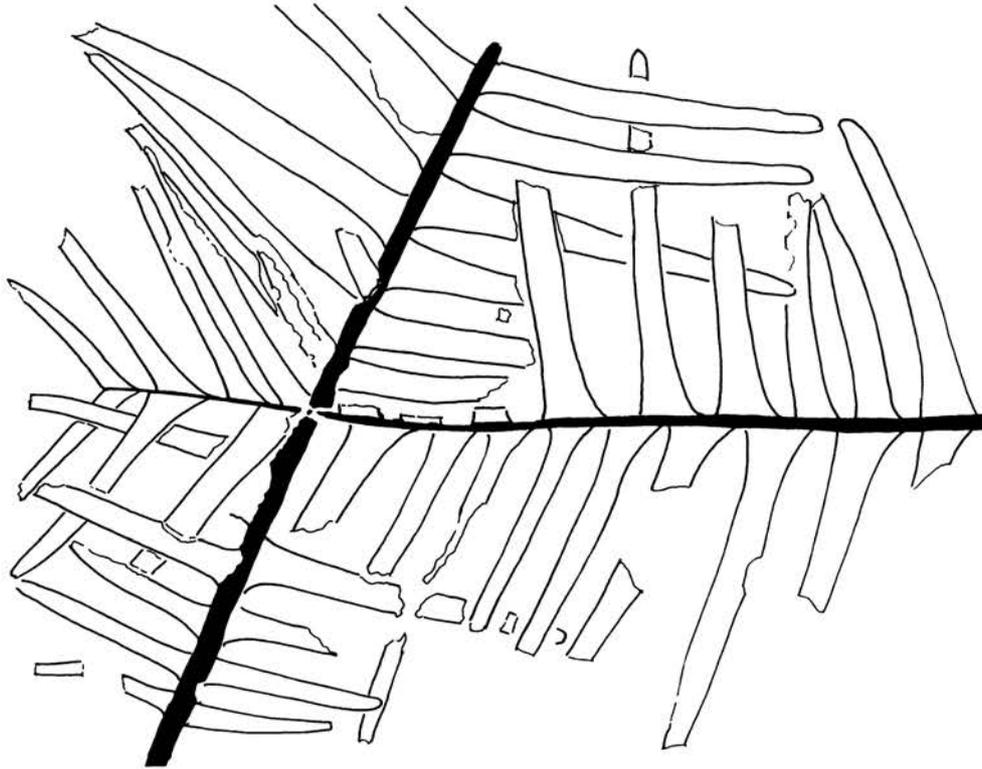


Fig. 31. *Pseudoctenis herriesi* Harris

Block in Geology Department, Reading University, Beckles Collection No. 1204,  $\times 1$ . Unlocalised but in a matrix resembling the Whitby Plant Bed. About 3 cm. at the top of the erect leaf are omitted.

Veins fairly distinct, running from base to apex without branching or anastomosing, nor ending in the margins, running parallel with margins at base of pinna and slightly converging towards the apex of a tapering pinna. In middle region of a pinna concentration of veins typically 32 per cm. below, 48 per cm. near apex. Lowest concentration noted 25 per cm. near base of a large pinna, up to 50 in small pinnae. No ducts or resin masses occurring between veins, but epidermal and mesophyll cells often filled with resinous matter which adheres to the cuticle.

Surface sculpture of lamina consisting of broad ridges with elongated bulging cells along the veins separated by furrows of equal or slightly greater width between the veins; hairs not apparent.

Cuticles of medium thickness, upper about  $2\mu$ , lower about  $1\mu$  (measured in folds). Upper

cuticle showing neither hairs nor stomata. Veins rather obscurely marked by narrower cells with thickened longitudinal walls. Cells rectangular or polygonal, often forming obscure longitudinal rows. Walls obscurely marked, sometimes appearing as a broad band, sometimes as a clear line with or without the broad band. Sculpture obscure, but cells along veins sometimes showing one or more longitudinal striations. No papilla present; scattered cells occupied by dark material apparently belonging to the cell contents.

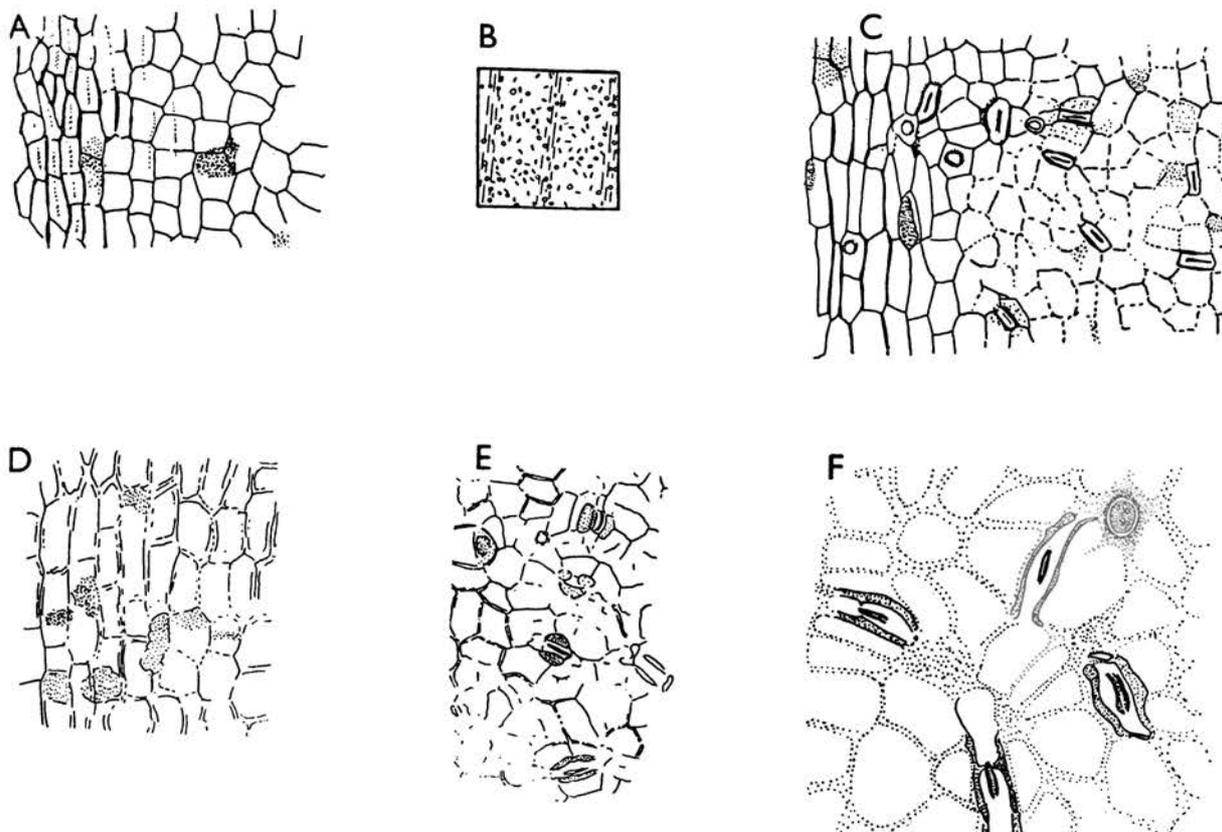


Fig. 32. *Pseudoctenis herriesi* Harris

A, upper cuticle, V.26913,  $\times 200$ . B, 1 sq. mm. of lower cuticle showing three veins; stomatal apertures shown by short black lines, trichomes by rings, V.26912,  $\times 18$ . C, lower cuticle, V.26912,  $\times 200$ . D, upper cuticle of holotype; cell outlines appear broad. E, lower cuticle of holotype, Herries Colln., Yorkshire Museum,  $\times 200$ . F, lower cuticle, V.26912,  $\times 400$ .

A-C, F are from Saltwick. D, E, unlocalised but possibly from Whitby. All the figures are from Harris (1946a, text-fig. 6).

Lower cuticle showing fairly conspicuous bands of elongated cells along the veins; stomata confined to broad strips between the veins but stomatal strips ill-defined. Cells between the veins polygonal; outlines usually very obscurely shown by broad slightly thicker bands. Sides of cells straight, surface not markedly sculptured; no papilla present. Stomata fairly numerous, scattered, irregularly orientated. Guard cells only slightly sunken, forming a very shallow rectangular pit. Subsidiary cells very irregular, not at all specialised except for a thickened margin next to the guard cells. Guard cells thickened round the aperture, but the rest of the exposed surface is usually thin. Occasional cells occupied by dark matter as on the upper surface. Encircling cells absent.

Trichome bases rather numerous, both on and between veins; consisting of a normal sized or rather small cell with a circular, thickened scar.

HOLOTYPE. Specimen figured Harris (1946a, text-figs. 4, 5 C, D, 6 B, E). Unlocalised but very possibly from Whitby. Herries Collection, Yorkshire Museum.

OCCURRENCE. In addition to the holotype *Pseudoctenis herriesi* is known from the following localities; all Lower Deltaic:

Whitby Long Bight; fallen block from above the main plant bed, V.26909-11, V.27069.

Saltwick, Waterfall plant bed; just above the Dogger (cuticle fragments), V.26912-13.

Beast Cliff at about 54° 21' 45" N. at the foot of the Cliff; at about the middle of the Lower Deltaic; a cuticle fragment, V.26914.

Marske Quarry; V.42398 also specimens in Lane collection in sandstone with no cuticles.

Roseberry Topping; sandstone of main scarp; several fine leaves, V.42399-401.

Eston Moor, Upsall Quarry; cuticle fragment, V.28302.

The following are unlocalised:

Specimens 1204 and 12011 in the Beckles Collection, Reading University; unlocalised but very possibly from Whitby.

No. 8976, an exceptionally fine leaf, Damon Collection; unlocalised but possibly Whitby.

DISCUSSION. Most of the fragments are from leaves which must have been very large, but there are two (Text-fig. 31) on a slab (Beckles Collection No. 1204, Reading University) which are from leaves of only moderate size.

COMPARISON. *P. herriesi* differs from most species of *Pseudoctenis* in its expanded pinna base; its blunt pinna apex and its fine, crowded and unbranched veins, as well as in its cuticle. The Yorkshire *P. lanei* occasionally has pinnae which are not contracted at the base, but it is then still distinguishable by other characters. The imperfectly known '*Pseudoctenis* sp. A' may have similarly shaped pinnae, but differs in its more distant veins, much thicker cuticle, strongly marked isodiametric cells above and papillose cells below. *P. depressa* Harris from the Greenland Lower Liassic also has slightly expanded pinna bases and unbranched veins, but the pinnae are much broader and the veins less crowded.

*P. herriesi* looks like certain specimens of *Pterophyllum thomasi* of Yorkshire and no doubt many specimens of other floras, but it is at once distinguished from this and all true species of *Pterophyllum* by its cuticle.

### *Pseudoctenis locusta* Harris

Text-fig. 33

1949 *Pseudoctenis locusta* Harris, p. 575, text-figs. 7, 8 c.

DIAGNOSIS. (Based on holotype only, from Harris 1949). Length of leaf unknown; width in part known 10-11 cm. Pinnae ovate-lanceolate about 6 cm. × 2 cm., widest a little above the middle and then tapering to a very obtuse apex. Base slightly contracted. Margins entire, slightly thickened. Veins very prominent, rather thick, about half of them simple, the rest forking once at a varied level. Most of the veins running into the lateral margins and there dying out, a number ending just short of the terminal margin. Anastomosis of veins very rare. Substance of lamina thin, forming a brown translucent film, interstitial ducts (probably discontinuous) present between veins; lamina showing numerous scattered dark bodies (trichomes, and possibly also stomata).

Cuticle fairly thick on both sides but weak and difficult to prepare. Upper cuticle probably without stomata or trichomes, composed of more or less isodiametric cells. Lateral walls broad, very ill defined and merging into the surface of the cell. Surface wall without a papilla or striations. Lower cuticle showing fairly evenly distributed trichomes and also stomata in the

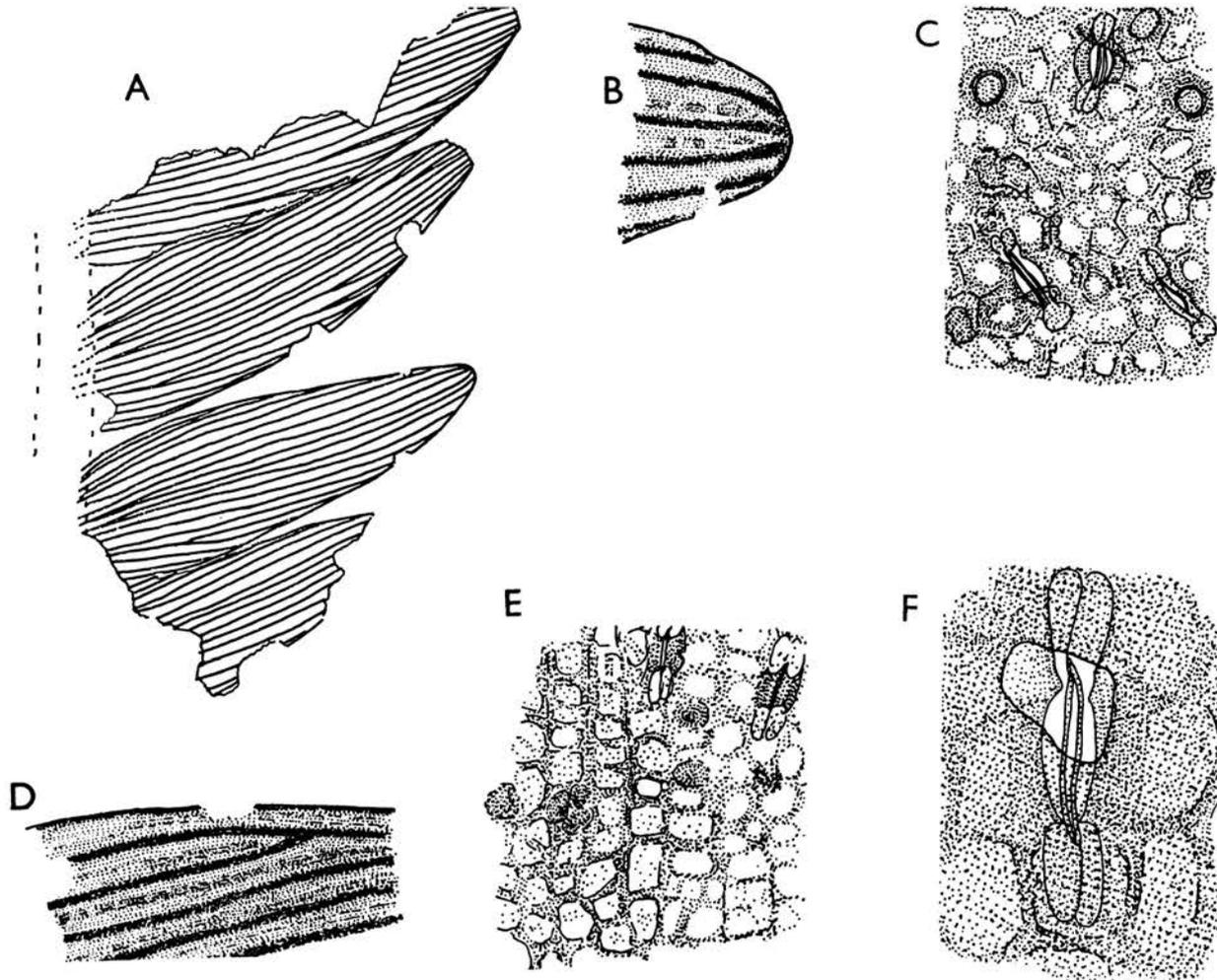


Fig. 33. *Pseudoctenis locusta* Harris

A, whole specimen, the dotted vertical lines represent a groove, probably the impression of the rachis,  $\times 1$ . B, apex of third pinna,  $\times 5$ . C, lower cuticle, between veins,  $\times 200$ . D, the only vein anastomosis (second pinna); interstitial ducts are more or less distinct,  $\times 5$ . E, lower cuticle, over a vein,  $\times 200$ . F, stoma showing the pit, guard cells and obscure outlines of subsidiary cells,  $\times 500$ . Probably from the Gristhorpe Bed.

All the figures represent the holotype (K.214, Sedgwick Museum, Cambridge) and are taken from Harris (1949, text-figs. 7, 8).

interstices of the veins. Epidermal cells isodiametric, anticlinal walls exceedingly broad, but rather better defined than those of the upper cuticle, periclinal wall only slightly less thick than anticlinal walls, more or less flat, without any papilla or striations. Cells along the veins nearly square, forming well-marked longitudinal rows, cells of interstitial region polygonal, forming ill-marked rows. Stomata scattered, not forming rows, mostly orientated parallel to the veins, but some irregularly orientated. Guard cells sunken, but part or whole of aperture exposed in a

fairly large pit. Aperture rather long ( $50\mu$ ), total length of stoma including poles  $100\mu$ . Subsidiary cells forming an ill-defined rather elongated group, wall along the sides of the pit often rather thickened, but subsidiary cells otherwise like ordinary epidermal cells. Encircling cells not recognised, ordinary epidermal cells near stomata unspecialised. Trichomes rather numerous, evenly scattered over both veins and interstices, each consisting of a cell with a thickened surface, bearing a ring about  $20\mu$  wide. Free part of trichome unknown.

HOLOTYPE. The only specimen. K.214 in the Leckenby Collection, Sedgwick Museum, Cambridge.

DISCUSSION. *P. locusta* is represented only by the holotype. It bears the label '*Otozamites latifolius* Phillips' in Nathorst's writing and also a pencil note by another hand, '? Only one of this specimen in England'. The specimen is unlocalised but the matrix looks like the Gristhorpe Bed and its associates *Nilssonia compta*, *Cladophlebis denticulata* and *Kylikipteris arguta* are typical of the Gristhorpe flora and have not been found together elsewhere. It is thus nearly certain it is from the Gristhorpe Bed of the Middle Deltaic. The rachis is not seen, but only a deep groove which is taken to represent it. The upper cuticle has very largely been destroyed, probably by varnish, but where two pinnae overlapped it is still present. The substance has suffered natural oxidation to a brown translucent film and even the lower cuticle was difficult to prepare. Attention is drawn in the diagnosis to interstitial ducts, and the one vein anastomosis is figured.

COMPARISON. There is no Yorkshire leaf resembling *P. locusta*. The most similar *Pseudoctenis* is the Japanese *P. brevipennis* Oishi (1940) in which, however, the veins are twice as crowded. A few species of *Ctenis* from E. Asia are rather similar, notably *C. yabei* Oishi (1932); and *C. uwatokoii* Toyama & Oishi (1935), but in these the veins anastomose frequently. *P. locusta* does indeed look rather like Phillips' sketch of '*Otozamites latifolius*' but the original is a typical leaf of *O. acuminatus* and the veins are represented inaccurately.

### *Pseudoctenis oleosa* Harris

Text-figs. 34, 35

1949 *Pseudoctenis oleosa* Harris, p. 580, text-figs. 8 A, B, 9. (Figures repeated here.)

EMENDED DIAGNOSIS. Leaf very large, but total length unknown, width in typical specimens probably exceeding 40 cm. Petiole channelled, 15 mm. wide; rachis and petiole marked with longitudinal ridges. Pinnae large, but becoming smaller towards leaf apex; typical pinnae about 15 mm. broad near the base, length 12–possibly 25 cm.; largest pinnae 30 mm. broad (length unknown); small ones from near leaf apex about 5 mm.  $\times$  10 cm. Pinna elongated-lanceolate, base contracted but soon attaining its full width and then either maintaining its width for 10 cm. or tapering evenly from near the base. At distal end pinna tapering evenly to a sharp point. Margins entire, somewhat thickened, especially in large pinnae. Pinna base often asymmetric, upper margin distinctly contracted; lower varied, contracted or slightly decurrent. Pinnae arising at a wide angle of about  $70^\circ$ – $80^\circ$  in lower part of leaf, but at a more acute angle above; spacing of pinnae uneven; in some leaves adjacent pinnae separated by gaps of nearly 1 cm., but more commonly in contact and occasionally overlapping.

Veins often inconspicuous, forming grooves or ridges on both sides of lamina and intervals between veins sometimes showing obscure ridges also. Pinna base typically with about eight

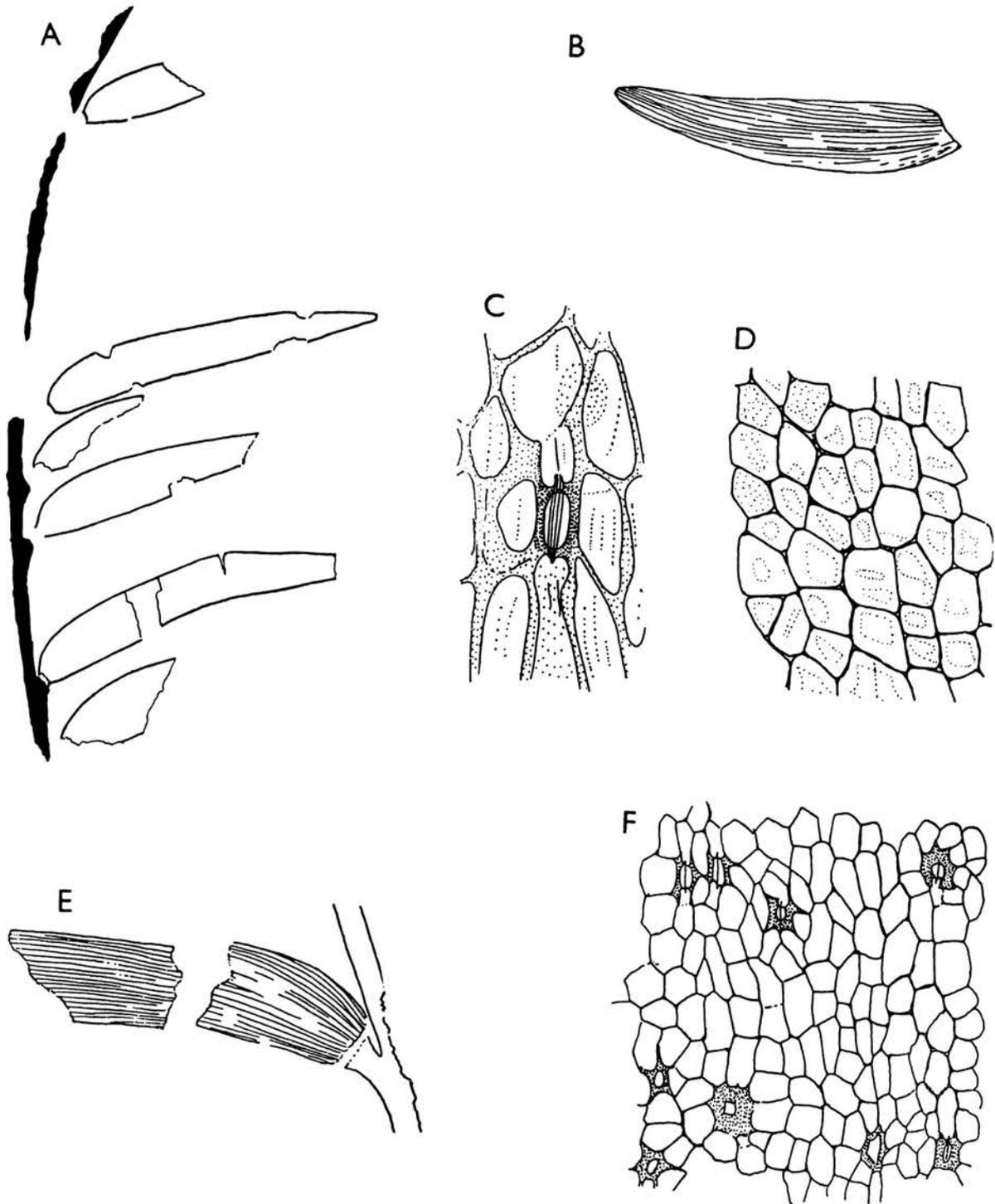


Fig. 34. *Pseudoctenis oleosa* Harris

A, holotype, drawn from part and counterpart; the pinnae of the left side are folded under those shown and are omitted, V.27713,  $\times \frac{1}{2}$ . B, small isolated pinna, V.27714,  $\times 1$ . C, stoma from holotype,  $\times 500$ . D, upper cuticle of holotype; thinner regions of cells are outlined in dots,  $\times 200$ . E, pinna of holotype (counterpart shown in A),  $\times 1$ . F, lower cuticle of holotype; the veins which are unrecognisable run vertically,  $\times 200$ .

Both specimens are from Burniston Wyke. All the figures are from Harris (1949, text-figs. 8, 9).

diverging veins, in middle region of leaf veins diverging only slightly or almost parallel, many vein branches ending in margins. Concentration of veins in middle region typically about 14 per cm. increasing to about 25 near apex. Veins forking frequently in basal region and occasionally in middle region, but scarcely at all near apex. No vein anastomosis observed. Substance of lamina thick, opaque, margin unspecialised in small pinnae, thickened and slightly recurved in large ones. Lamina on maceration yielding large amounts of resinous matter representing internal casts of numerous layers of mesophyll cells; (such matter, however, is absent from the petiole and rachis).

Cuticles of lamina thick, upper about  $4\mu$ , lower about  $2\mu$  (measured in folds) but often fragile. Upper composed of uniform isodiametric cells not forming rows; veins barely distinguishable. Anticlinal walls prominent, corners of cells thickened so as to give a somewhat rounded shape to the cell. Periclinal wall somewhat convex but not thickened to form a papilla, surface usually showing a thin strip or area, but without striations. Stomata and trichomes absent.

Lower cuticle with a marginal region 0.2 mm. wide lacking stomata and resembling the upper cuticle, and the rest (with generally distributed stomata) which is uniform and shows the veins scarcely, if at all. Trichomes absent, stomata evenly scattered, equally common along the veins, not forming files but longitudinally orientated. Epidermal cells polygonal, isodiametric, smaller than those of the upper side; not forming obvious rows. Anticlinal walls prominent, often flanked by thickenings extending on to the periclinal wall. Periclinal wall convex but not papillate, surface often marked with a few longitudinal striations; surface often unevenly thick, one region of irregular shape being thick, another thin.

Stomata sunken, surrounded by an irregular ring of subsidiary cells, usually forming an elongated group. Terminal subsidiary cells little specialised but lateral ones usually thickened towards the pit. Pit rather small, usually narrow with a very thick wall along the sides of the aperture, but thinner walls at the poles. Stomatal pit occasionally circular and almost evenly thickened. Aperture of guard cells fairly short ( $20-30\mu$  long), entirely sunken; poles of guard cells beneath the surface but occasionally visible, narrow, making the total length of the stoma  $50-80\mu$ . Encircling cells absent, or only irregularly present and unspecialised.

Trichomes probably absent; hypodermal cells absent on both sides. Cuticle of rachis and petiole very thick, fairly strong, showing elongated cells with very thick and prominent anticlinal walls and with longitudinal striations on the periclinal walls.

HOLOTYPE. V.27713, figured Harris (1949, text-figs. 8 A, B, 9).

OCCURRENCE.

Upper Deltaic:

Burniston Wyke at  $54^{\circ} 19' 19''$  N. fallen blocks from near top of cliff.

Lower Deltaic:

Roseberry Topping.

Near Whitby.

DISCUSSION. *P. oleosa* was known from a few specimens at one point in Burniston Wyke but there are several much better ones in the abundant material collected by Hamshaw Thomas at Roseberry Topping in about 1912. Some of the Roseberry specimens are just like the Burniston ones, but others represent rather larger leaves and they are also better preserved.

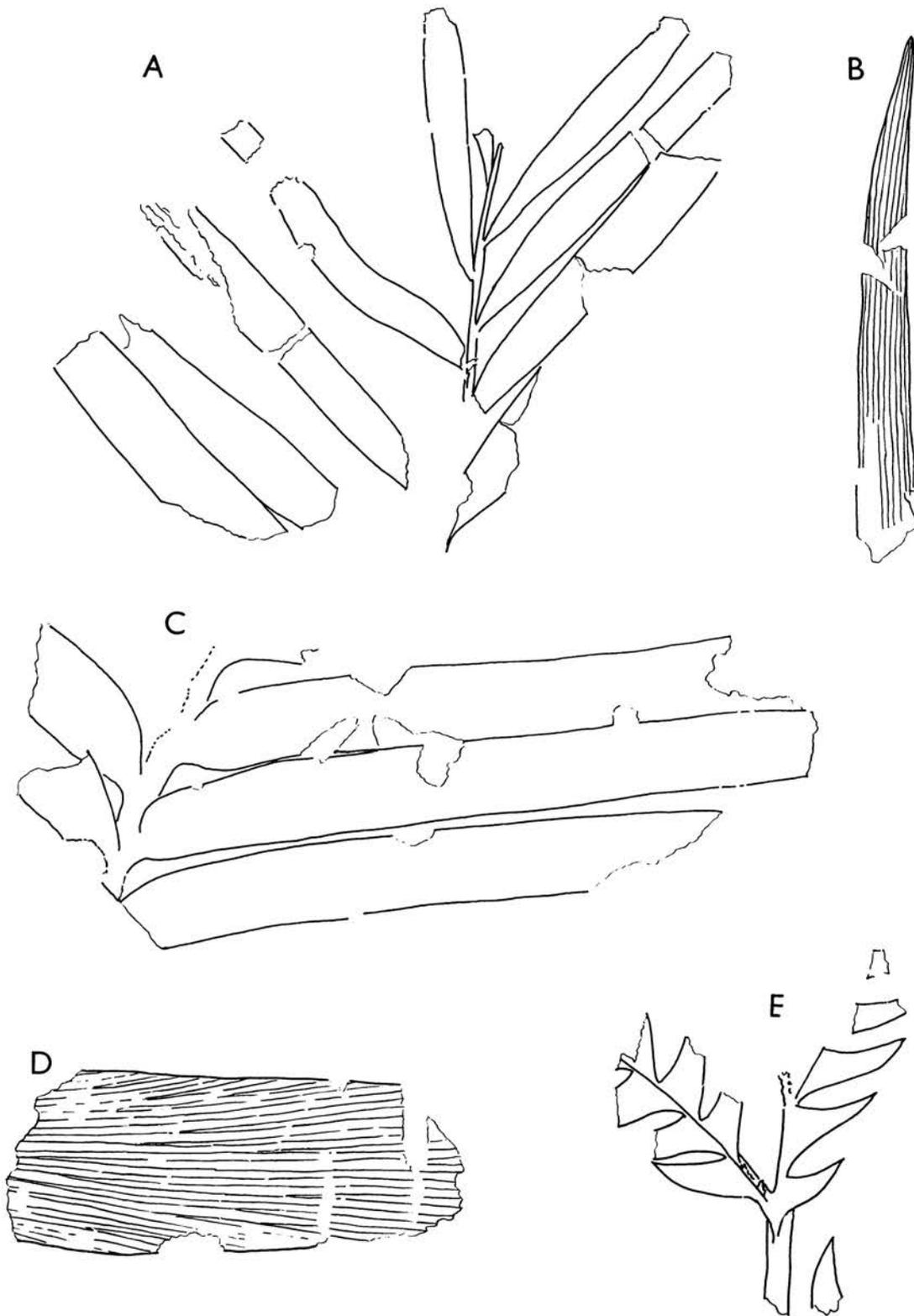


Fig. 35. *Pseudoctenis oleosa* Harris, *Ctenozamites leckenbyi* (Leckenby)

A–D, *Pseudoctenis oleosa*. A, apex of leaf, the veins are about 15 per cm., V.45462,  $\times 1$ . B, apex of pinna, V.45462,  $\times 1$ . C, middle region of a leaf with crowded pinnae. The veins are about 13 per cm., V.45463,  $\times 1$ . D, widest pinna fragment, V.45464,  $\times 1$ . E, *Ctenozamites leckenbyi*, forked leaf apex, V.45465,  $\times 1$ .

A–D from Roseberry Topping. E from the Gristhorpe Bed.

Every specimen on maceration shows solid casts of mesophyll cells. On the upper side these are seen as evenly distributed discs (occurring over veins as well as between them); on the lower side there are more sparsely distributed and less solid discs which avoid the stomata and in addition there are collapsed remnants of other cells. The vascular tissue is not represented. It is sometimes possible to rub some of these mesophyll remains off from the cuticles, but some always remain, making their study confusing.

The original Burniston specimens were mistaken for *Zamites gigas* until their cuticles were examined, but the larger leaves in the Hamshaw Thomas collection are unlike anything else in the flora. It is to be noted that the pinnae at the leaf apex may look like *Podozamites lanceolatus*. *P. oleosa* has only half the concentration of veins seen in *Z. gigas* and its cuticle is entirely different. Large specimens of *P. oleosa* are very different from anything in Yorkshire or other floras as far as I know, but a good many living Cycads must have similar looking leaves. However in nearly all living Cycads there is a layer of hypodermal fibres under the upper epidermis, but here the fact that the palisade mesophyll cell-casts stick to the upper cuticle without there being any sign of hypodermal cells is evidence that none existed.

COMPARISON. It is distinguished from *Pseudoctenis lanei* by its much broader pinnae and less crowded veins. In *P. lanei* the pinna base is less contracted and though there may be some resinous casts of mesophyll cells, they are less prominent. *P. herriesi* has expanded pinna bases and narrower pinnae. The imperfectly known *Pseudoctenis* sp. A has pinnae of similar width but a blunt apex and more parallel and unbranched veins. The lower cuticle shows thickened, or papillose cells. *Pseudoctenis* sp. B of unknown form has a papillose upper surface and strongly striated lower surface. Since I had confused *P. oleosa* with *Zamites gigas* I checked all the specimens of *Z. gigas* available but all proved to be correctly determined (including those from the Upper Deltaic.)

### *Pseudoctenis lanei* Thomas

Pl. 4, figs. 8, 9; Text-figs. 36, 37

- 1909 *Zamites* sp. cf. *Buchianus*, Lane, p. 173, plate. (Photo ? reduced.)  
 1910 *Zamites buchianus* Ett.: Lane, p. 264. (Name in list.)  
 1913 *Pseudoctenis lanei* Thomas, p. 242, pl. 24, fig. 4; pl. 26. (Good leaves.)  
 1913a *Pseudoctenis lanei* Thomas: Thomas, p. 199. (Name in flora list for Roseberry Topping; no description.)  
 1932 *Pseudoctenis lanei* Thomas: Harris, p. 88, text-fig. 36 E-J. (Figure of stomata of one of Thomas's specimens.)  
 ?1940 *Pseudoctenis lanei* Thomas: Oishi, p. 322, pl. 24, figs. 1-3. (Japanese specimens.)  
 1950 *Pseudoctenis lanei* Thomas: Harris, p. 1007, text-figs. 4 A, 5-7. (Form and cuticle of Yorkshire specimen.)  
 1960 *Pseudoctenis lanei* Thomas: Thomas & Harris, p. 150, pl. 4, figs. 25, 28. (Cuticle; relation to *Androstrobus prisma*.)

DIAGNOSIS (slightly emended). Leaf large, length probably over 1 m., width up to about 30 cm. in middle region, but narrowing to 10 cm. above. Lower pinnae smaller and shorter; petiole 10-15 mm. wide, without pinnae, expanding to a base 25 mm. wide. Rachis gradually tapering, marked on both sides with numerous fine longitudinal ridges, otherwise smooth. Cuticle of rachis very thick, showing rectangular cells with thick anticlinal walls and flat, non-papillose surface walls. Stomata rare, trichome bases rare. Rachis bearing pinnae laterally, in lower parts of leaf pinnae arising at an angle of up to 70° or 80°, but frequently less; angle becoming reduced to about 30° near the apex. Pinnae never crowded, separated by a distance about equal to their own width. Pinnae linear-lanceolate; in lower part of leaf 6-10 mm. broad;

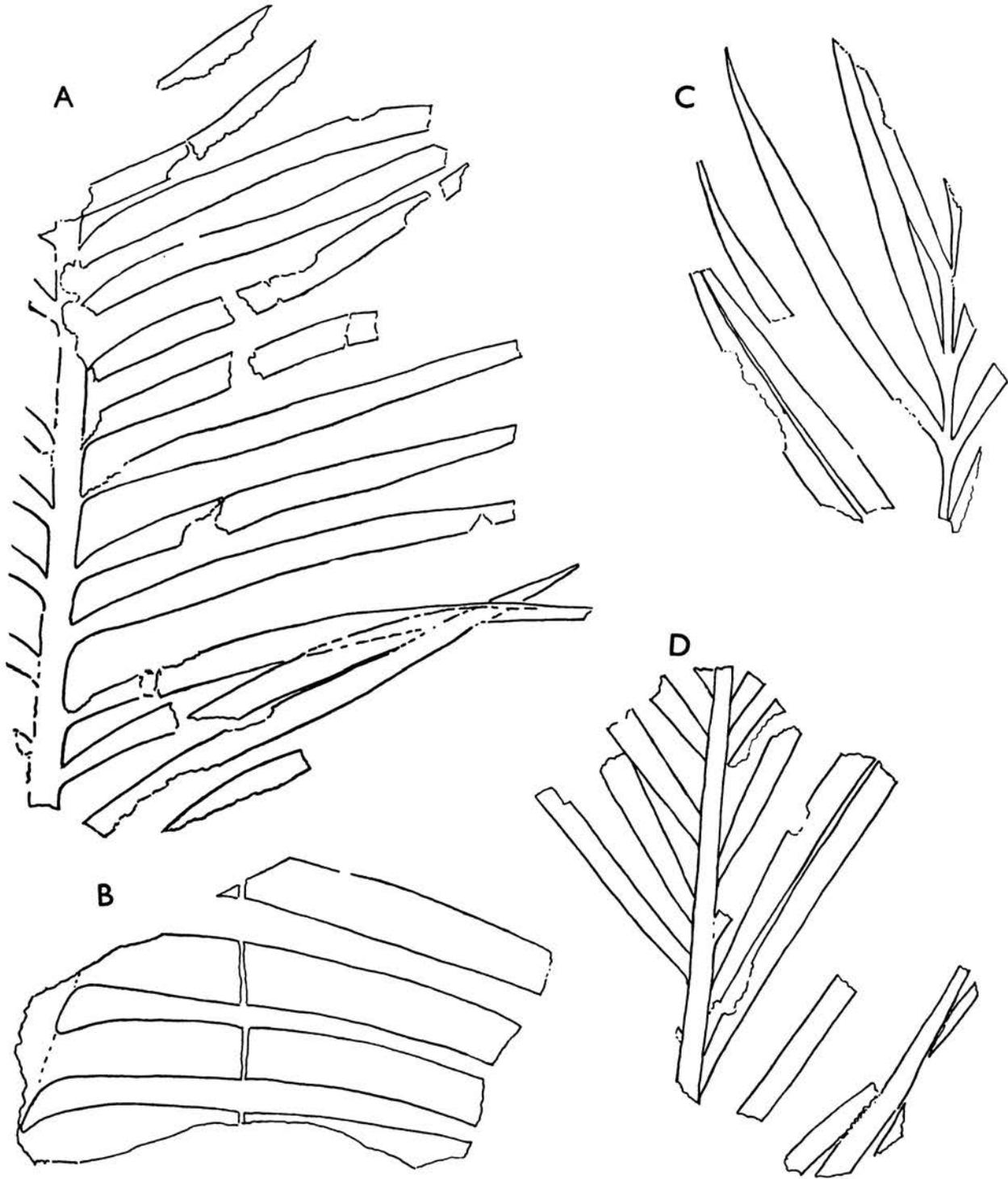


Fig. 36. *Pseudoctenis lanei* Thomas

A, unlocalised specimen in Yorkshire Museum, Herries Colln., no. 1131, reduced to 0.6 of natural size. A small part of the left side is omitted. B, fragment from middle or lower part of leaf, Hasty Bank, V.28300,  $\times 1$ . C, near apex of leaf, Hasty Bank, V.28299,  $\times 1$ . D, middle region of leaf, Hasty Bank, V.28298,  $\times 1$ .

All the figures are from Harris (1950, text-figs. 4-6).

in upper part of leaf 4–6 mm. broad. Pinna base rather contracted, gradually widening to a maximum breadth in the middle regions and then gradually tapering to an acuminate apex. Lower pinnae less contracted at the base and reaching a maximum width rather quickly. Upper margin of pinna always contracted at point of origin, never running up rachis. Lower margin always more or less decurrent, decurrence rather marked in lower pinnae, but scarcely noticeable in upper ones. Lateral margins of pinna somewhat thickened and often slightly recurved. Veins moderately conspicuous or inconspicuous, forking rather freely near the pinna base, and then only occasionally. In distal part of pinna, vein number reduced by the lateral veins running into the margins. Vein anastomoses absent apart from rare exceptions. Concentration of veins in middle of pinna about 17 per cm. (range 15–23), rather higher near apex. No interstitial ducts apparent. Lamina thick, surface cells often bulging, those along veins like others. Lamina yielding internal casts of rounded cells on maceration, but no larger resin bodies, lamina showing no marked peculiarities by transmitted light.

Cuticles rather thick (up to  $2\mu$ ). Upper cuticle showing uniform cells, veins not recognisable, cells not as a rule forming recognisable rows. Cells nearly isodiametric polygons, lateral walls very broad and usually prominent. The whole lateral and often some part of the inner wall preserved. Outer wall usually bulging but not papillose, more or less sculptured with ill-defined corrugations and sometimes showing a thin central area and broad thick border extending in from the sides. Cell surface sometimes showing a longitudinally running central thin strip. Trichomes and stomata absent. Lower cuticle composed of nearly uniform polygonal cells or slightly elongated rectangular cells which tend to form longitudinal rows. Veins not recognisable, stomata evenly and thinly scattered. Epidermal cell outlines broad and rather strongly marked, but often less conspicuous than those of upper cuticle. Cell surface varied, but usually convex. A proportion of the cells strongly thickened to form large thick-walled papillae; proportion of papillate cells varying from three-quarters to one-tenth, rarely almost absent. When strongly developed, papillae often projecting over walls of adjacent cells. Papillae not, as a rule, related to the stomata in position, nor tending to overhang them. Surface of weakly or non-papillate cells more or less sculptured with irregular corrugations or more or less definite longitudinal striations.

Stomata rather sparse (about 50 per sq. mm.), almost evenly scattered but with a tendency to be arranged in longitudinal files. Stomata longitudinally or obliquely orientated, rarely transverse. Guard cells deeply sunken. Guard cells about  $80\mu$  long ( $70\mu$ – $90\mu$ ) with an aperture  $30\mu$  long. Surface of guard cell thin around the aperture, but thickened along the sides of the guard cells (parallel with the aperture); poles of guard cells thin but usually outlined by a ridge of cuticle. Stomatal pit usually broad, round or irregular, formed by about two lateral subsidiary cells on each side and one terminal cell at each end. Opening of stomatal pit often wide and round, but often also contracted to a rectangular slit; opening not as a rule constricted by a cutinised rim. Lateral subsidiary cells probably reaching to near the surface and then replaced by lateral encircling cells which form the top of the pit, no polar encircling cells present. Lateral encircling cells unspecialised. Trichomes rare, base consisting of a small thickened cell with a circular scar, free part unknown. Marginal region of lower side specialised, lacking stomata, showing longitudinal rows of non-papillose epidermal cells.

*Note.* It is possible that the stomata are wrongly interpreted in the diagnosis, and that the subsidiary cells both form the pit and also extend out on to the general surface. In this case no

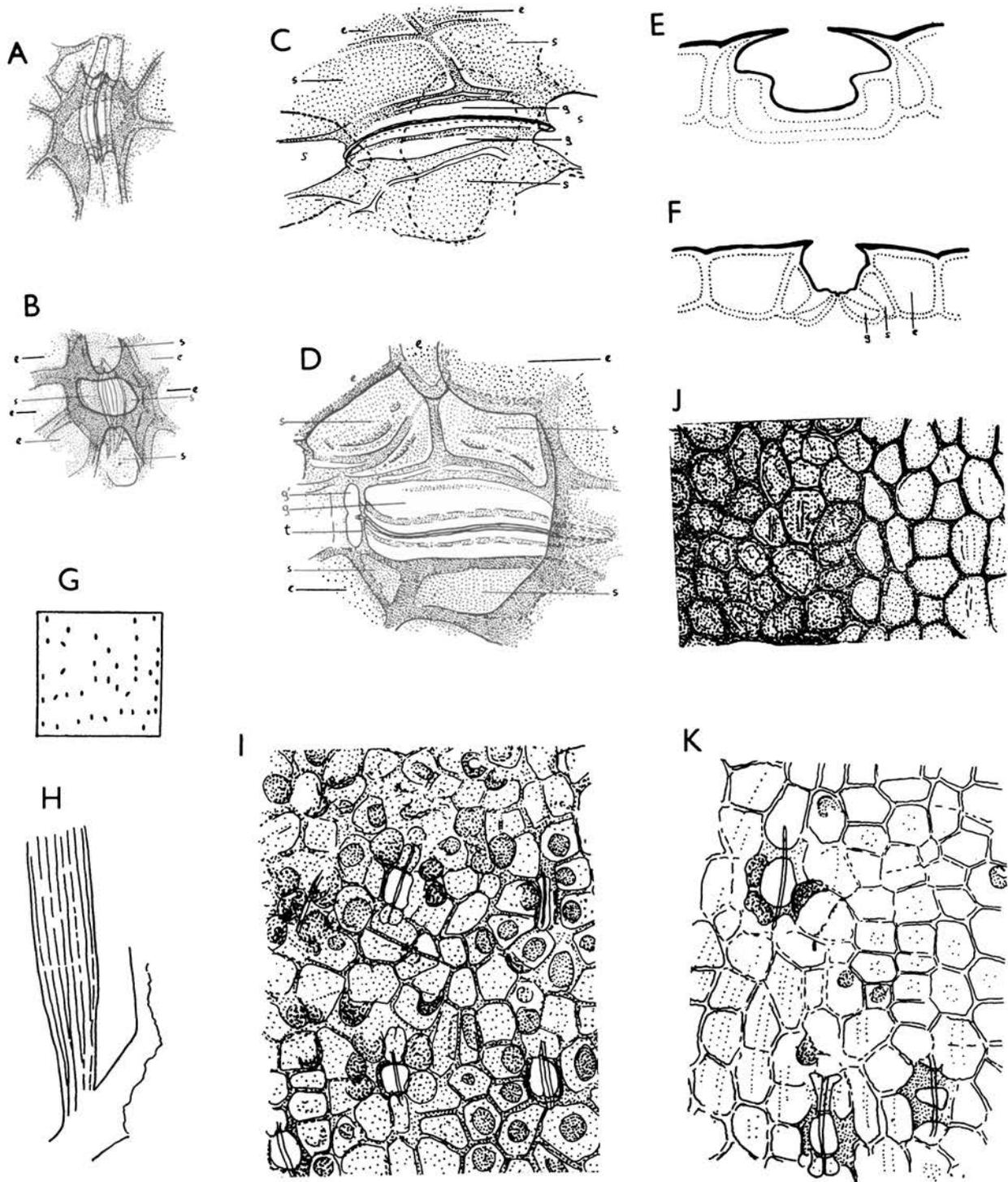


Fig. 37. *Pseudoctenis lanei* Thomas

A, normal stoma viewed from inside,  $\times 400$ . B, normal stoma viewed from outside,  $\times 400$ . C, normal stoma from inside,  $\times 1000$ . D, abnormally exposed stoma,  $\times 1000$ . E, imaginary longitudinal section, and F, imaginary transverse section through A or B. G, distribution and orientation of stomata in 1 sq. mm. of lower surface of specimen in Text-fig. 36 A. H, venation of pinna base, V.28301,  $\times 2$ . I, lower cuticle from a specimen with well developed papillae, V.28298a,  $\times 200$ . J, upper cuticle, the cells on the left still have their inner walls, V.28298a,  $\times 200$ . K, lower cuticle from leaf in Text-fig. 36 A with feebly developed papillae,  $\times 200$ . In figures A-F which are taken from Harris (1932, text-fig. 36) *e*—encircling cell, *g*—guard cell, *g'*—pole of guard cell, *s*—subsidiary cell, *t*—transverse thickening of cuticle of guard cell. Figs. G-K are from Harris (1950). A-F are from Yorkshire and the figures are published by permission of the publishers of *Meddelelser om Grønland*. G, K, Yorkshire (unlocalised). H-J, Hasty Bank.

encircling cells are present. The interpretation given here is preferred because certain unusually open stomata appear to show both subsidiary and encircling cells.

LECTOTYPE. Specimen figured by Lane (1909 : 173, pl.). Middlesbrough Museum.

OCCURRENCE.

Middle Deltaic:

Gristhorpe Bed (at a single point).

Lower Deltaic:

Marske Quarry (H. H. Thomas' original locality).

Hasty Bank.

Roseberry Topping.

Carlton Quarry (Lane).

Beast Cliff, fallen block, near  $54^{\circ} 23' 0''$  N.

Beast Cliff *Ctenozamites* Bed at  $54^{\circ} 23' 41''$  N.

Westerdale, Esklets Crag.

DISCUSSION. *P. lanei* is represented by magnificent leaves at one point in the Gristhorpe Bed (though they crumbled hopelessly when extracted). It is locally abundant too in certain layers at Hasty Bank and Roseberry Topping and was there associated with *Androstrobus prisma*. The evidence for attributing these two fossils to the same plant is given on p. 161.

The numerous fragments now studied include all parts of the leaf. There is some variability in the angle of insertion of the pinnae in the middle and lower parts, but it is always acute near the apex. The pinna base is always distinctly constricted and there the veins branch. The cuticle varies somewhat in thickness, but the stomata are nearly uniform. In many leaves papillae are scarcely developed, but some show them rather conspicuously and there may be trichome bases in small numbers also. The specimens from the different localities show a similar range of variation.

COMPARISON. *P. herriesi* and *P. oleosa* are the most similar among the Yorkshire species. *P. herriesi* is distinguished by its more or less expanded pinna base, more obtuse pinna apex and the undivided veins at the pinna base. Its epidermal cells are longer and its stomata less sunken. In *P. oleosa* the base of the pinna is more contracted than in *P. lanei* (contracted below as well as above); its substance is more heavily impregnated with resinous matter and there is often a broader band of thickened cuticle around the stomatal pit. The pinnae of *P. oleosa* are much broader.

The Japanese specimens determined by Oishi (1940) as *P. lanei* are very similar, but one difference is that the rachis appears as a groove instead of being flat (though this might be caused in preservation). The veins stated to be about 13 in each pinna are more crowded (25 per cm.) than in normal Yorkshire specimens.

Of other species certain specimens attributed to *P. eathiensis* are very close, e.g., those figured by Seward (1911, pl. 4, fig. 67; pl. 8, fig. 32; pl. 10, fig. 47) which cannot at present be satisfactorily distinguished from it. The holotype of *P. eathiensis* (Seward 1911, pl. 10, fig. 45) is however outside its range, having stiff-looking pinnae at right angles to the rachis, and fewer veins per cm. *P. footeana* (Feistmantel) which as Seward & Sahni (1920) remark, looks like *P. eathiensis*, also looks like *P. lanei*.

*Pseudoctenis* sp. A

Pl. 3, figs. 5, 6; Text-fig. 38 A-D

The only hand-specimen (V.44877) is a fragment which, though apparently distinct from all known species, is too incomplete to merit description as a new species.

DESCRIPTION. Isolated pinna; at least 9 cm. long (base missing); width 13 mm. below, tapering to 8 mm. above, apex obliquely truncate. Veins 11, unbranched, nearly parallel, all ending in the terminal margin without forming projections. Lamina coriaceous, epidermal cells clearly visible and indicating the veins. No interstitial ducts or resin bodies visible between veins. Interior of lamina not resinous. Cuticles thick, upper showing small isodiametric cells with very thick and conspicuous walls. Cells along the veins rectangular and forming longitudinal rows. Cell surface flat, not sculptured. Thin-walled hypodermal cells visible, especially along the veins. Trichomes absent, but a very few stomata present between the veins. Lower cuticle showing numerous stomata between veins, none over veins. Cells over veins more or less rectangular and forming longitudinal rows, cell walls moderately conspicuous, cell surface thickened but not forming a definite papilla, often showing about two longitudinal ridges. Many cells appearing dark as though occupied by solid contents. Cells of interveinal areas isodiametric, outlines moderately conspicuous. Cell surface strongly thickened to form a solid flat papilla, or occasionally a prominent papilla with a minute central cavity. Cell surface not longitudinally striated.

*Pseudoctenis* sp. A is well distinguished from all the Yorkshire species of *Pseudoctenis* by its strongly papillate epidermal cells between the veins on the lower side. Its cuticle looks rather like that of *Eretmophyllum pubescens* and the possibility was considered that it might belong to that or to *E. whitbiense*. The fragment differs in shape however from a typical *Eretmophyllum* leaf and the cuticles also differ slightly. *E. pubescens* differs in having distinct papillae on its upper epidermal cells, while *E. whitbiense* is distinguished by its more strongly prominent hollow papillae on the lower side.

*Pseudoctenis* sp. A is known from a single specimen from the Beast Cliff *Otozamites* Bed. Cuticle fragments which match it closely are known from Snilesworth, Arnsgill 3. Both localities are Lower Deltaic.

*Pseudoctenis* sp. B

Pl. 3, figs. 7, 8; Text-fig. 38 E, F

This species is known only from a number of cuticle fragments obtained by macerating the coal from an old coal pit. The fragments show very characteristic cuticle structure but leave the form of the leaf unknown except that the lamina forms long segments over 5 mm. wide. The veins run at about 10 per cm.

Both cuticles are thick. The upper has no stomata and shows almost uniform small polygonal cells, each with a very conspicuous solid papilla. Towards the leaf margin the papillae are less prominent but instead parallel striae become conspicuous. Very often the cells form longitudinal rows and the papillae of adjacent cells may merge to form elongated dark bars. The lower cuticle has evenly scattered stomata, the veins being obscurely marked. The epidermal cells are small and isodiametric and have either no papillae or rather poorly developed papillae. They

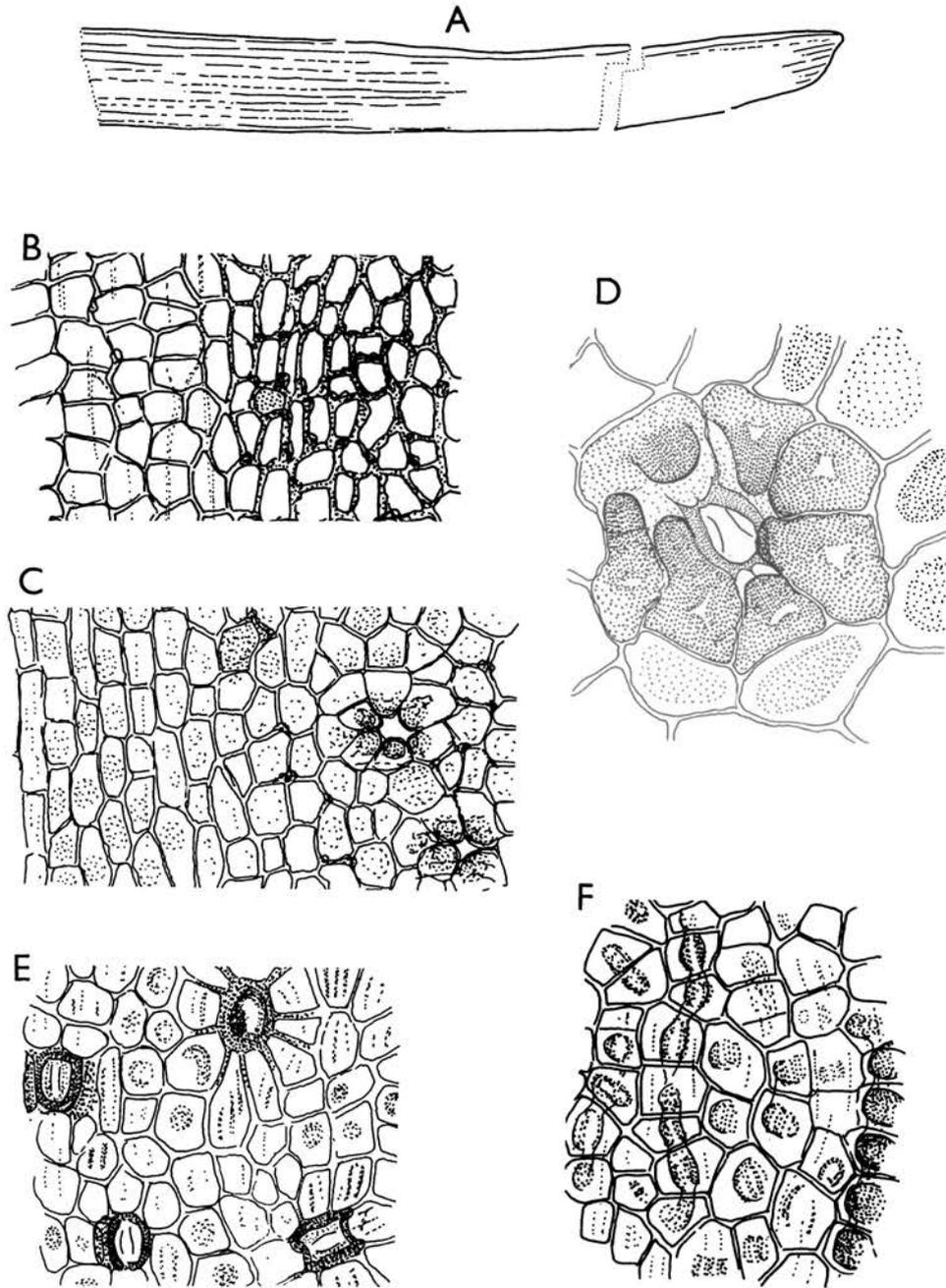


Fig. 38. *Pseudoctenis* spp.

A-D, *Pseudoctenis* sp. A. A, detached pinna, V.44877a,  $\times 1$ . B, upper cuticle with a vein to the left where hypodermal cells are visible, V.44877a,  $\times 200$ . C, lower cuticle with a vein to the left, V.44877a,  $\times 200$ . D, stoma, some of the papillae are irregular, V.44877a,  $\times 500$ . E-F, *Pseudoctenis* sp. B. E, lower cuticle (away from margin), V.45512,  $\times 200$ . The rounded stoma at the top is exceptional. F, upper cuticle (away from margin), same fragment. Near the margins, papillae are undeveloped but there are strong longitudinal striae.

A-D from Beast Cliff *Otozamites* Bed. E-F, Snilesworth R. Rye, Old Coalpit.

have instead very conspicuous longitudinal striations. The stomata are mostly longitudinally orientated and the guard cells are sunken in a round or rectangular pit formed by about six subsidiary cells. The mouth of the pit is strongly thickened and may form a raised more or less even ring, or the thickening may be uneven and form a conspicuous dark papilla on each subsidiary cell.

**OCCURRENCE.** Lower Deltaic. Snilesworth, R. Rye, old coal pit. Its fragments are locally frequent.

**COMPARISON.** *Pseudoctenis* sp. B is certainly distinct from any other species known in Yorkshire. It greatly resembles *P. cteniforme* (Nathorst) from the Rhaetic of Sweden, re-described by Florin (1933) as *Pseudopterophyllum cteniforme*. They do, however, appear to be distinct species. *P. cteniforme* has more conspicuous papillae on the under side; Florin specifically states that it is without longitudinal striations, but in *Pseudoctenis* sp. B every fragment shows striations very conspicuously.

There is no direct evidence that the leaf producing these fragments had the form of a *Pseudoctenis*; all that the fragments show is that the lamina is elongated, with veins running parallel with the margins. It was included mainly because of the close resemblance of its cuticle to *P. cteniforme*.

#### *Pseudoctenis* spp.

Small fragments of cuticle showing parallel veins and stomata of the Cycadean type occur in many macerations and appear to represent a good many species. They are not described in this work because there is too little to indicate the form of the leaf, and many fragments are indeed so small that they do not exclude the possibility that the veins form an elongated network as in *Ctenis*.

### Genus CTENOZAMITES Nathorst 1886 : 122

The name *Ctenopteris* Saporta (or of Brongniart) is inadmissible because it is the homonym of a Recent fern described much earlier, see Harris (1916*b*) but see also Antevs (1914 : 5).

**EMENDED DIAGNOSIS.** Leaf large, elongated. Main rachis simple or forking in middle region of leaf, bearing simple pinnae both above and below the point of forking. Lamina of pinnae decurrent on to main rachis, lamina divided into rhomboidal or triangular or falcate segments, division between segments extending near to or up to the rachis; base of segments not contracted, one segment occurring on main rachis between pinnae. Lamina arising on upper side of pinna rachis. Veins several, nearly equal, parallel or slightly divergent, forking, ending in margins; tracheids scalariform. Resin and interstitial ducts absent. Substance thick and coriaceous. Cuticles thick, stomata confined to lower epidermis, scattered in areas between veins, variably orientated, not forming rows.

Guard cells at the base of a rounded pit formed by about six subsidiary cells. Subsidiary cells forming a rounded or irregular group, size often uneven; sides of stomatal pit thickly cutinised and mouth raised as a thick ring; inside of ring constricted by a thin rim of cuticle or rim replaced by lobes of thin cuticle opposite subsidiary cells. Epidermal cell walls straight or undulating, but not markedly sinuous.

**TYPE SPECIES.** *Odontopteris cycadea* Berger (1832).

REMARKS. Four or five species of *Ctenozamites* have been described satisfactorily and these make a compact genus and to these may be added ten doubtful species mentioned below. Nathorst believed *Ctenozamites* to be close to *Ptilozamites* and since he published this view the new facts about the cuticle and the forking of the rachis in *C. cycadea* give this idea strong support. Forking of the rachis would appear to be a frequent but inconstant character in this group. It normally occurs in *Ptilozamites nilssoni* Nathorst, and in an exceptionally large leaf it occurs twice (Harris 1932). On the other hand it is normally or invariably absent in *P. heeri* Nathorst. In *C. cycadea* it may occur near the base of a large leaf (Harris 1961*b*) though there is nothing to show how constant forking may be in this position. It sometimes occurs near the apex of the leaf as in a specimen figured without comment by Schenk (1887, pl. 3, fig. 13). In *C. leckenbyi* a forked leaf apex is known but in both of these species simple leaf apices are more usual. *Ptiloctenia ketoviae* Delle (1959) which resembles *C. cycadea* in form and cuticle, though with smaller pinnules is known to fork near the leaf apex. Clearly forking or its absence constitutes no difference between *Ptilozamites* and *Ctenozamites*. It appears to me that Delle's *Ptiloctenia ketoviae* is another species of *Ctenozamites* close to *C. cycadea* and I have named it *C. ketoviae*.

The only general difference between *Ctenozamites* and *Ptilozamites* is that the one is bipinnate, the other simply pinnate. This difference separates them easily but is unlikely to have botanical importance, and it seems possible that they might be no more than two sections of a single natural genus. The general character of the cuticle of these leaves is Cycadean, though not exclusive to that family, and what we know of the anatomy of the lamina and rachis of *C. cycadea* is Cycadean too. We know nothing about other organs of any species of *Ctenozamites* but Harris (1932) attributed to *Ptilozamites* the strangely organised fructification now called *Harrisothea marsilioides* Lundblad (1961). *Harrisothea* has nothing in common with a cycad male cone or sporophyll, and if this attribution is correct *Ptilozamites* and presumably *Ctenozamites* cannot be placed in any recognised Gymnosperm family, except possibly the Pteridosperms.

The four satisfactorily known species of *Ctenozamites* are:

*Ctenozamites cycadea* (Berger) Schenk (see p. 95 for references).

*Ctenozamites leckenbyi* (Leckenby) Nathorst (see p. 91 for references).

*Ctenozamites sarrani* (Zeiller) (Zeiller's *Ctenopteris sarrani*); see Zeiller (1903) and Sze (1956). (Probably not of Corsin (1950), see under *C. cycadea* on p. 95).

*Ctenozamites wolfiana* (Gothan) for *Ctenopteris wolfiana* Gothan (1914).

To these we may now add:

*Ctenozamites ketoviae* (Delle) nov. comb. for *Ptiloctenia ketoviae* Delle (1959).

The four following species from the Jurassic of Europe are either inadequately known or belong to other genera:

*Ctenopteris changarnieri* Saporta (1886).

*Ctenopteris dagincourti* Saporta (1886), considered to be a *Thinnfeldia* by Gothan (1914: 142), but may prove to be a *Ctenozamites*.

*Ctenopteris* ? *falcata* Nathorst = *Ptilozamites falcata*.

*Ctenopteris girardoti* Saporta (1886).

The six following species from the Cretaceous of America were described as species of *Ctenopteris* by Fontaine (1889) under the names *C. angustifolia*, *C. insignis*, *C. integrifolia*, *C. longifolia*, *C. minor* and *C. virginensis*. Berry (1911) united them all under the name *C. integrifolia* and Gothan (1914) pointed out that they differ from *C. cycadea* in lacking pinnules on the main rachis between the pinnae (Zwischenfedern) and he considered they should be placed in another genus. I would agree with Berry in uniting the species and with Gothan in considering that these fossils belong to a distinct genus.

#### Key to the Yorkshire species of *Ctenozamites*

- |  |   |                       |
|--|---|-----------------------|
| (1) Pinnules typically less than 5 mm. broad | . | <i>C. megalostoma</i> |
| Pinnules typically over 5 mm. broad          | . | 2                     |
| (2) Pinnules 1-2 times as long as broad      | . | <i>C. cycadea</i>     |
| Pinnules 2-5 times as long as broad          | . | <i>C. leckenbyi</i>   |

Other diagnostic characters:

*C. megalostoma*, very large stomatal pit often with cutin lappets, epidermal cells often papillose, hypodermis present.

Neither of the other two have hypodermis, epidermal papillae or strongly developed cutin lappets, the rim being evenly developed as a rule.

*C. leckenbyi*, apex of pinnule often with a mucro nearly 1 mm. long and with subsidiary points, margins slightly reflexed, cell walls slightly wavy.

*C. cycadea*, apex of pinnule obtuse or acute but not mucronate or with strong subsidiary points, margins flat, cell walls straight.

#### *Ctenozamites leckenbyi* (Leckenby) Nathorst

Pl. 4, figs. 6, 10; Text-figs. 35 E, 39, 40

The following are all Yorkshire specimens:

- 1864 *Ctenis leckenbyi* Leckenby (ex Bean MS), p. 78, pl. 10, fig. 1.  
 1867 *Odontopteris leckenbyi* (Leckenby) Zigno, p. 111. (Discussion.)  
 1875 *Odontopteris leckenbyi* (Leckenby): Phillips, p. 218, lign. 41. (Imperfect copy of Leckenby's figure.)  
 1886 *Ctenozamites leckenbyi* (Leckenby) Nathorst, p. 122. (Name.)  
 1900 *Ptilozamites (Ctenozamites) leckenbyi* (Leckenby) Seward, p. 238. (Description and discussion.)  
 1903 *Ctenopteris leckenbyi* (Leckenby) Zeiller, p. 51. (Discussion.)  
 1908a *Ctenozamites leckenbyi* (Leckenby): Nathorst, p. 5, pl. 1, figs. 3-5. (Cuticle.)  
 1913 *Ptilozamites (Ctenozamites) leckenbyi* (Leckenby): Thomas & Bancroft, p. 194, pl. 19, figs. 16, 17; pl. 20, fig. 12. (Cuticle.)  
 1914 *Ctenopteris leckenbyi* (Leckenby): Gothan, p. 143 (Comparison.)  
 1943 *Ctenopteris leckenbyi* (Leckenby): Harris, p. 515, text-figs. 4-6. (Form, emended diagnosis and cuticle.)

DIAGNOSIS (modified from Harris 1943). In middle and upper parts of leaf main rachis stout, longitudinally furrowed, bearing pinnae at an angle of 45° or less, lower parts of leaf unknown. Segments of lamina (pinnules) in large leaves, typically 3-4 cm. long × 1 cm. broad, distinctly falcate; segments in smaller leaves relatively shorter, rhomboidal or triangular and 1.5-1.8 cm. long × 0.7-1.0 cm. wide. Margins of segments slightly curved downwards, often very slightly reflexed, apex acute, often mucronate and often with a few smaller teeth. About six veins entering the base of a segment, veins forking once or twice and running at a concentration of about 20 per cm.; veins mostly ending at the apex or in the lower margin near the apex.

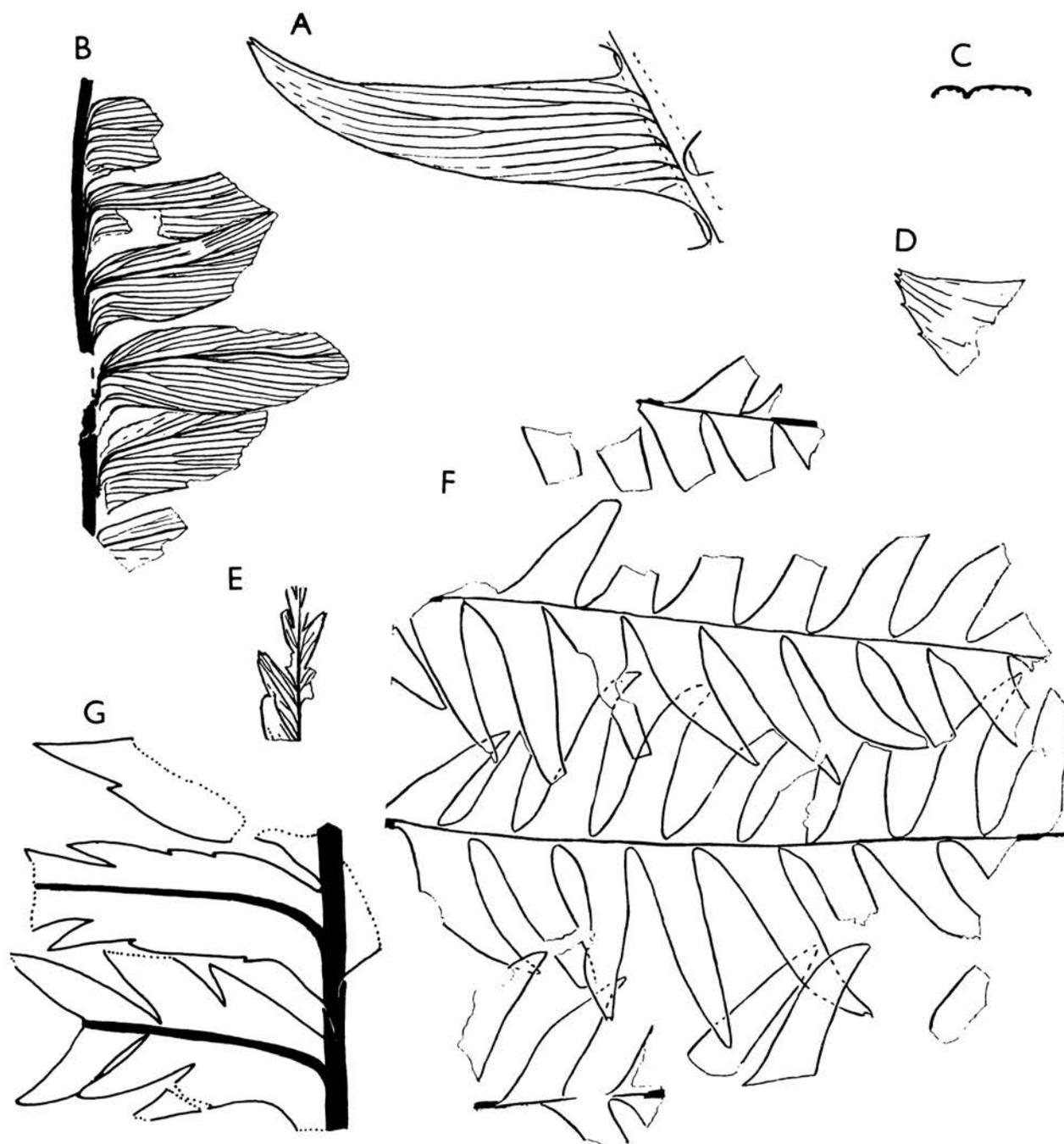


Fig. 39. *Ctenozamites leckenbyi* (Leckenby)

A, one segment from F,  $\times 2.5$ . B, fragment believed to be from leaf apex, V.21876. C, imaginary cross section through a pinna of B to show the sunk pinna rachis (midrib),  $\times 1$ . D, apex of a segment (total length 15 mm.), V.26868,  $\times 2.5$ . E, fragment from near apex of a pinna, V.21876,  $\times 1$ . F, fragment showing parts of four pinnae. The leaf is drawn as seen from above and the pinna rachises are largely concealed. Segments exposed by removing upper ones are shown by broken lines, V.21874,  $\times 1$ . G, near leaf apex, compare it with B. Specimen in J. Walton Colln., Botany Dept., Glasgow University.

All the specimens are from the Gristhorpe Bed. Figs. A-F are from Harris (1943, text-figs. 4, 5).

Cuticle robust, up to  $9\mu$  thick above and  $4\mu$  below. Upper epidermis without stomata, veins obscurely marked by longer cells. Cell outlines strongly marked, almost straight or slightly waved; consisting of a prominent median ridge and broad borders, borders interrupted by small pits. Surface of cells between veins usually granular, cells over veins often showing obscure longitudinal striae. Papillae absent.

On under side, stomata occurring in broad bands between veins. Cells on under side as on upper side, but those along veins more elongated, those between veins often irregular or in groups. Hypodermal fibres absent, even on upper side. Stomata scattered in their bands typically 30–50 per sq. mm., guard cells often orientated longitudinally. Subsidiary cells often about six, irregular in size and position, sometimes very small; exposed surface sometimes unthickened, but usually somewhat thickened all over; or if rather large, inner half thickened and outer half thin. Encircling cells often present, but irregular, unspecialised, and seldom forming a complete ring. Subsidiary cells forming a deep pit, pit rounded or polygonal, sides strongly thickened and at the general surface forming a raised ring of solid cuticle about  $20\mu$  wide from which a thin rim of cuticle extends inwards and constricts the aperture. Aperture of pit usually round, but often oval (elongated transversely to the guard cells), occasionally constricted by ingrowths opposite the subsidiary cells to a narrow slit; aperture of pit seldom over  $8\mu$  wide and often much less. Guard cells completely sunken, usually strongly cutinised along the contact with the lateral subsidiary cells as broad crescent shaped thickenings about  $50\mu$  long; aperture of guard cells about  $15\mu$  long; thin regions over guard cell poles about  $12\mu$  long.

LECTOTYPE. Leckenby Coll., No. 245, Woodwardian Museum, Cambridge. Figured by Leckenby (1864, pl. 10, fig. 1).

OCCURRENCE. The good specimens of *C. leckenbyi* are all from the Gristhorpe Bed (where however it is uncommon). There are also fairly good specimens in the Beast Cliff *Ctenozamites* Bed (at  $54^{\circ} 23' 41''$  N, near Ravenscar). Cuticle fragments agreeing with *C. leckenbyi* are widespread throughout the Deltaic Series and it is one of the more commonly met species in the relatively barren Upper Deltaics. Its localities are distributed as follows:

Upper Deltaic	12 localities
Middle Deltaic Gristhorpe Series	10 localities
Middle Deltaic Sycharham Series	2 localities
Lower Deltaic	10 localities

There is a rather small pinna (J. 1137) from Stonesfield, Oxfordshire, in the Oxford Museum which appears to belong to this species. The Stonesfield Slate is younger than part at least of the Upper Deltaic and includes the zones of *Tulites subcontractus* and *Morrisoceras morrisoni* of the Middle Bathonian.

DISCUSSION. *Ctenopteris leckenbyi* is only occasional in the Gristhorpe Bed but in the course of time a considerable number of specimens from there has been collected. All but the smallest agree in their relatively narrow segments and also in their reflexed margins and minute apical teeth. No specimen is large enough to indicate the length of the leaf. One specimen (Text-fig. 35 E) shows dichotomy but this is at the top of a leaf and we do not know whether dichotomy occurs in the main rachis.

An unusual specimen (Text-fig. 39 B) shows lamina segments with midribs and contracted bases. They were earlier described as pinnules (Harris 1943) but are now regarded as

pinnae from a leaf apex. This explanation is supported by the specimen in Text-fig. 39 G which is evidently from near the top of a leaf. The upper pinnae in Text-fig. 39 G are becoming small and imperfectly segmented and the uppermost seems similar to the lowest in Text-fig. 39 B. Thus the 'midribs' in Text-fig. 39 B are reduced pinna rachises.

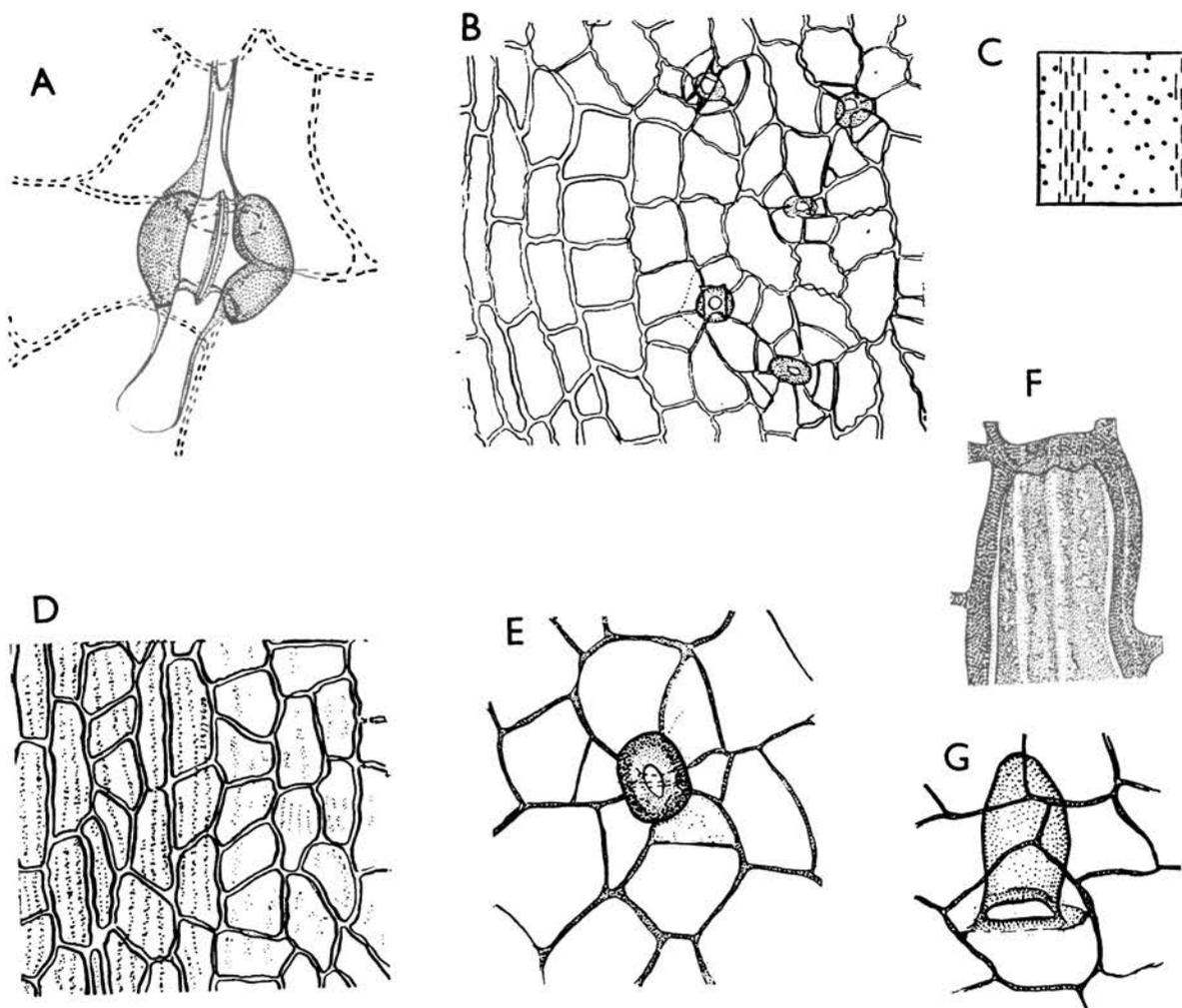


Fig. 40. *Ctenozamites leckenbyi* (Leckenby)

A, stoma (seen from inside), structures below surface level shown by broken lines, V.21881,  $\times 800$ . B, lower epidermis (vein on left), V.21877,  $\times 200$ . C, 1 sq. mm. of the lower cuticle, veins indicated by vertical shading, stomata by black dots, V.21877,  $\times 20$ . D, upper epidermis (vein on left), V.21877,  $\times 200$ . E, stoma (seen from outside), V.21877,  $\times 400$ . F, part of a cell of the upper epidermis, V.21877,  $\times 800$ . G, hair on upper surface, V.21875,  $\times 400$ .

All specimens are from the Gristhorpe Bed. All figures from Harris (1943).

Cuticle fragments from several localities show the outlines of palisade mesophyll cells underneath the upper epidermis, sometimes so conspicuously as to obscure the epidermal cells. In addition there may be a single dark body of unknown nature in the middle of each of these cells recalling a nucleus, but rather larger than a nucleus would be expected to be (Pl. 4, fig. 10). Similar palisade cells are known in *C. cycadea* (see Harris 1961) where also they abut

on to the upper epidermis without there being any hypodermis. Presumably these mesophyll cells are seen because of some exceptional impregnation of their walls or contents which has made them resist maceration.

Some variation was noted in stomatal structure. In typical Gristhorpe Bed specimens, about one stoma in fifty has an extremely wide pit forming a ring up to  $40\mu$  wide and this pit is not at all constricted, the inner parts of the subsidiary cells and the guard cells being exposed. A few other stomata were noted in which the pit is of normal size but the rim constricting it is unevenly lobed, the lobes being opposite subsidiary cells.

COMPARISON. Typical specimens of *C. leckenbyi* are readily distinguished from the other Yorkshire species by the characters given in the key (p. 91), and even small fragments of cuticle appear to be determinable.

### *Ctenozamites cycadea* (Berger) Schenk

Pl. 4, figs. 3, 7; Text-figs. 41, 42

None of the following is from Yorkshire:

- 1832 *Odontopteris cycadea* Berger, pp. 23, 27, pl. 3, figs. 2, 3. (Rhaeto-Liassic, Germany.)
- 1835 *Filicites cycadea* (Berger) Brongniart, p. 387, pl. 129, figs. 1, 2. (Lower Lias, France.)
- 1836 *Odontopteris bergeri* Goepfert, p. 219. (Change of name.)
- 1847 *Pterophyllum crassinerve* Schenk in Germar, p. 123, pl. 15, fig. 5. (Lias, Germany.)
- 1847 *Pterophyllum hartigianum* Schenk in Germar, p. 123, pl. 15, fig. 4. (Lias, Germany.)
- 1866 *Odontopteris cycadea* Berger: Brauns, p. 51, pl. 13, fig. 5. (Rhaeto-Liassic, Germany.)
- 1873 *Ctenopteris cycadea* (Brongn.) Saporta, p. 355, pl. 40, figs. 1, 2. (New genus from Brongniart MS, species attributed to Brongniart. Lias, France.)
- 1876 *Ctenopteris cycadea* (Brongn.): Nathorst, p. 37, pl. 6, figs. 5, 7. ('Upper Rhaetic' or Lower Lias, Sweden.)
- 1877 *Ctenopteris cycadea* (Brongn.): Heer, p. 125, pl. 51, fig. 13. (Lias, Switzerland.)
- 1882 *Ctenopteris cycadea* (Brongn.): Staub, p. 249, plate. (Lias, Hungary.)
- ?1883 *Ctenopteris cycadea* (Brongn.): Heer, pl. 4, fig. 12. (Indeterminable fragment. Lias, Switzerland.)
- 1886 *Ctenozamites bergeri* (Goepfert) Nathorst, p. 122. (New name.)
- 1887 *Ctenozamites cycadea* (Brongn.) Schenk, p. 5, pl. 3, figs. 11-16a; pl. 4, fig. 18; pl. 6, fig. 30; pl. 7, fig. 36; pl. 8, fig. 43; pl. 9, fig. 54. (Lower Jurassic, Persia.)
- 1891 *Ctenopteris cycadea* (Brongn.): Saporta, p. 400, pl. 292, figs. 2-6. (Lias, France.)
- 1900 *Ctenopteris cycadea* (Brongn.): Zeiller, p. 101, text-fig. 75. (Drawn from Staub 1882.)
- 1904 *Ctenopteris cycadea* (Brongn.): Seward, p. 36, pl. 3, fig. 1, 1a, also text-fig. 2 as *Thinnfeldia rhomboidalis*. (Lower Lias, England.)
- 1909 *Ctenopteris cycadea* (Brongn.): Salfeld, p. 16, pl. 1, fig. 10; pl. 2, fig. 21. (Lower Lias, N. Germany.)
- 1914 *Ctenopteris cycadea* (Brongn.): Antevs, p. 4. (Brief description of cuticle.)
- 1914 *Ctenopteris cycadea* (Brongn.): Gothan, p. 142. (Comparison.)
- 1919 *Ctenopteris cycadea* (Berger): Antevs, p. 35, pl. 4, figs. 30-34. (Lower Lias, Sweden.)
- 1947 *Ctenopteris cycadea* (Brongn.): Carpentier, p. 6, pl. 6, figs. 1-5; pl. 11, fig. 12. (Lower Lias, France.)
- 1950 *Ctenopteris cycadea* (Brongn.): Corsin, p. 258, pl. 11, fig. 3, 3A; pl. 12, figs. 6-11; text-fig. 6. (Rhaetic, France.)
- 1950 *Ctenopteris* cf. *sarrani* Zeiller: Corsin, p. 252, pl. 11, fig. 4; pl. 13, figs. 1-9; text-fig. 3A. (Rhaetic, France. Specimens regarded here as large *C. cycadea*.)
- 1961b *Ctenopteris cycadea* (Berger): Harris, p. 151, pls. 31, 32, text-figs. 1, 2. (Form and structure. Lower Lias, England.)
- 1962 *Ctenopteris* sp. (cf. *cycadea-sarrani*) Daber, p. 129, pl. 3, figs. 4-7; pl. 4, fig. 5; text-fig. 3. (Fragments and cuticle. Lias, N.E. Germany.)

DIAGNOSIS (based largely on Liassic specimens). Leaf about 1 m. long, main rachis about 2 cm. wide below the dichotomy, longitudinally ribbed, pinnae arising at an angle

greater than  $45^\circ$ . Segments of lamina typically rhomboidal and about  $20 \times 10$  mm. and arising at a wide angle but in outer parts of pinnae becoming triangular and about  $10 \times 7$  mm. and arising at a smaller angle. Apex of segment usually obtuse, margins entire and not denticulate near the apex, margins flat or incurved. About six veins entering each normal sized segment, veins forking once or twice, nearly parallel and mostly ending in outer margin. Hypodermis absent. Cuticle moderately thick, lower cuticle much thinner than upper; stomata confined to lower epidermis, generally distributed or veins weakly distinguished by their absence along narrow strips. Upper cuticle showing almost uniform polygonal cells; veins very slightly indicated by longer cells. Cell walls moderately clearly marked, rather broad, straight, not interrupted by pits; cell surface not or scarcely striated, granular or almost smooth, occasionally showing an obscure papilla. Trichomes often absent, but sometimes frequent; if present, base consisting of a small oval cell on top of other cells, bearing a ring scar; free part unknown. Lower cuticle showing polygonal or irregularly elongated cells; surface not striated nor papillate. Cell walls moderately distinct, nearly straight. Stomata scattered, incompletely dicyclic, orientation varied. Subsidiary cells about six, irregular in size and position, sometimes small, exposed surface usually somewhat thickened. Encircling cells uneven in size and irregular in position. Subsidiary cells forming a pit with strongly thickened sides  $20-25\mu$  wide and probably raised at the general surface; mouth of pit small, often polygonal and slightly constricted by a thin rim of cuticle. Guard cells seldom much cutinised.

LECTOTYPE. Specimen figured by Berger (1832, pl. 3, fig. 2).

OCCURRENCE.

Upper Deltaic:

Cloughton Stone Quarry, Riccal Dale and Roppa Gulley (The last two localities each provided one small fragment).

Lower Deltaic:

Hasty Bank (occasional).

Roseberry Topping (locally frequent—well represented in the Hamshaw Thomas Collection and in the Burton Collection, Middlesbrough Museum).

DESCRIPTION. Fragments of *C. cycadea* are fairly numerous at Hasty Bank and at Roseberry Topping. In all these specimens the pinnules are fairly broad and in all the margins of the pinnules are flat. Some variation was noted among the specimens at Roseberry Topping. Apart from the obvious differences in size of pinnules shown in Text-fig. 41, some have an entire apex, but some (Text-fig. 42 D and E) show slight irregularity which suggests denticulation of the kind seen more strongly in *C. leckenbyi*.

Some of the Yorkshire specimens have thick cuticles (the upper  $8\mu$  thick, the lower  $4\mu$ ) but in others the upper is thin and the lower so delicate as to be difficult to prepare. In certain Yorkshire specimens also, the lower cuticle has for some reason vanished entirely leaving the mesophyll as a black powder on the upper cuticle. In certain leaves from the Liassic e.g., the English one, Brit. Mus. no. 40674 and the French one 11612, figured by Saporta (1891, pl. 292, fig. 6) and prepared by Dr. Archangelsky, the lower cuticle is missing also.

The Yorkshire specimens also vary in the size of their epidermal cells and it happens that a leaf with a rather thick cuticle has the smallest cells and one with a thin cuticle has the largest. In the thin cuticle, cell outlines are rather finely and faintly marked instead of being thick and

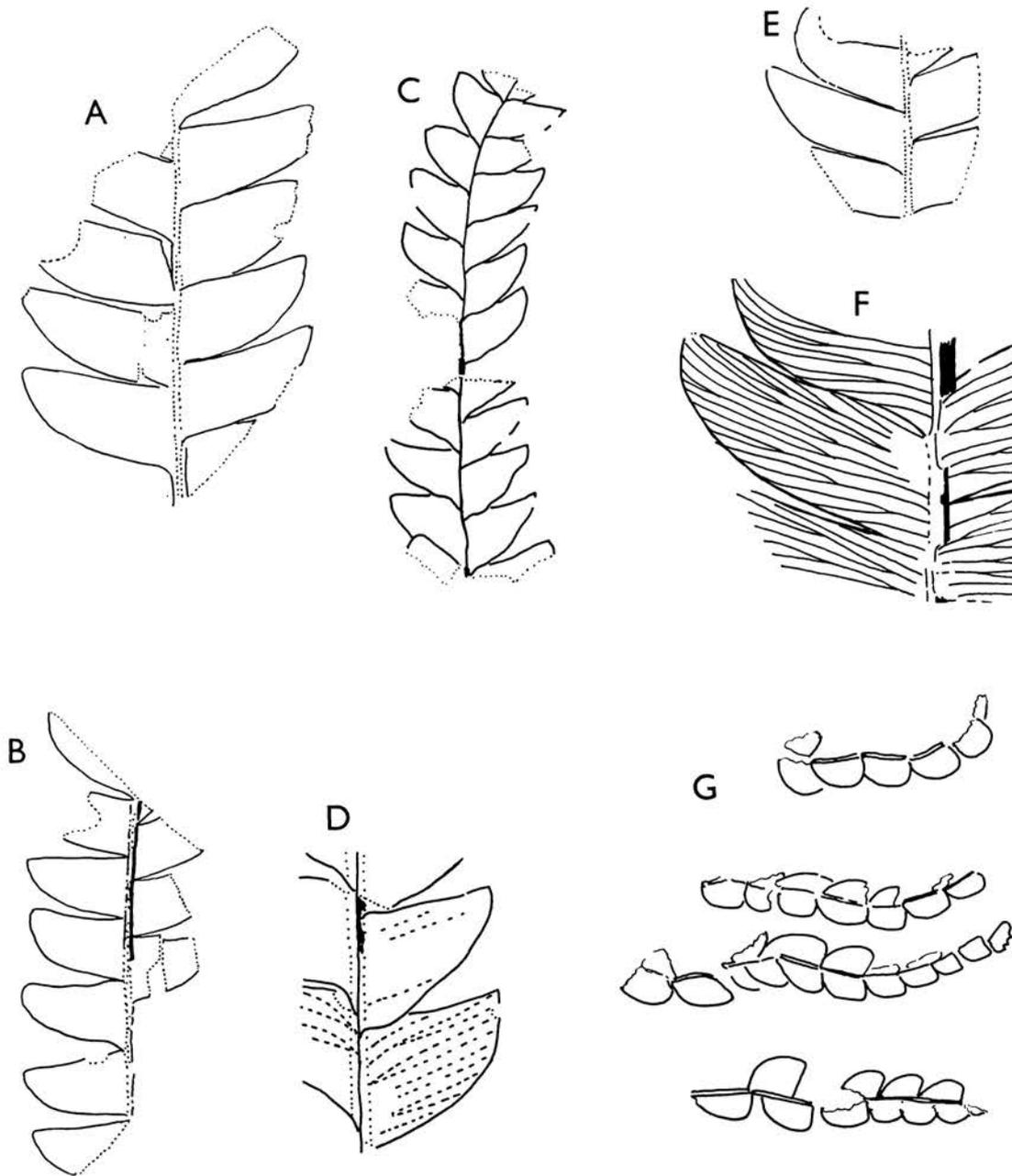


Fig. 41. *Ctenozamites cycadea* (Berger)

A, B, E, specimens in the Burton Colln., Middlesbrough Museum; probably from Roseberry Topping,  $\times 1$ . C, V.28548, from Hasty Bank,  $\times 1$ . D, details from C,  $\times 2$ . F, details from E, V.45586,  $\times 2$ . G, leaf fragments from Hasty Bank, V. 44869,  $\times 1$ .

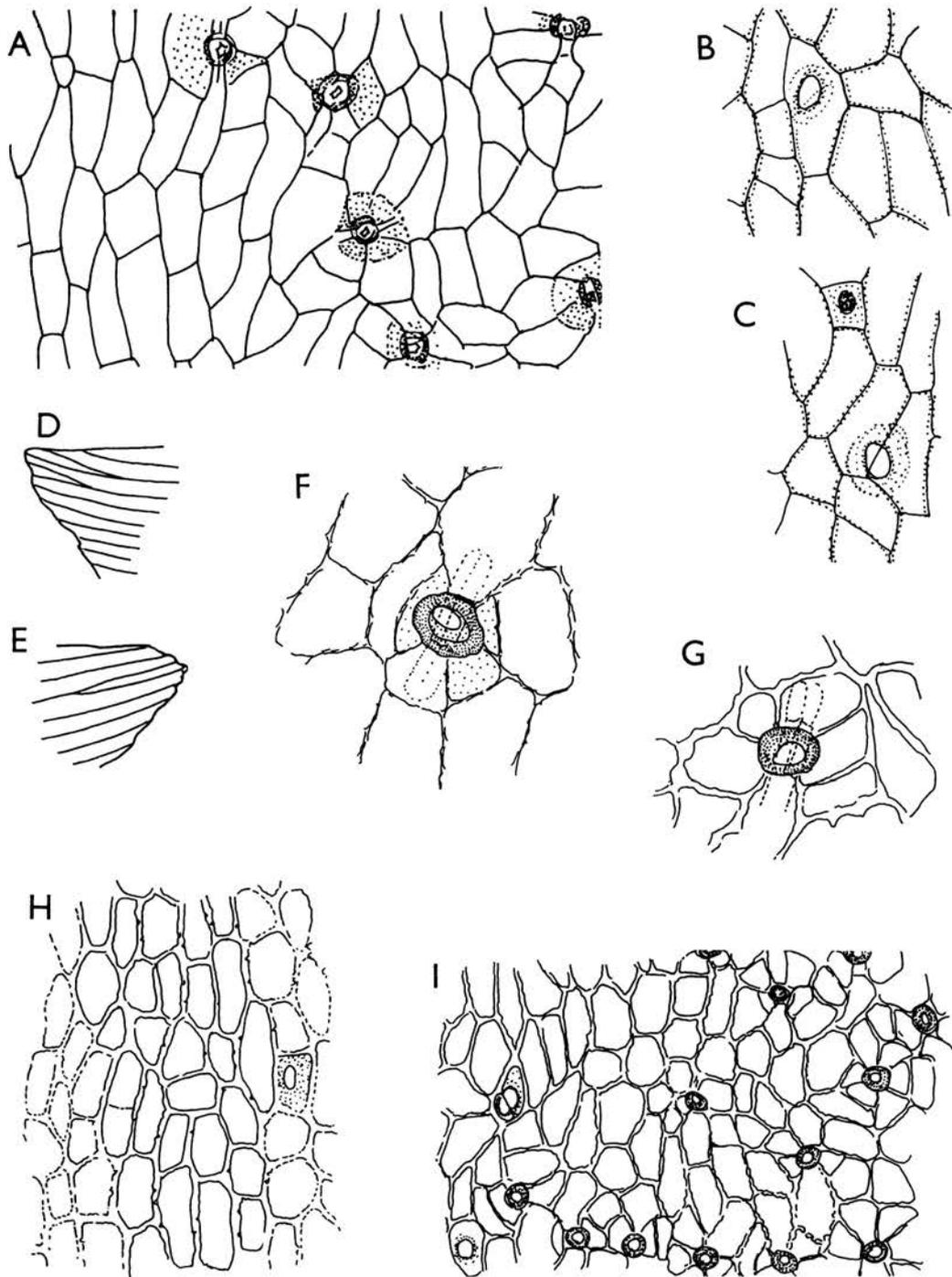


Fig. 42. *Ctenozamites cycadea* (Berger)

A, lower cuticle (unusually thin and with large cells), specimen shown in Fig. 41 E. V.45586,  $\times 200$ . B, C, upper cuticle of same specimen showing trichome bases,  $\times 200$ . D, E, pinnule apices from specimens in block shown in Pl. 4, fig. 7, V.44867,  $\times 4$ . F, stoma from same specimen as in A,  $\times 400$ . G, stoma from same specimen as in I,  $\times 400$ . H, upper cuticle (thick and with small cells), V.45587,  $\times 200$ . I, lower cuticle of same pinna as H, there is a vein on the left with two trichome bases, V.45587,  $\times 200$ .

A-C, F are from a specimen in the Burton Colln., Middlesbrough Museum; probably from Roseberry Topping. D, E, G-I are from Roseberry Topping.

obvious and in the thin one also the subsidiary cells have a slightly thicker surface than other cells. No such difference is apparent in the thickly cutinised leaf. In some leaves a few stomata show an unevenly lobed rim recalling that typical in *C. megalostoma*.

No cuticle shows any imprint of hypodermal cells and in the petrified English Liassic specimen (V.36330) the palisade mesophyll abuts on the upper epidermis. Some of the Yorkshire leaves on maceration yielded recognisable palisade and spongy mesophyll cells and this confirms the absence of hypodermis.

The frequency of trichome bases varies greatly, apparently in different parts of a single leaf. In some preparations none was seen on the upper side and very few below, but in others they are frequent above and numerous below. The same is true of Saporta's specimens, one of Dr. Archangelsky's preparations from Saporta's pl. 192, fig. 6 shows about 25 per sq. mm. and some of these are more elaborate than those figured here. Other small preparations showed few or none.

It may be pointed out that although all the Yorkshire specimens have a flat lamina and so apparently do nearly all the figured specimens, one English Liassic leaf figured accurately by Seward (1904, pl. 3) shows strongly recurved pinnules. This curvature is very uneven and I suspect is merely caused by withering after death, while the minute recurving of the margin in *C. leckenbyi* is regular and appears original.

COMPARISON. The Yorkshire specimens look just like the figures listed above and agree also in their cuticles. They differ in age, being Bathonian to Bajocian while the previous ones are all Lower Liassic or else of undetermined age.

*Ctenozamites megalostoma* sp. nov.

Pl. 3, figs. 3, 4. Text-fig. 43

DIAGNOSIS. (Size and form of leaf unknown, leaf only known from isolated pinnules.) Pinnules rather small, typically 5 mm. long  $\times$  3 mm. broad, arising from pinna rachis at a small angle. Pinnule straight or only slightly falcate, apex acute often with minute teeth; margins flat. Pinnule showing about six parallel veins in distal part, veins forked below, running at a concentration of about 20–30 per cm. Cuticle moderately thick, typically  $4\mu$  thick above,  $3\mu$  below (measured in folds). Stomata usually confined to lower epidermis, in ill-defined bands between the veins; in some leaves a few scattered stomata occurring on upper side. Cell outlines clearly marked on both sides, nearly straight, seen as a broad, prominent ridge occasionally interrupted by pits. On upper side cell surface obscurely granular, middle of cell often thickened to form an ill-defined solid papilla; on under side papillae absent even in leaves where papillae occur above; cuticular striae absent or obscure. On upper side, veins very obscurely marked. On under side veins marked by a few rows of elongated cells. On upper side all cells usually slightly elongated, on under side cells between veins isodiametric or variously elongated. Hypodermis present, on upper side often distinct and forming elongated cells under the whole epidermis; on lower side confined to the veins and margins.

Stomata scattered, about 40 per sq. mm., orientation often longitudinal. Subsidiary cells often about six, irregular in size and position, exposed surface unthickened. Encircling cells, if present, unspecialised. Subsidiary cell pit with very strongly thickened sides, forming a raised ring of solid cuticle about  $30\mu$  wide internally,  $45\mu$  wide externally. Interior of ring typically

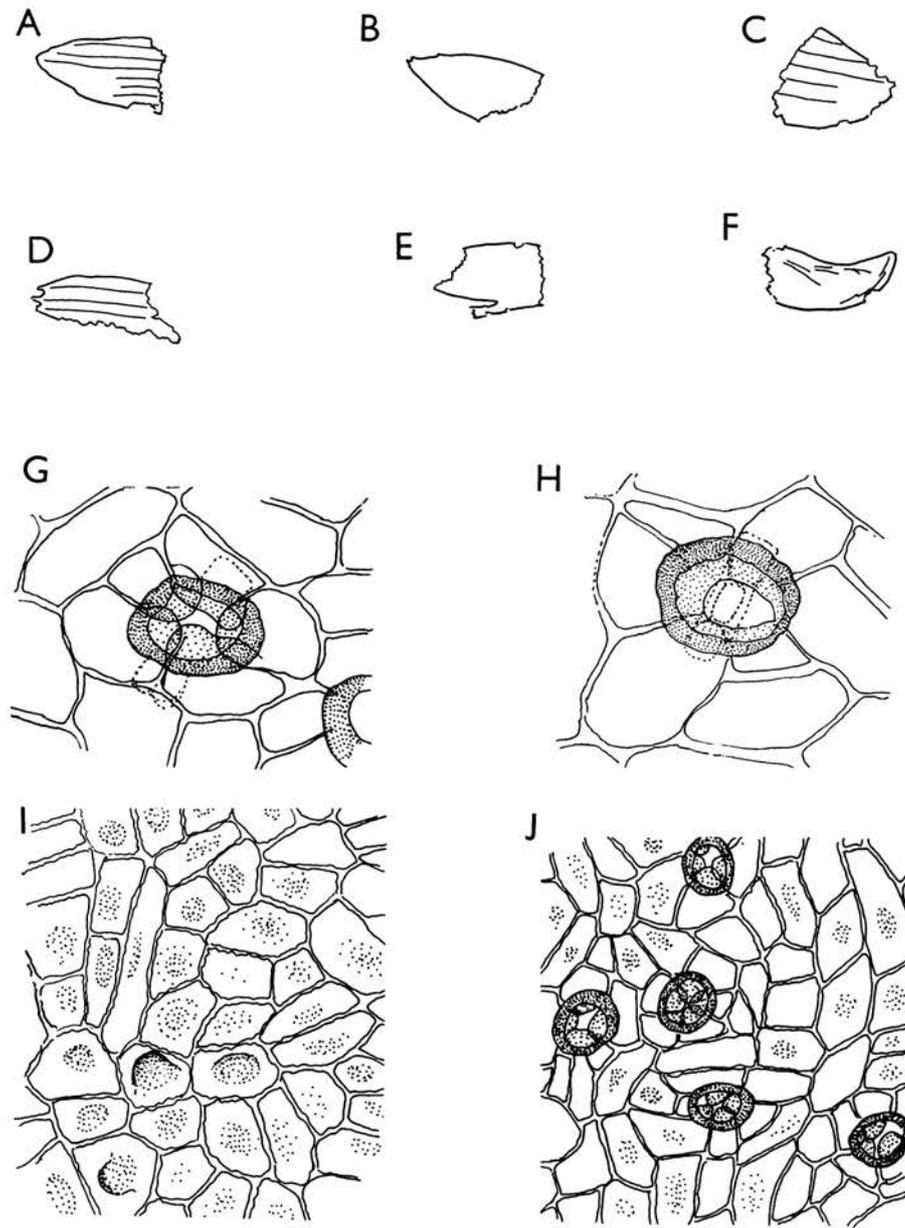


Fig. 43. *Ctenozamites megalostoma* sp. nov.

A-F, fragments of pinnules, all  $\times 3$ . A, B, Eston Moor Quarry, V.45590. C, Sniles-worth, Wheat Beck 3, one of the broadest fragments, V.45591. D, Wheat Beck 3, the apices of the teeth are broken off, V.45510. E, Wheat Beck 3, a little of the pinna rachis is present, V.45592. F, Hartoft 4, the surface is folded, V.45593. G, H, two stomata from the fragment shown in A,  $\times 400$ . I, upper cuticle of A,  $\times 200$ . J, lower cuticle of A,  $\times 200$ . The holotype is shown in A, G, H, I, J.

constricted by a lobe of cuticle opposite each subsidiary cell, or lobes more or less confluent. Exceptionally, lobes represented by an evenly developed diaphragm pierced by a round or oval hole. Guard cells often showing a crescent-shaped thickening  $25\mu$  long along their contact with subsidiary cells. Aperture of guard cells about  $12\mu$  long. Trichomes usually absent but a very few unicellular trichome bases occurring on a few leaves.

HOLOTYPE. V.45590 (Text-fig. 43 A, B, G-J).

OCCURRENCE. *C. megalostoma* is widespread in the Yorkshire Deltaics and occurs in all divisions but is much less frequent than *C. leckenbyi*. Its distribution is as follows:

Upper Deltaic . . . . .	6 localities
Middle Deltaic Gristhorpe Series .	1 locality
Middle Deltaic Sycharham Series . . . .	2 localities
Eller Beck Bed and Hydraulic Limestone	2 localities
Lower Deltaic	7 localities

The type locality is Eston Moor, Beacon Quarry, where it is frequent. It is also frequent at Snilesworth, Wheat Beck Loc. 3. Both of these are Lower Deltaic.

DISCUSSION. Fragments of *C. megalostoma* are locally common. Its main interest is that its stomata show in some of their forms the usual structure of a *Ctenozamites* stoma, but in others they are like normal stomata of *Lepidopteris*; I do not, however, suggest close affinity with *Lepidopteris*.

By no means all the fragments show clear hypodermal fibres or large stomata with well developed lappets closing the ring and these fragments are thus imperfectly separated from the other Yorkshire species, but most are clearly enough separated. The main distinguishing features are:

- (1) The small size of the pinnules;
- (2) The very large stomatal ring;
- (3) The lobes, rather than a continuous rim of cuticle constricting the stomatal pit;
- (4) The hypodermal cells; where these are visible they form an absolute distinction from the other two species described here.

*Ctenozamites wolfiana* Gothan (1914) from the Lower Lias of S.W. Germany has pinnules of similar size, but the stomatal ring is smaller. The figures are not clear enough to give evidence on the other characters mentioned above.

### *Ctenozamites* sp. A

Pl. 3, figs. 1, 2

Three cuticle fragments were found which agree in most respects with *C. megalostoma* but differ too much to be identified. The fragments show that the pinnule apex is mucronate as in *C. megalostoma* and *C. leckenbyi*. All three fragments are thicker than in *C. megalostoma* and in all the stomatal rim is entire with a round hole. In one fragment the surface is strongly striate, in another weakly striate and the last is merely finely granular. One shows traces of hypodermal cells.

OCCURRENCE. Upper Deltaic, Gristhorpe Bay, foot of Upper Deltaic Cliff (two rather different fragments); Flask Inn, roadside ditch.

## Genus CTENIS Lindley &amp; Hutton 1834:63

DIAGNOSIS (freely translated from Florin 1933 : 81). Leaf once pinnate, pinnae [usually] with entire margins, inserted laterally on the rachis. Pinnae with no midrib but with several more or less parallel veins which anastomose and which reach the margins of the pinna. Lamina with stomata on its lower side, stomata in broad zones separated by narrow zones with few or no stomata along the veins. Upper surface with corresponding zones but few or no stomata. Epidermal cells orientated irregularly, cuticular striations always present. Basal cells of trichomes (probably simple) occurring on under side. Stomata haplocheilic, guard cells more or less sunken. Surface of guard cells thinly cutinised at the sides of the aperture but more thickly towards its ends and forming cross bars which join the more strongly cutinised dorsal lamellae of the guard cells and which bound the thinly cutinised and strongly raised polar parts of the guard cells. Four to seven subsidiary cells making contact with the guard cells and forming a rampart round the stomatal pit, no distinct papillae occurring round the stoma. (I have inserted the word 'usually' in the first sentence.)

TYPE SPECIES. *Cycadites sulcicaulis* Phillips 1829.

DISCUSSION. The better known species of *Ctenis* seem a coherent group but we still know nothing of the plant beyond the leaf. Florin (1933) presented a strong case for regarding *Ctenis* as a member of the Cycadales and two additional facts can now be added which are consistent with this view. The tracheids of the leaf vein are scalariform and are accompanied by a few very large fibres. The guard cells have the type of lignified thickenings found in Recent Cycads and most other Gymnosperms.

The lamina in *Ctenis* seems to be rather more delicate than in most Recent Cycads. The Yorkshire species at least lack any layer of hypodermal fibres (but it may be noted that the Recent *Bowenia* has none either).

Florin, in the diagnosis given above, refers to the veins ending in the margins. This statement can now be expanded (for *C. sulcicaulis* and for *C. kaneharai*). The pinna margins have a fibre bundle which is not vascular. In the lower parts of the pinna the veins avoid the fibre bundle, but near the apex a few of them end very near it or in it. The number of the veins is reduced distally, but more by vein fusion than by marginal ending.

The fact that petioles and leaf bases have rarely been figured suggests that they may be much rarer fossils than the tops of leaves. It could be that in *Ctenis*, as in so many Recent Cycads, the leaves hang on the plant and gradually break up, the bases remaining on the stem indefinitely. This would contrast with, say, *Nilssonia*, where leaves are shed and where leaf bases are common fossils. This suggestion is put forward in the hope that *Ctenis* leaf bases will be looked for elsewhere, and their rarity either confirmed or disproved.

The leaf genera nearest *Ctenis* are *Quervainia* Harris (1932) which differs only in having a midrib in the pinnae and *Pseudoctenis* which differs in having no vein anastomoses in its pinnae (see p. 71 for discussion of this point).

Keys to Yorkshire species of *Ctenis*

## 1. On leaf.

- |  |   |   |   |                  |
|--|---|---|---|------------------|
| (1) Pinnae with lobed or toothed margins | . | . | . | <i>C. exilis</i> |
| Pinnae with entire margins               | . | . | . | 2                |

(2)	Pinnae up to 5 mm. broad, veins 25 per cm.	. . . . .	<i>C. reedi</i>
	Pinnae over 5 mm. broad, veins about 10-20 per cm.	. . . . .	3
(3)	Base of pinna usually contracted	. . . . .	<i>C. kaneharai</i>
	Base of pinna expanded	. . . . .	<i>C. sulcicaulis</i>
2. On cuticle.			
(1)	Rampart round stoma circular and complete	. . . . .	2
	Rampart round stoma elongated and incomplete	. . . . .	3
(2)	Cell walls even and straight	. . . . .	<i>C. sulcicaulis</i>
	Cell walls jagged	. . . . .	<i>C. exilis</i>
(3)	Cell walls straight	. . . . .	4
	Cell walls jagged or sinuous	. . . . .	5
(4)	Cuticular striae strongly developed	. . . . .	<i>C. kaneharai</i>
	Cuticular striae weak	. . . . .	<i>C. reedi</i>
(5)	Cell walls jagged only	. . . . .	<i>C. exilis</i>
	Cell walls sinuous	. . . . .	<i>C. stewartiana</i>

*Ctenis sulcicaulis* (Phillips) Ward

Text-figs. 44, 45, 46 c

All the following are Yorkshire specimens:

- 1828a *Zamia longifolia* Brongniart, p. 94 (*Nomen nudum*.)  
 1829 *Cycadites sulcicaulis* Phillips, p. 148, pl. 7, fig. 21. (Poor figure.)  
 1834 *Ctenis falcata* Lindley & Hutton, p. 63, pl. 103. (Good figure of good specimen.)  
 1856 *Ctenis falcata* L. & H.: Zigno, p. 196, pl. 25, figs. 1-3. (Good Yorkshire specimens.)  
 1868 *Ctenis falcata* L. & H.: Schenk, p. 220, pl. 25, fig. 4. (Cuticle of Yorkshire specimen.)  
 1874 *Ctenis falcata* L. & H.: Schimper, p. 521, pl. 107, fig. 8. (Veins of a pinna.)  
 1875 *Ctenis falcata* L. & H.: Phillips, p. 218, pl. 7, fig. 21. (As 1829.)  
 1900 *Ctenis falcata* L. & H.: Seward, p. 235, pl. 8, fig. 2. (Good leaf.)  
 1905 *Ctenis sulcicaulis* (Phillips) Ward, p. 113. (Name only; specimens figured in pl. 25, fig. 9; pl. 26 are here regarded as distinct.)  
 1913 *Ctenis falcata* L. & H.: Thomas & Bancroft, p. 193, pl. 19, fig. 19; pl. 20, fig. 13. (Cuticle figured and discussed.)  
 1917 *Ctenis sulcicaulis* (Phillips): Seward, p. 582, ? text-fig. 626 (cf. Seward, 1911, pl. 4, fig. 62.)  
 1933 *Ctenis sulcicaulis* (Phillips): Florin, p. 64, pl. 7, figs. 1-6; pl. 8, fig. 1; text-figs. 21B, 23A. (Good specimens, cuticles, diagnosis, discussion.)

The following specimens identified as *Ctenis sulcicaulis* are from other regions:

- 1905 *Ctenis sulcicaulis* (Phillips) Ward, pp. 113, 149, pl. 25, fig. 9; pl. 26; pl. 38, figs. 7, 8. (Jurassic, Oregon, U.S.A.)  
 1955 *Ctenis sulcicaulis* (Phillips): Pantic, p. 214, pl. 5, fig. 1. (A smaller leaf. Jurassic, Serbia.)  
 1963 *Ctenis sulcicaulis* (Phillips): Samylina, p. 84, pl. 15. (Typical form. Jurassic, E. Siberia.)

EMENDED DIAGNOSIS. Leaf large, length possibly 70 cm., width in middle region at least 15-25 cm. Pinnae numerous, at least 14 cm. long in middle region of leaf but shorter near apex. (Basal pinnae not known). Pinnae arising almost at right angles in lower part and at about 1 cm. apart, but in middle region pinnae arising at an angle of 60°-70° and nearly in contact; angle reduced near apex and pinnae often more crowded. Pinnae straight or distal parts curved slightly forwards. Margins of pinnae nearly parallel over proximal half but tapering evenly in distal half, sometimes becoming slightly narrowed at 2-4 cm. from the rachis. At pinna base upper margin running straight towards rachis and then expanded for the basal 1-2 mm.; but in pinnae from lower part of leaf upper margin sometimes distinctly contracted near its insertion. Lower margin of pinna always considerably decurrent; typically extending as a narrow

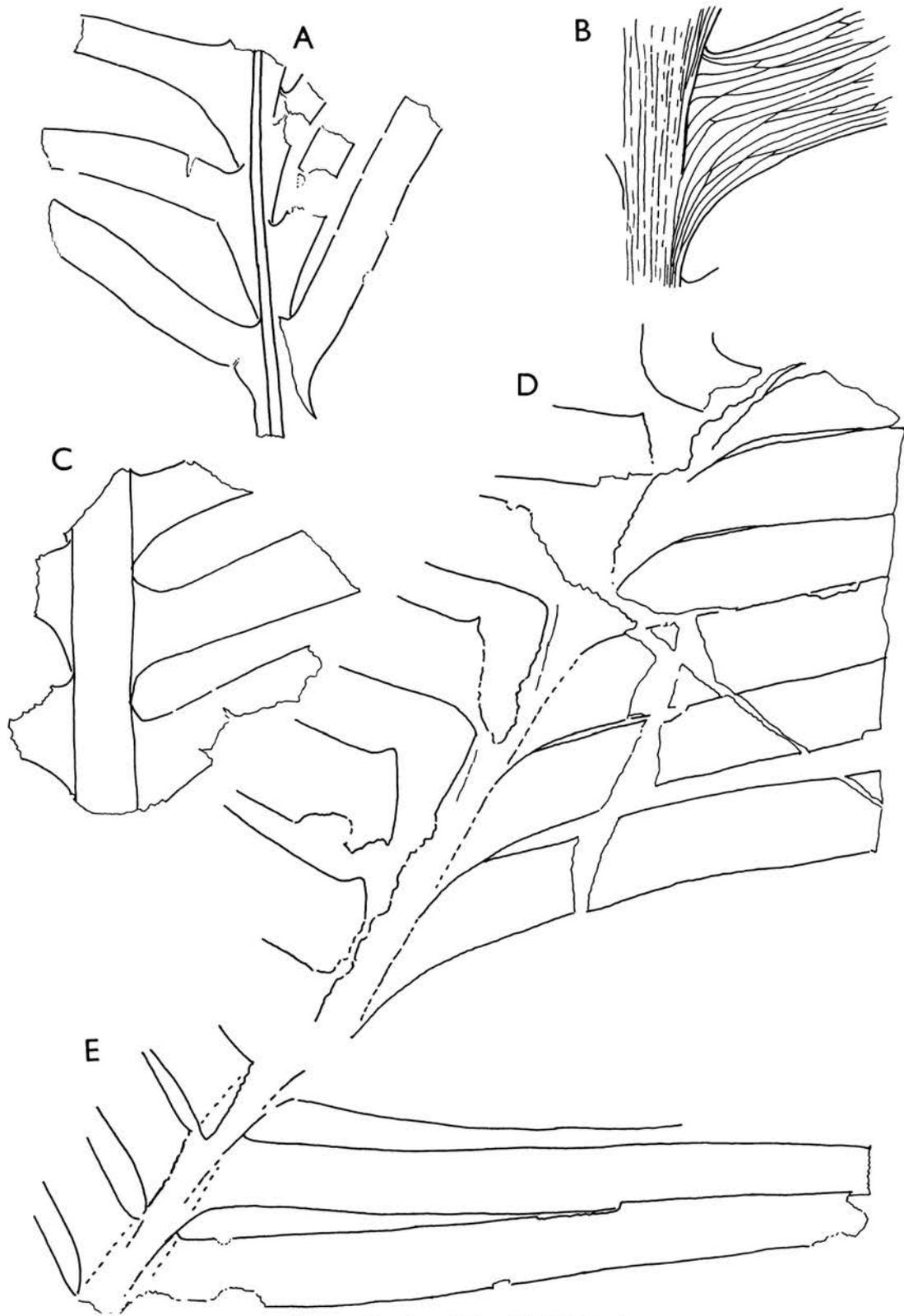


Fig. 44. *Ctenis sulcicaulis* (Phillips)

A, fragment from near top of a leaf, V.25865,  $\times 1$ . B, base of a pinna, 39205,  $\times 2$ . C, fragment from lower part of a leaf, V.44858,  $\times 1$ . D, E, pinnae from upper and lower parts of the fragment seen in 39025. The whole fragment is 37 cm. long.

A, C, Gristhorpe Bed. B, D, E, imperfectly localised but almost certainly from the Gristhorpe Bed.

flange overlapping the upper margin of the next pinna below. Width of pinna typically 10–15 mm., but at leaf apex, pinnae becoming only half as broad; pinnae known to taper distally to 2–3 mm., apex not known (? acute). Margins of pinnae flat but distinctly thickened by a fibre bundle. Rachis up to 1 cm. wide in lower part of lamina, tapering above, but width exaggerated by decurrent pinna bases; surface of rachis marked with longitudinal furrows. Veins 12–21 in a typical pinna, nearly parallel but anastomosing at intervals of about 1–2 cm., traversing the lamina at a concentration of about 18 per cm. At base of pinna, veins diverging in directions parallel to nearest pinna margin; towards apex of pinna veins converging slightly and becoming more crowded, though fewer. At margins of pinna outermost vein running parallel with the marginal fibre bundle, not anastomosing with it; towards apex marginal veins ending separately in or near the fibre bundle. Veins usually conspicuous on both surfaces, often forming two ridges separated by a furrow.

Cuticle of moderate thickness on both sides (measuring 2–5 $\mu$  in folds). Upper epidermis without hairs or stomata; cells along veins rectangular forming 2–4 longitudinal rows; cells between veins isodiametric or irregular polygons. Cell walls straight, longitudinal walls of cells along veins conspicuous but transverse walls and walls of cells between veins often inconspicuously marked by an obscure broad ridge. Cell surface flat, cells along veins showing longitudinal striations but cells between veins usually showing coarse mottling only.

Lower epidermis showing a small number of scattered hair bases and about 100 stomata per sq. mm. in the areas between the veins. Cells along veins rectangular, forming 2–4 longitudinal rows, often not markedly distinguished from other cells; cells between veins polygonal, often irregularly elongated. Walls of all cells conspicuously marked by a broad or a fine ridge, straight, scarcely interrupted by pits. Surface of cells flat; cells along veins showing conspicuous longitudinal striations, cells between veins showing a mottled surface or rather faint parallel striations particularly near stomata.

Stomata evenly scattered in areas between veins, not aggregated in clumps; not arranged in any regular order, variably concentrated. Stomata typically incompletely dicyclic, often with two polar subsidiary cells and about four lateral ones; neighbouring stomata occasionally sharing a subsidiary cell. Guard cells entirely sunken but middle region exposed in a pit typically 30–50 $\mu$  wide. Aperture of stoma about 50–60 $\mu$  long; surface of guard cells thinly cutinised in the middle parts but with a transverse bar or fold of thickening at the ends of the aperture separating the deeply sunken aperture from the raised poles. Subsidiary cells irregular in size and position, usually small when divided from an encircling cell. Subsidiary cells forming the round stomatal pit; margin of pit conspicuously raised as a continuous circular rampart, occasionally rampart elongated and poorly developed over the poles of the guard cells. Encircling cells often developed in a lateral position, unspecialised. Trichome bases consisting of a small epidermal cell usually without any definite surface marking, free part of trichome lost before preservation.

Elongated hypodermal cells present along margins of pinnae but probably absent elsewhere.

LECTOTYPE. Specimen figured by Phillips (1829, pl. 7, fig. 21).

OCCURRENCE. Middle Deltaic Gristhorpe Series—Gristhorpe Bed. (Origin of most hand-specimens). Cloughton Wyke *Solenites* Bed; specimens collected by Halle and figured by Florin, also by Hamshaw Thomas and myself.

Cuticle fragments resembling *C. sulcicaulis* are known from three other localities in the Middle Deltaic Gristhorpe Series and two in the Lower Deltaic.

DISCUSSION. *C. sulcicaulis* is represented by many magnificent slabs, mostly from the Gristhorpe Bed. It has been well figured, but the first figure (Phillips 1829, pl. 7, fig. 21) though showing the very characteristic shape of the pinna base, was imperfect in that it showed no clear vein anastomoses; Lindley & Hutton (1834) showed anastomoses clearly but they made no comment on them, nor did Phillips (1875) when he accepted the Lindley & Hutton name and figure and repeated his own early figure. It has been suggested to me that this error makes Phillips' figure unworthy as a designation of the holotype (and so the name *sulcicaulis* invalid) but I do not agree. The figure is fairly good otherwise and neither Phillips, Lindley & Hutton, nor anyone else have seen reason to doubt that the figure represents what was called *C. falcata*. I therefore accept the name *sulcicaulis*. Ward (1905) made this point too.

Florin gives an excellent account of this species but I have slightly altered his diagnosis to accommodate facts provided by certain additional specimens. There are still gaps in our knowledge caused by imperfect collecting. Although a number of leaf apices have been found and figured, no one seems to have found a leaf base; Zigno (1856) figured pinnae from the lower part of the lamina but probably not its base. I think I may have seen a leaf base but the specimen broke up and I regrettably kept no fragments. I remember it as having a broad rachis bearing short spine-like pinnae. As suggested on p. 102 leaf bases of *Ctenis* may be rarely preserved as fossils.

More surprisingly no specimen shows the complete length of a pinna nor have I seen any specimen showing the apical half of a pinna, though many have been preserved showing the rachis and inner parts. In the diagnosis the length of a pinna is estimated (assuming that it tapers evenly) to be 14 cm. but it might well be 20 cm. in a large leaf. The estimate of length of the leaf is based on the taper of the rachis in fragments about 30 cm. long, but the decurrent pinna margins make this taper difficult to measure accurately.

Florin observed that the veins of this species (and the very similar *C. nilssoni*) often form two ridges separated by a furrow. However, other veins, apparently just as well preserved, appear single. Some more information can now be given about the veins; it is provided by certain Gristhorpe specimens which had undergone oxidative decay before preservation. Here the cuticle forms a light brown or golden membrane enclosing the vascular elements. Such specimens were mounted in balsam without further treatment. The most translucent of these specimens (presumably the ones which had suffered most decay) merely show the cuticles enclosing fibres and tracheids and often the bundles have separated into their elements. The scalariform bars of the tracheids are then plain. Darker specimens show the tracheids in a more compact mass flanked by fibres. These fibres are pointed, about  $40\mu$  wide and about 1 mm. long. It appears that no more than 1-3 fibres accompany a small vein on each side of the xylem but a large vein probably has more. In still less rotted bundles the xylem forms a central mass in which scalariform bars are just visible and this xylem is flanked by much darker masses of fibres on either side. The fibres form the two ridges noticed by Florin and the collapsed xylem forms the furrow between them. In other, more compact looking bundles it seems that some fibres lie above (or below) the xylem. When veins anastomose both fibres and tracheids cross over. The marginal fibre band includes no tracheids, and when a vein ends by the margin, tracheids meet the fibre bundle but they do not continue along it.

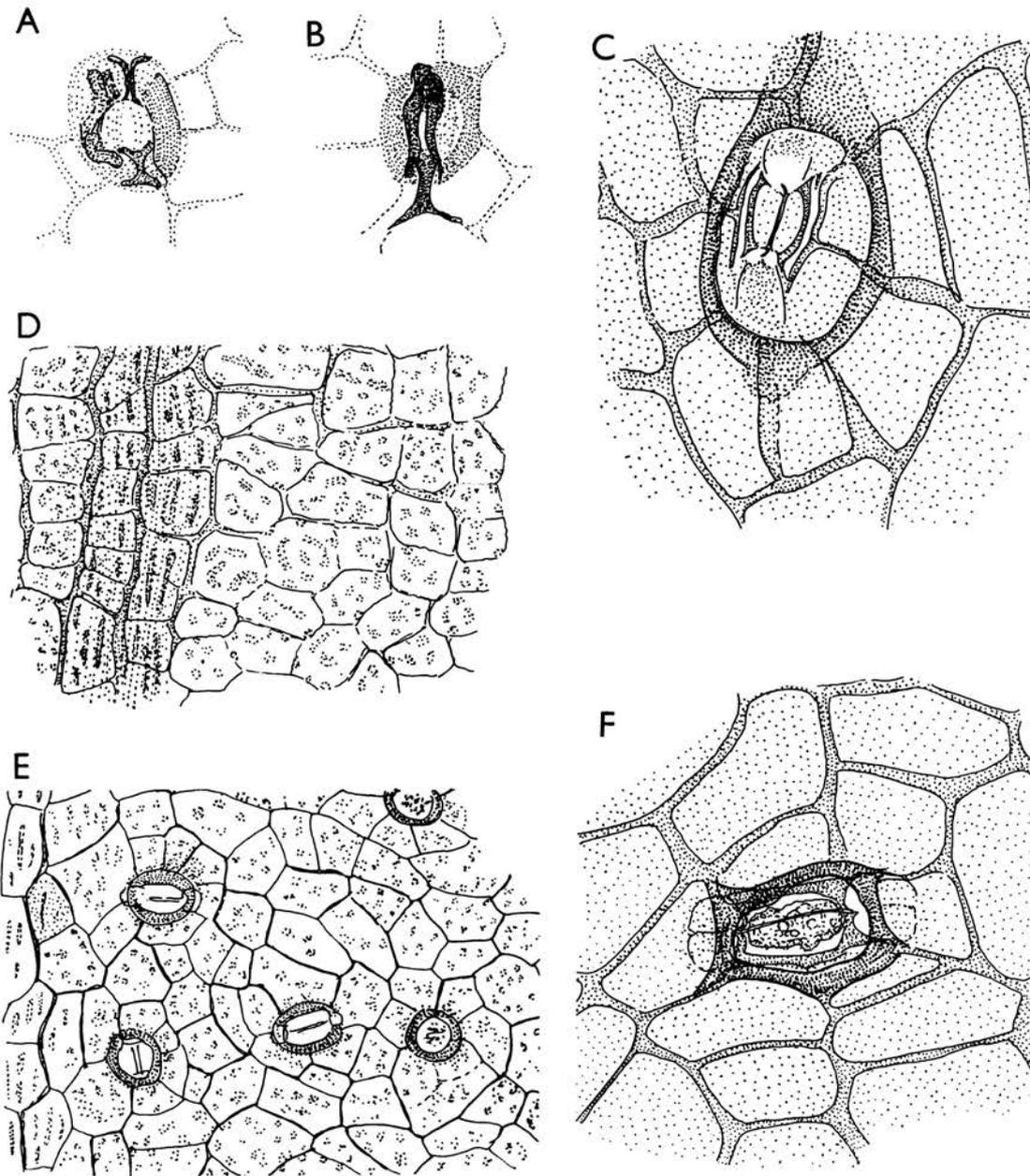


Fig. 45. *Ctenis sulcicaulis* (Phillips)

A, B, two stomata in a piece of unmacerated epidermis showing the guard cell thickenings, V.45369,  $\times 400$ . C, F, more exposed and more protected stomata of V.25879,  $\times 400$ . There is some wax round the aperture of F. D, E, upper and lower cuticles of V.25879,  $\times 200$ . In each there is a vein to the left. All specimens are from the Gristhorpe Bed.

*Stomatal structure.* The stomata shown from a cuticle preparation in Text-fig. 45 E, F, are typical of those of V.2879; but others from this specimen differ, some being more protected, others as exposed as in Text-fig. 45 C or even slightly more exposed. In one extreme stoma no rampart is developed at all. All the previously figured stomata have been normal ones, with well developed ramparts. A similar range was observed in *C. nilssoni* (see Harris 1937, text-fig. 36).

In exposed stomata such as the one in Text-fig. 45 C the guard cells are more cutinised than usual. The thinnest part of their cuticle is at the poles, and the next thinnest is a strip looking like a hinge line just outside the lateral thickenings. The general surface between the aperture and the lateral thickenings usually looks slightly thicker than the poles. The transverse bars at the ends of the aperture are usually conspicuous but I believe that they do not represent originally thicker cuticle but are the result of strong curvature just here which commonly results in a fold.

In exposed stomata where the rampart round the mouth of the pit is very wide, the subsidiary cell walls can be traced past it and along to the guard cells. Where the rampart forms a narrow ring the subsidiary cells end underneath it, very close to the lateral thickenings of the guard cells. In 1932 I gave an interpretation of the stoma of *C. nilssoni* in which the subsidiary cells were supposed to be concealed in the sides of the pit and only exposed exceptionally where the pit was wide with sloping sides, but Florin (1933) gave a different interpretation in which the subsidiary cell forms the sides of the pit and extends on to the surface, whether the sides of the pit are vertical or oblique. Florin's interpretation is here adopted for description as it is the simpler.

In the naturally cleared leaves of the Gristhorpe Bed (already mentioned as showing tracheids and fibres), the stomata are seen as dark spots and in a few fragments where the two epidermises had separated through decay the lower shows the lignine lamellae of the guard cells very clearly (Text-fig. 45 A, B). A Recent gymnosperm such as a Cycad stained for lignine shows corresponding lateral and polar lamellae. These thickenings are exactly as expected but they have rarely been reported from fossils because the oxidative maceration needed to clear the cuticle destroys them. Pant (1960) however, figured them in similarly preserved *Glossopteris* fragments.

Various authors have noticed swellings in the lamina of *Ctenis* and they were at first regarded as sori of the fern type. Florin regards them as fungal fructifications; he speaks of them as parasitic but in the present material they are more likely to be saprophytes, or if parasites ones which attacked late in the life of the leaf since there is no visible host reaction in the epidermal cells.

COMPARISON. Many species of *Ctenis* are at once distinguished from *C. sulcicaulis* by their absolutely broader or relatively broader pinnae and broader vein meshes. The following have rather similar form:

*C. nilssoni* (Nathorst) Harris; see Harris (1932) and Florin (1933). Rhaetic of Sweden and East Greenland.

*C. minuta* Florin. See Harris (1932), as *C. fallax*, and Florin (1933). Rhaetic of Sweden and East Greenland.

*C. yamanarii*. Kawasaki (1926, 1939). Liassic of Korea.

*C. sulcicaulis* (Phillips) Ward 1905 (i.e. The American specimens figured under this name).

*C. hungarica* Staub (1896). Lias of Hungary.

Of these *C. nilssoni* is discussed further below.

*C. minuta*, a leaf of very similar form, is at once distinguished by its cuticle. The stomata are clumped and individual stomata are relatively exposed. As in other species with clumped stomata the epidermal cells near the stomata are folded.

*C. yamanarii*. A leaf of unknown structure, probably has considerably shorter pinnae and only the longest (when broken off) look like broken off pinnae of *C. sulcicaulis*. The specimen from Oregon described as *C. sulcicaulis* by Ward also represents a smaller leaf than the Yorkshire *C. sulcicaulis*.

*C. nilssoni* agrees with *C. sulcicaulis* (as far as we know the two species) in size, shape, venation, general characters and fine details of the cuticle and the problem is how to distinguish the two if indeed we are to continue to do so. Florin states that a few stomata occur on the upper epidermis of some preparations of *C. nilssoni*; in *C. sulcicaulis* they are normally absent but I have seen what I believe is one; since many preparations of *C. nilssoni* show none, there is no easy distinction here. The striations are more conspicuous in *C. nilssoni* and the hair bases on the lower side are rather more numerous; but both these are characters which vary. Had their ages been similar the two would have been identified with confidence. Instead, I leave them as they are for further study, but it is clear that with such similar leaves determination of the one or the other has no stratigraphic value.

*Ctenis laxa* (Rhaetic) and *C. nathorsti* (Möller) from the Lower Lias, both described by Florin (1933) have cuticles which are moderately similar to that of *C. sulcicaulis*, but both are at once distinguished by their pinnae.

*C. nathorsti* has pinnae which are only slightly decurrent and tend to be broader and with wider vein meshes.

*C. laxa* has a much wider pinna and meshes 2–3.5 mm. wide.

### *Ctenis reedi* Harris

Text-figs. 46 A, B; 47

1947a *Ctenis reedi* Harris, p. 659, text-figs. 4E, 5.

EMENDED DIAGNOSIS. Leaf of moderate size, length not known, width at least 15 cm. Pinnae attaining a length of at least 8 cm., rachis attaining a width of at least 4 mm. Pinnae arising at right angles in lower or middle part of leaf but at an angle of about 40° towards the apex. In lower part, pinnae rather distant, separated by gaps as wide as themselves but gaps becoming narrow in upper part. Pinnae straight or curving slightly forwards, margins nearly parallel over proximal half but tapering distally to an acute apex, sometimes becoming rather wider at about 2 cm. from the rachis. Width of pinna in lower part of leaf 4–7 mm.; towards leaf apex width diminished to 3–4 mm. Basisopic margin of pinna always decurrent, acroscopic margin neither ascending nor descending the rachis to any considerable extent. Margins of pinnae thickened with fibres, not recurved. Veins slender and inconspicuous, appearing single, traversing the lamina at a concentration of about 25 per cm.; anastomosis irregular, occurring at intervals of 1–5 cm.

Upper cuticle without stomata, about 3 $\mu$  thick (measured in folds), lower considerably thinner. Upper showing rather uniform polygonal cells, slightly elongated over the veins,

isodiametric or irregular between veins. Occasional cells along veins thickened, forming trichome bases. Cell outlines not very conspicuously marked by a rather fine ridge, but becoming broad near pinna margins. Cell outlines straight, unpitted; cell surface flat, obscurely mottled rather than striated. Lower cuticle showing stomata evenly scattered in areas between veins, trichome bases frequent along veins, occasional between veins. Veins marked by a few rows only of narrow cells. Cells between veins obscurely sculptured but those along veins

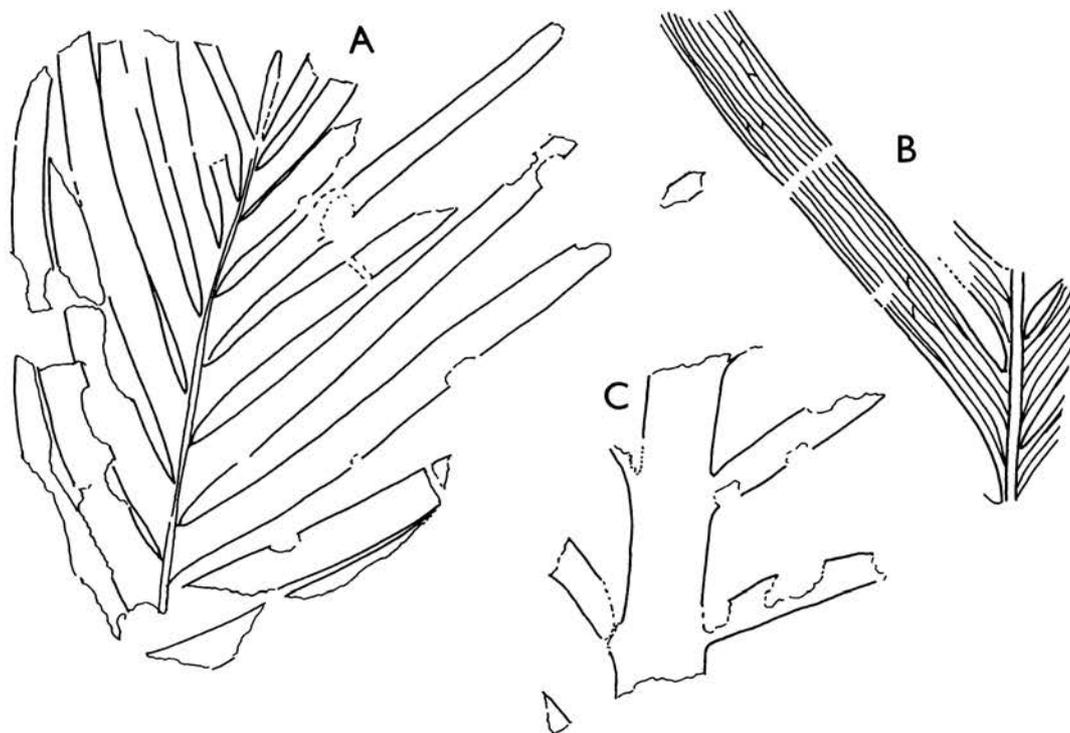


Fig. 46. *Ctenis reedi* Harris, *C. sulcicaulis* (Phillips)

A, *C. reedi*, specimen in Geology Dept., Leeds University,  $\times 1$ . B, veins of one of the pinnules of A,  $\times 3$ . Probably from the Gristhorpe Bed. C, *C. sulcicaulis*, fragment from lower part of lamina, V.44857,  $\times 1$ . Gristhorpe Bed.

showing distinct parallel striae. Cells near stomata not folded. Stomata variably orientated, scattered and not forming groups, monocyclic or partly dicyclic. Subsidiary cells of uneven size and irregularly placed but often with about four lateral and two polar ones; neighbouring stomata occasionally sharing a subsidiary cell. Stomatal aperture sunken, about  $25\text{--}35\mu$  long, surface of guard cells thinly cutinised in middle parts but with transverse ridges separating the aperture from the poles. Poles usually with a small area exposed on the surface. Subsidiary cells forming a shallow oval stomatal pit, lateral margins of pit thickened but scarcely forming a raised rampart above general surface; no thickening occurring round or over poles of guard cells as a rule. Hypodermal cells, where present, unspecialised. Trichome bases on lower surface usually showing a ring on the thickened surface, free part missing.

**HOLOTYPE.** Specimen figured Harris (1947a, text-figs. 4 E, 5). Reed Collection, Yorkshire Museum.

**OCCURRENCE.** Neither of the two specimens known is properly localised, but the matrix

of both can be matched with that of the Gristhorpe Bed (Middle Deltaic Gristhorpe Series), and it may be presumed that this is their origin. Cuticle fragments agreeing with *C. reedi* were found in one Lower Deltaic locality; Westerdale Stockdale. They are, however, scarcely well enough characterised to be identified with confidence.

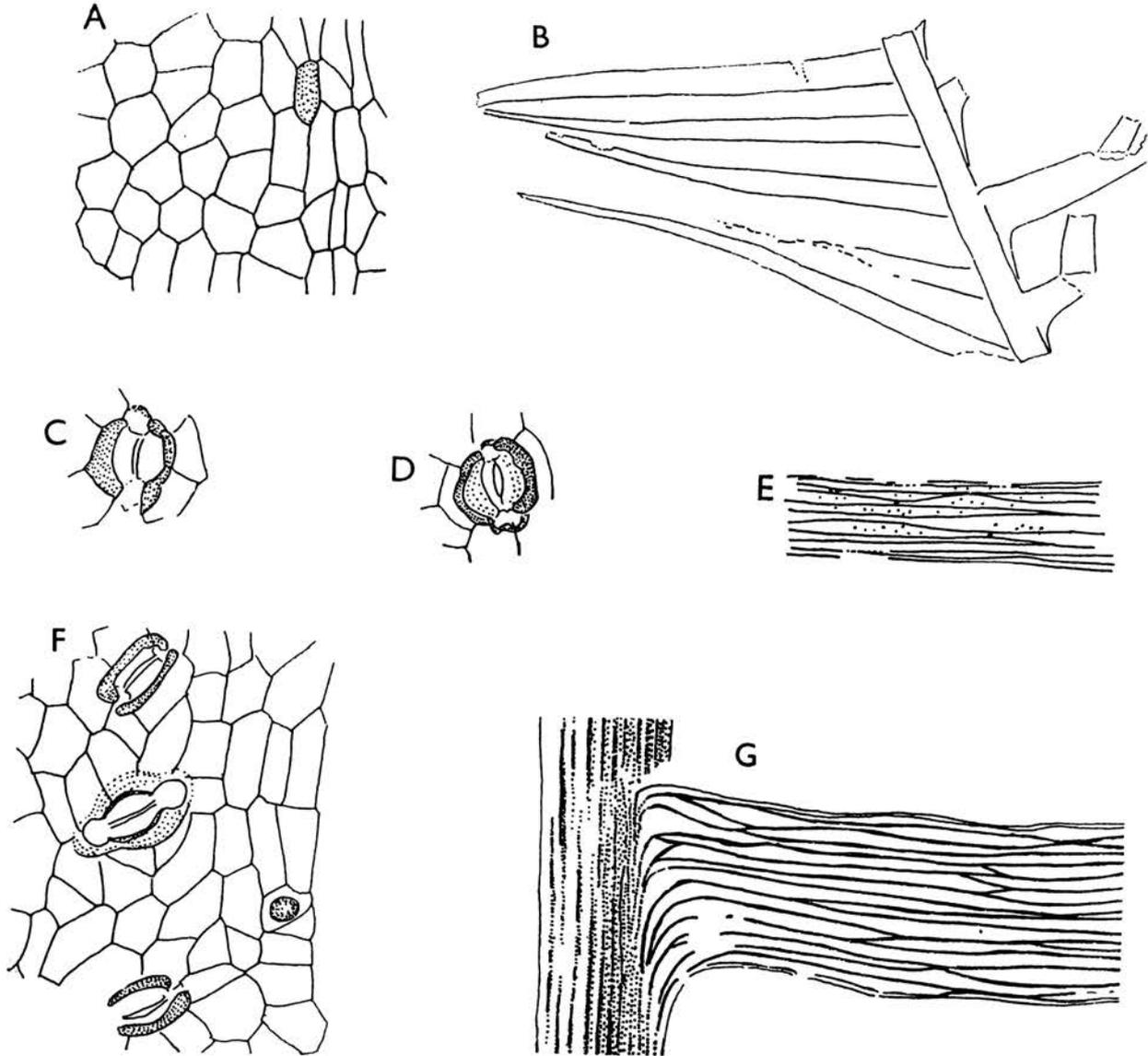


Fig. 47. *Ctenis reedi* Harris

A, upper cuticle, there is a vein on the right, slide B,  $\times 200$ . B, the holotype specimen, Reed Colln., Yorkshire Museum,  $\times 1$ . C, D, two stomata, slide B,  $\times 200$ . E, narrow distal part of a pinna, showing the veins and some of the small dark bodies (possibly fungi),  $\times 4$ . F, lower cuticle, slide A,  $\times 200$ . G, basal part of a pinna and the strongly grooved midrib,  $\times 4$ .

Probably from the Gristhorpe Bed. All the figures are from Harris (1947a, text-figs. 4, 5).

DISCUSSION. *C. reedi* was described from one specimen in the Yorkshire Museum and another has now been found in the collection of the Geology Department of Leeds University. Neither is localised. The holotype had associates characteristic of the Gristhorpe Bed but its

matrix was unfamiliar to me. I now realise that such a matrix does occur at a few points in the Gristhorpe Bed. The Leeds specimen is preserved in a matrix which looks more typical of the Gristhorpe Bed and it is thus likely that both came from that classic locality.

Neither specimen gave good cuticle preparations. The holotype had been damaged by varnish while the Leeds specimen was pitted with pyrites. However it gave preparations which revealed a good deal and it is valuable in showing the form of the leaf apex. The holotype showed little lumps of unknown nature between the veins, but the Leeds one did not, so they have been omitted from the diagnosis. They may be fungi, as suggested by Florin for another species.

COMPARISON. *C. reedi* resembles *C. sulcicaulis* (and probably occurs in the same locality) and the possibility was considered that it might be an extreme form of it. No intermediate specimens are known, however, and the finding of a second specimen very like the first makes the possibility less likely. The distinguishing characters of *C. reedi* are:

(1) The pinnae are half as wide, 4–7 mm. instead of 7–15 mm. Their length is possibly half as great also. The whole leaf is much smaller.

(2) The veins are about half as many per pinna but slightly more concentrated and are less prominent.

(3) A few trichomes occur on the upper surface (none in *C. sulcicaulis*).

(4) The stomata are less sunken, the rampart formed by the subsidiary cells is much less prominent and normally interrupted at the poles and the guard cell poles reach the surface.

(5) Striations are less prominent in *C. reedi*.

Very few leaves of the other floras resemble *C. reedi* in their narrow pinnae and crowded veins; the most similar being those listed on p. 103 under *C. sulcicaulis*. In only one of these are the pinnae as narrow as in *C. reedi*, and their veins as crowded; and this is *Ctenis intermedia* (Kryshstofovich & Prinada), see Samylina (1963). Unfortunately we have no fine details of *C. intermedia*.

### *Ctenis kaneharai* Yokoyama

Text-figs. 48, 49

1906 *Ctenis kaneharai* Yokoyama, p. 29, pl. 9, fig. 1, 1 A, (Holotype, Manchuria.)

1933 *Ctenis kaneharai* Yokoyama: Yabe & Oishi, p. 226. (Mention.)

1940 *Ctenis kaneharai* Yokoyama: Oishi, p. 296, pl. 24, fig. 1. (Japan.)

1950 *Ctenis kaneharai* Yokoyama: Harris, p. 1001, text-figs. 1–3, 4 B. (Yorkshire leaves and cuticles.)

?1961 *Ctenis kaneharai* Yokoyama: Kimura, p. 29, pl. 6, figs. 1, 2. (Lower Cretaceous, Japan.)

EMENDED DIAGNOSIS. (Based largely on Yorkshire specimens.) Leaf large, width in middle region 30–40 cm. (length unknown). Rachis up to 1 cm. wide, longitudinally striated, bearing pinnae laterally. (Base of rachis and petiole unknown.) Pinnae numerous, 15–20 cm. long in middle region of leaf, but shorter towards leaf apex and leaf base (basal pinnae not known); width of pinna from middle region of leaf typically 17 mm. but less towards apex and base. Pinnae in lower part of leaf arising at 80°–90° and separated by gaps of 1.0–1.5 cm.; arising at an angle of 60°–80° in middle region of leaf and often almost in contact; arising at an angle of 45° and in contact near leaf apex. Pinnae straight, usually increasing in width to a maximum at about one fifth the distance from the rachis to apex and then tapering evenly at about 1 mm. per cm. of length to the apex. Apex appearing acute, but actually rounded in a

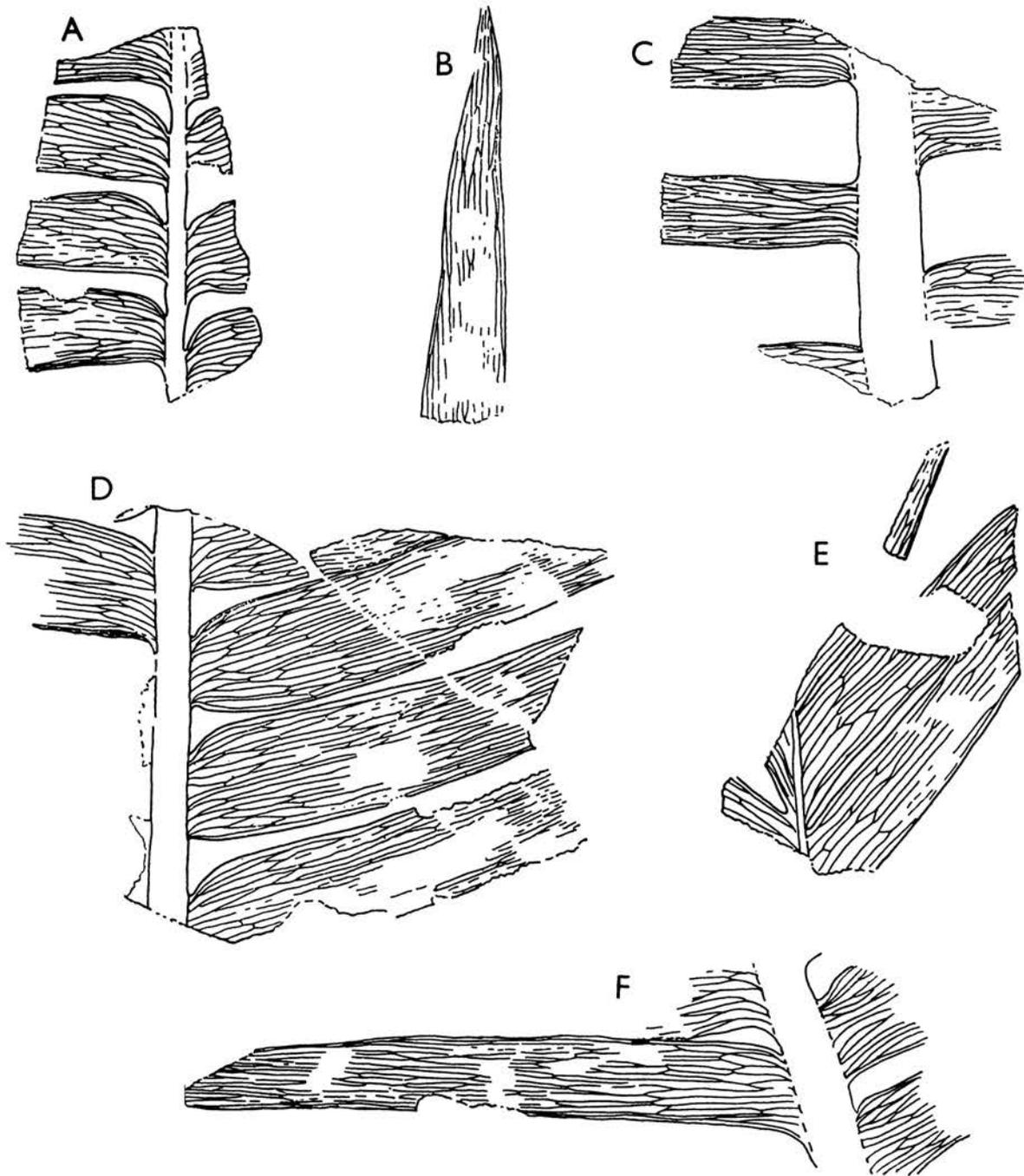


Fig. 48. *Ctenis kaneharai* Yokoyama

A, upper part of leaf, V.28291,  $\times 1$ . B, apex of pinna, V.28289,  $\times 2$ . C, lower part of leaf, V.28288,  $\times 1$ . D, middle region of leaf, lower margin of pinnae contracted, V.28290,  $\times 1$ . E, fragment from near leaf apex, V.28293,  $\times 1$ . F, fragment from middle region of leaf, lower margin of pinnae decurrent, V.28292,  $\times 1$ . All the specimens are from Hasty Bank. All the figures are from Harris (1950, text-figs. 1, 2).

semicircle of 1 mm. diameter. Pinna margin entire, slightly thickened and depressed but not inrolled. Form of pinna base varying with part of leaf. In lower and middle parts of leaf, basisopic margin usually slightly contracted or running straight to the rachis, rarely slightly expanded; acrosopic margin always distinctly contracted so that the pinna is always narrower at its attachment than about 3 cm. out. In upper part of leaf basal contraction of pinna less marked; basisopic margin slightly contracted or expanded, acrosopic margin slightly contracted or running straight to rachis, not expanded. Veins rather prominent on lower side but becoming fine and inconspicuous towards pinna apex, concentration occasionally 10 per cm., typically 13-15 per cm. but more crowded towards pinna apex. Vein meshes 1-3 cm. long. Towards pinna apex veins reduced in number by anastomosis and by some ending near the marginal fibre bundle. Veins usually forming a single ridge but occasionally double. Cuticle fairly tough, about  $3\mu$  thick measured in folds. Upper cuticle lacking stomata but with a few trichome bases mostly along veins. Veins distinguished by about four rows of conspicuously elongated cells; cells between veins irregularly polygonal, sometimes forming packets of sister cells. Cell outlines marked by broad, conspicuous and straight walls of even thickness. Cell surface flat, not papillate but marked with conspicuous striations, striations longitudinal along veins, longitudinal or oblique between veins.

Lower cuticle showing veins clearly distinguished by about four rows of more elongated cells. Cells between veins polygonal, isodiametric or irregular. Stomata scattered in intervenal areas, but often tending to avoid the region of the veins and often forming small clumps of 3-6 rather than being evenly dispersed. Epidermal cell outlines marked with narrow but prominent ridges, walls nearly straight but sometimes appearing jagged where striations cross them. Cell surface conspicuously sculptured with parallel striations, striations longitudinal along veins but often tending to encircle any stomatal clumps. Near stomata, striations often very coarse and more marked than cell walls.

Stomata typically occurring at a concentration of 60-80 per sq. mm.; apertures orientated irregularly. Stomata usually monocyclic, often with 2 polar and 3-5 lateral subsidiary cells forming a wide and shallow stomatal pit. Guard cells with a moderately sunken aperture about 20-30 $\mu$  long; surface of guard cells thin but with a slight thickening along aperture and strong lateral thickenings and often with clearly marked transverse thickenings (folds) at the ends of the aperture; poles thin, normally reaching the surface. Subsidiary cells showing a slightly developed ridge or rampart opposite the guard cell thickenings but usually with no thickening at the poles. Encircling cells occasional and unspecialised. Trichome bases usually frequent both on veins and interstices, consisting of a small cell showing a ring-shaped mark 15 $\mu$  wide; free part of trichome lost before preservation. Trichome base usually associated with another small cell not bearing a trichome.

HOLOTYPE. Specimen figured by Yokoyama (1906, pl. 9, fig. 1).

OCCURRENCE. *Ctenis kaneharai* occurs chiefly in the Lower Deltaic but also in the Middle Deltaic (Bathonian) of Yorkshire. Hand-specimens are abundant at Roseberry Topping and at Hasty Bank and rare at Farndale Hill House Nab (all Lower Deltaic). Cuticle fragments (less confidently identified as *C. kaneharai*) were obtained from eight additional Lower Deltaic localities, where they are sometimes abundant. A single small fragment was obtained from the Middle Deltaic Sycharham Series and one from the Middle Deltaic Gristhorpe Series.

The Manchurian holotype specimen may be Bathonian, but the Japanese ones are rather younger, one in the Tetori Series of the Upper Jurassic, the other Lower Cretaceous.

DISCUSSION. About twenty additional Yorkshire hand-specimens have been studied since 1950 and very numerous cuticle fragments. The additional specimens add somewhat to knowledge of the leaf form and give more idea of the length of a typical pinna, and the cuticle preparations add to our knowledge of its range of variation. This range is the same in each locality. The upper cuticle varies in:

- (1) Thickness from 2–8 $\mu$  (measured in folds).
- (2) Cell shape, cells isodiametric to transversely elongated.
- (3) Anticlinal walls of cells; wall thick and continuous to thin and interrupted.
- (4) Trichome number, from a few to 30 per sq. mm.
- (5) Periclinal wall showing striations from moderately conspicuous to very conspicuous.

The lower cuticle shows similar variations to the upper, and in addition:

- (1) Stomatal concentration from 30–100 per sq. mm.
- (2) Guard cell aperture from 15–30 $\mu$  long.
- (3) Striations sometimes so conspicuous as to obliterate cell walls, but usually only moderately clear.

It is unlikely that the specimens represent more than one species because the middle of the range of each character is met most commonly in each locality and the different characters vary to some extent independently.

A few cuticle fragments were found in which very distinct prints of palisade mesophyll cells are imposed on the upper epidermis. Such specimens give evidence that no layer of sub-epidermal fibres exist. Certain cuticle fragments were only doubtfully identified with *C. kaneharai*. Two of these fragments, each from a different locality, have slightly more sinuous cell walls than is usual and one is unusual also in showing four dark round bodies 100 $\mu$  wide looking like resin just behind the pointed pinna apex. It seems most likely that these specimens are merely forms of *C. kaneharai*.

There is a large number of fragments from one locality (Fryup Dale) which differ from all specimens of *C. kaneharai* in being much more thickly cutinised, the upper side being 10–20 $\mu$  measured in folds. The shapes of the cells and their arrangement is, however, normal. In certain of these fragments cutinisation extends down to the palisade mesophyll. In some of these fragments also, cells along the veins show a distinctly thickened median papilla. It seems likely that these specimens represent an unknown species resembling *C. kaneharai* in certain respects.

COMPARISON. The Yorkshire specimens agree with the holotype of *C. kaneharai* from the Jurassic of Manchuria in the contracted bases of their pinnae but in none are the pinnae quite as broad as in the holotype. The Japanese Upper Jurassic specimen (Oishi 1940) is, however, more like the Yorkshire ones in size. The veins in the Manchurian specimen are rather less crowded, and in the Japanese one rather more crowded than in the Yorkshire specimens. As neither of these East Asiatic specimens shows the form of the pinna apex, nor any details of fine structure, it remains possible that the two are distinct from one another and that either or both are distinct from the Yorkshire ones. This can only be settled by further study of the

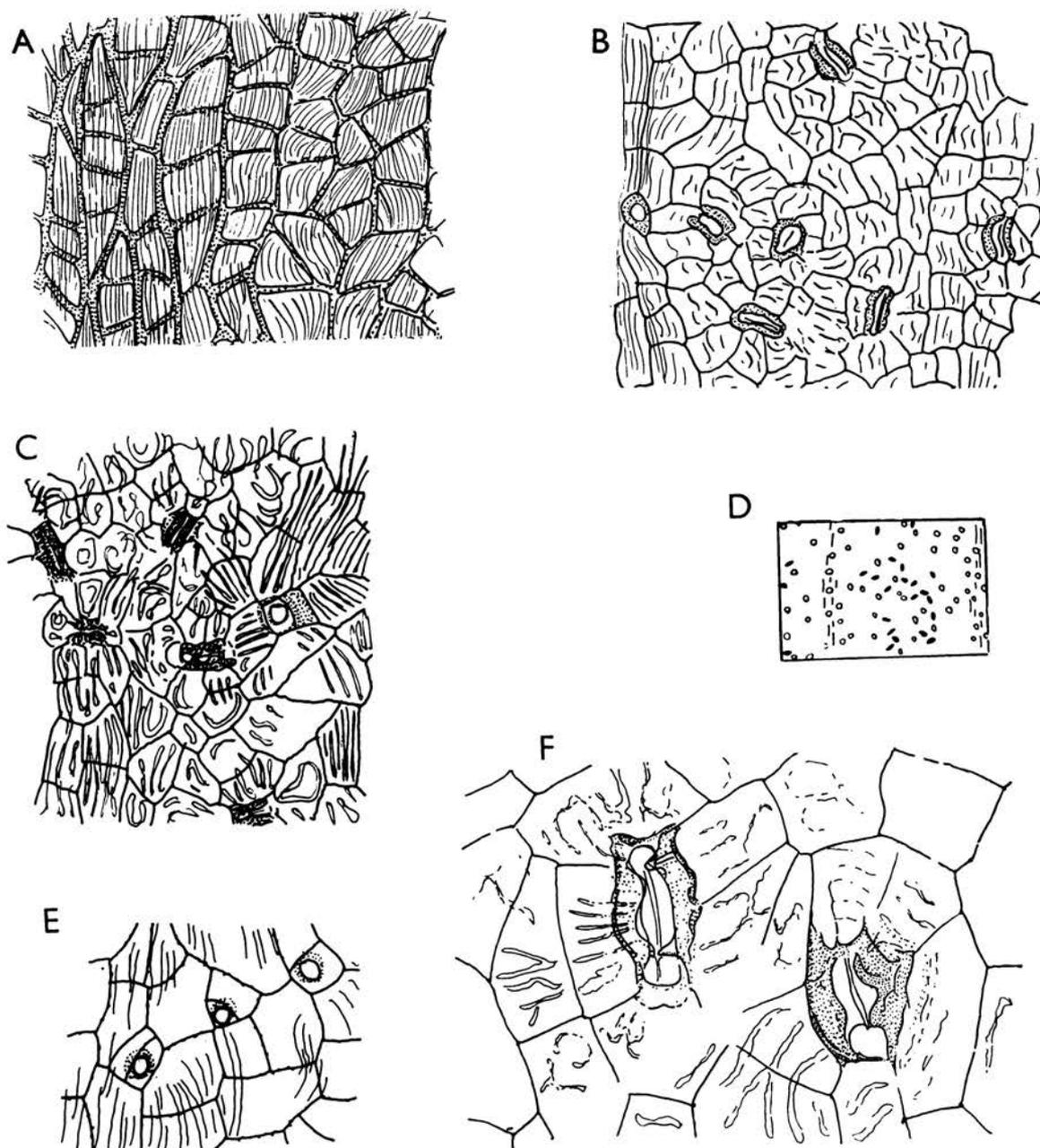


Fig. 49. *Ctenis kaneharai* Yokoyama

A, upper cuticle. B, lower cuticle, both from V.28290a (same specimen as Fig. 48 D),  $\times 200$ . A vein is on the left in each figure. C, lower cuticle of specimen with strongly marked striae, V.45623,  $\times 200$ . D, distribution and orientation of stomata (black ovals) and trichomes (rings) in a strip 1 mm. long, V.45624,  $\times 10$ . E, trichome bases on a vein, V.45624,  $\times 200$ . F, stomata, V.28294,  $\times 500$ .

A, B, F are from Hasty Bank and are from Harris (1950, text-figs. 3, 4). C-E are from Snilesworth Stonymoor Sike Coalpit.

Asiatic material, which is now less fully known than the specimens from Yorkshire. Kimura (1961) figured two specimens from the Lower Cretaceous of Japan which are probably distinct from the Yorkshire ones. Their pinnae agree in their bases and venation, but the pinna apex is very different, for the margins narrow quickly to meet at an angle of about  $50^\circ$  instead of gradually tapering and meeting at  $15^\circ$ – $20^\circ$ . This again raises the question, which of the various sets of specimens can be considered identical with the holotype.

The Yorkshire specimens are satisfactorily distinguished from *C. sulcicaulis* (with which they seem once to have been confused) by the following differences:

In *C. kaneharai* the pinna base is typically contracted, in *C. sulcicaulis* expanded, and indeed contraction on the basiscopic side is unknown. The pinnae of *C. kaneharai* are usually rather wider and at their widest 2–3 cm. from the rachis, and from there taper, but in *C. sulcicaulis* the proximal half has nearly parallel sides and only the distal half tapers. In *C. kaneharai* both the cuticles as a rule show much more conspicuous striations; trichome bases are more numerous and better developed and the stomata are different. In *C. kaneharai* the rampart is usually slightly developed and scarcely exists at the poles which are commonly exposed; in *C. sulcicaulis* the rampart is higher and usually round and the poles are concealed. A few abnormally exposed stomata occur in *C. sulcicaulis* which are like normal ones of *C. kaneharai*.

*Ctenis exilis* sp. nov.

Text-figs. 50, 51 D–G

DIAGNOSIS. Form of whole leaf unknown. Pinnae small, typically 4 cm. long and 7 mm. wide, base contracted, margins varied, entire, lobed, or bearing forward pointing teeth; teeth usually acute and up to 2 mm. long and about 1 mm. broad below, teeth occasionally themselves lobed. Margin of pinna flat but thickened with a fibrous band, veins fairly prominent, running at a concentration of 20–30 per cm.; the larger pinnae having up to 10 veins, but marginal teeth only two or one vein, average length of vein mesh about 1 cm. Veins ending by merging into the marginal fibre band. Cuticles well developed, upper about  $7\mu$  thick, lower about  $3\mu$  thick (measured in folds). Upper cuticle showing irregularly shaped cells, often elongated transversely. Veins either not distinguished or indicated by a file 1–2 cells broad of rectangular cells. Marginal region thickened. Trichomes absent or very few. Stomata occasional, 0–10 per sq. mm. Epidermal cell walls marked by broad and prominent ridges showing jagged thickenings and interrupted by pits, essentially straight and never more than slightly sinuous. Cell surface flat, marked by numerous parallel striae, or striae broken into rows of oval dots; striae of variable orientation but mostly longitudinal. Lower cuticle with a marginal thick region resembling that of the upper cuticle and often separated from the nearly uniform region over the rest of the lower surface by a line of crushing, veins either not indicated, or indicated as strips with fewer stomata, or in large segments by lines of crushing as well. Cells of irregular shapes, often transversely elongated, outlines clearly marked, walls essentially straight but always showing jagged and uneven thickenings. Cell surface flat, usually crossed by about six parallel striae, but near stomata striae fewer but more strongly developed. Stomata scattered and variably orientated but more commonly nearly transverse than longitudinal, trichome bases occasional, scattered both along veins and between them, absent from marginal regions.

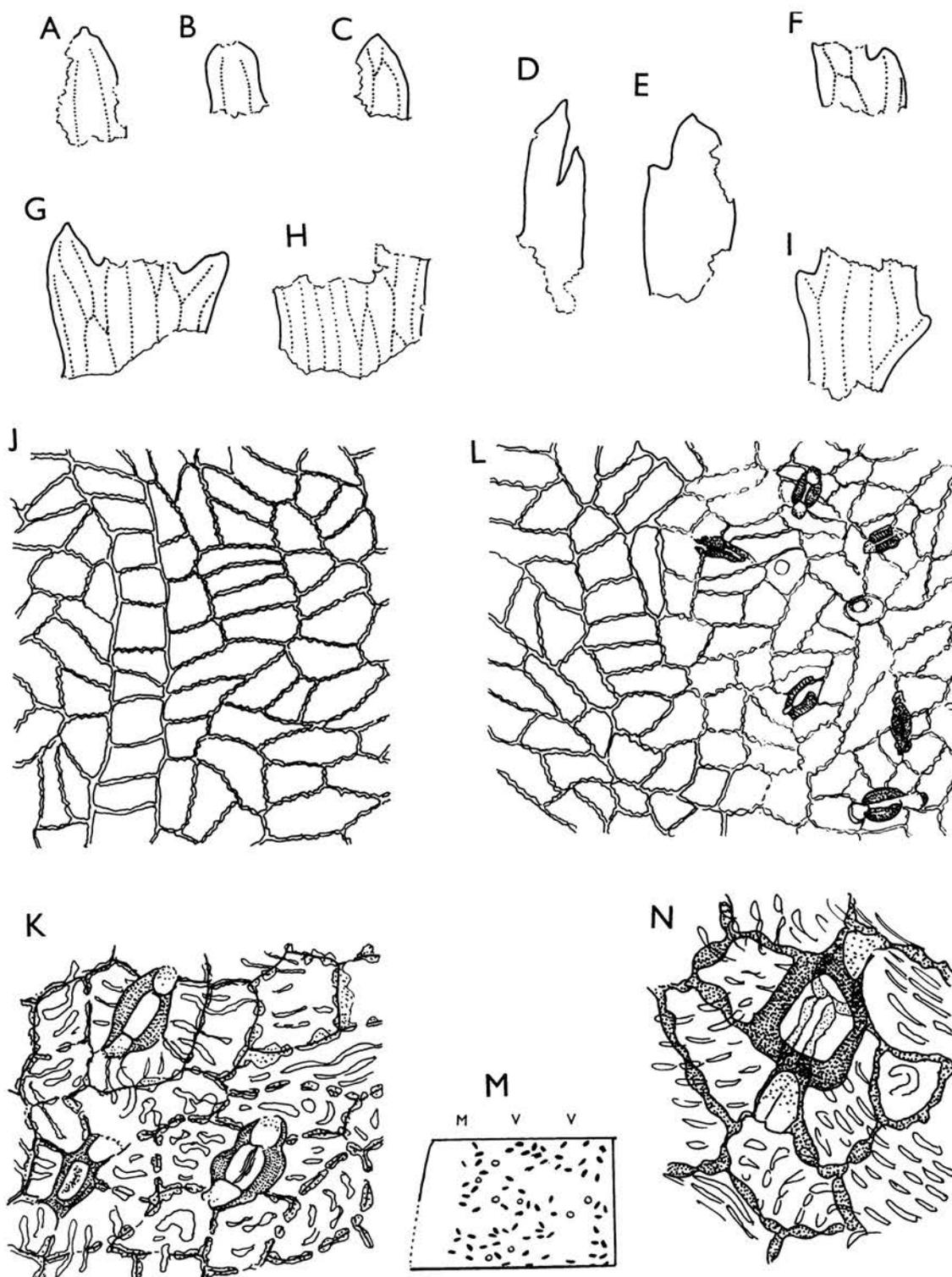


Fig. 50. *Ctenis exilis* sp. nov.

A-I, pinna fragments, all  $\times 6$ . A, holotype, V.45612. B, C, V.45613. D-G, V.45614. H, V.45615. I, V.45616. J, upper cuticle of holotype, a vertical line of cells left of the middle is above a vein,  $\times 200$ . K, three stomata of holotype,  $\times 400$ . L, lower cuticle of holotype, the marginal zone is to the left,  $\times 200$ . M, distribution of stomata and hair bases (rings) in a strip 1 mm. wide from the holotype; m = marginal zone, v = veins position indicated by upper cuticle. N, stoma on upper cuticle, V.45612,  $\times 400$ .

All specimens are from Beast Cliff Bed A.

Stomata monocyclic or imperfectly dicyclic. Subsidiary cells of uneven size and irregularly placed, lateral ones often large and extending nearly the length of the guard cells. Stomatal aperture sunken, about  $30\mu$  long. Lateral margin of stomatal pit strongly thickened with a raised rampart; rampart extending inwards opposite the ends of the guard cell aperture and sometimes crossing the guard cells, to form a rectangular ridge, but also continued less strongly round guard cell poles. Guard cell surface rather thin in middle parts but with lateral thickenings along the subsidiary cell borders and slight thickenings along the aperture. Transverse ridges present and separating the poles from the middle parts. A thin strip occurring outside the lateral thickenings but usually concealed by the subsidiary cell rampart. Guard cell poles often partly exposed, but sometimes entirely concealed. On lower surface most of stomata having an incomplete rampart and exposed poles, on upper, most having a ring-shaped rampart and concealed poles. Subsidiary cells usually smaller than other epidermal cells and surface slightly thicker but otherwise unspecialised, encircling cells where recognisable entirely unspecialised.

Trichome base consisting of a small cell with a somewhat thickened surface and bearing a ring-shaped scar about  $15\mu$  wide; trichome bases occurring singly, not associated with a second small cell.

The name refers to the small size of the pinnae.

HOLOTYPE. V.45612 (Text-fig. 50 A).

OCCURRENCE. *C. exilis* is rare; the type locality Beast Cliff Bed A of the Sycarham Series of the Middle Deltaic has so far yielded three more or less complete pinnae and a good many cuticle fragments. Minute cuticle fragments are known also from Gristhorpe at 15 ft. below the Millepore Bed (also Sycarham Series) and from two Upper Deltaic localities.

DISCUSSION. *C. exilis* was found gradually. The first specimens were tiny cuticle fragments macerated out of Beast Cliff Bed A. The one chosen as holotype (Text-fig. 50 A) was the best and as there were others similar, some expanding basally as though on to a rachis, they were all taken to be complete but very small pinnae, instead of as mere teeth of a pinna. Thus a narrow leaf like a small *Ptilophyllum pecten* was looked for when the locality was visited a second time but of course no such leaf was found. However, about 10 kg. of the bed was collected and macerated and yielded a generous supply of fragments some better than the holotype. These showed that the pinnae had toothed margins and when such a pinna was looked for, three rather imperfect ones were found.

Although fragments of *C. exilis* are fairly common in Beast Cliff Bed A, the chance of finding a really good leaf there is slight because the plants in this bed were all broken before they were deposited and the bed itself is a crumbly clay that does not cleave well.

*Ctenis exilis* resembles certain other species of *Ctenis* in cuticle, being intermediate between *C. kaneharai* and *C. stewartiana* but it is exceptional in its toothed margin. It might indeed be separated generically from *Ctenis* on this character but this would seem inadvisable in view of our imperfect knowledge of the form of *C. exilis* and also the fact that in some Recent Cycad genera (*Encephalartos*) some species have entire and others toothed pinnae.

COMPARISON. *C. exilis* differs from all species in its small dentate pinnae. It differs from most species in which the cuticle is described in its distinctly jagged cell walls, though in forms of *C. kaneharai* they may be nearly as strongly jagged, and in forms of *C. stewartiana* they may be on the borderline between strongly jagged and weakly sinuous.

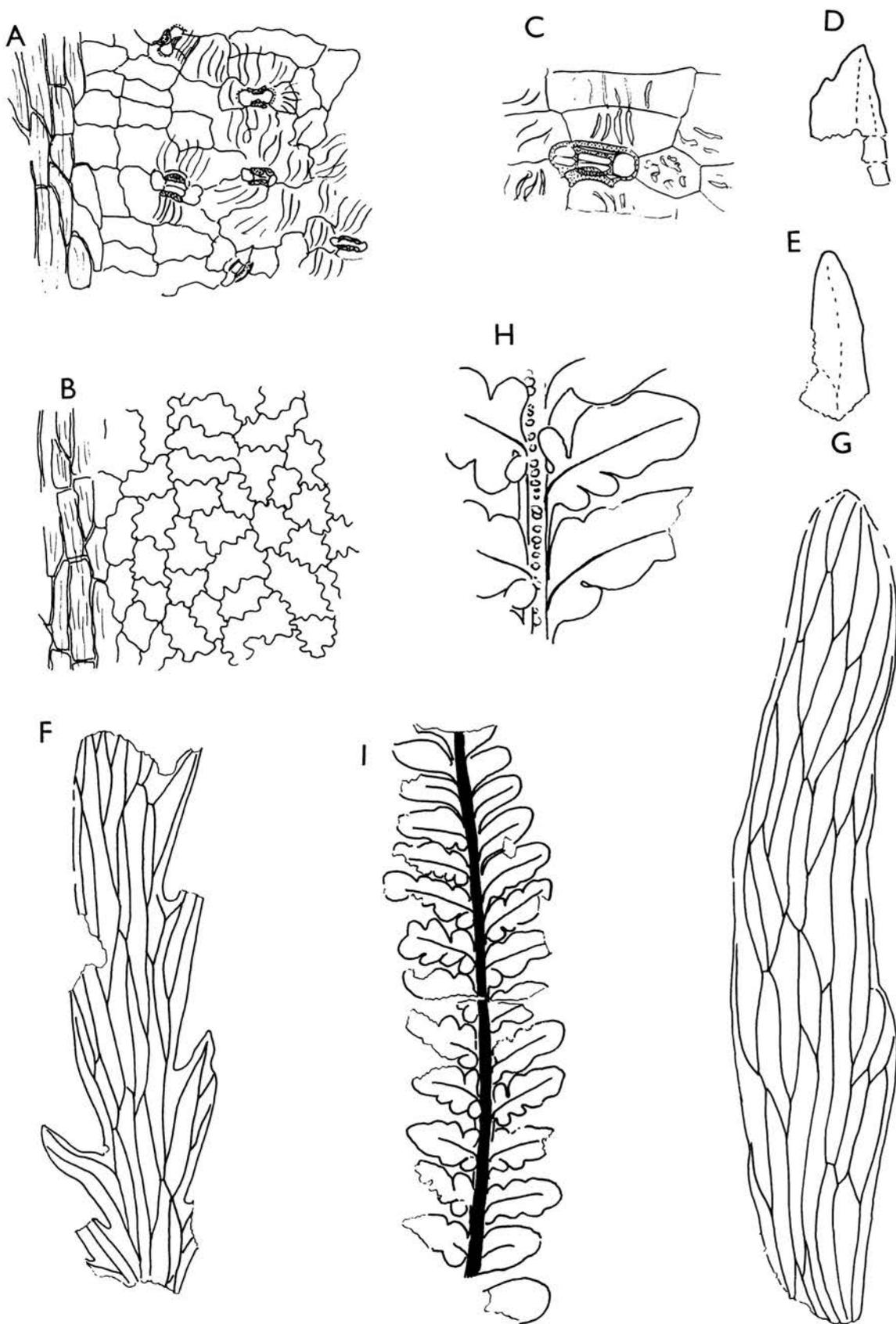


Fig. 51 see opposite.

*Ctenis* cf. *stewartiana* Harris

Text-fig. 51 A-C

- 1919 *Ctenis* sp., Antevs, p. 36, pl. 5, figs. 1-4.  
 1932 *Ctenis stewartiana* Harris, p. 12, text-fig. 6. (East Greenland.)  
 1933 *Ctenis stewartiana* Harris: Florin, p. 76, pl. 12, figs. 4-8; text-figs. 24 B, 26 A, 27 C, D. (Full diagnosis; Sweden.)

DESCRIPTION. A fragment of cuticle of about 2 sq. mm. was found which agrees in all its details with the published figures of *Ctenis stewartiana*. However, it shows two veins at 0.75 mm. apart while in typical *C. stewartiana* they are 1.5-2 mm. apart. This difference may perhaps be discounted because veins in *Ctenis* become closer near the apex of the pinnae.

The most striking point of agreement is in the sinuous cell walls, especially of the upper side and no other species of *Ctenis* which has been described shows such walls. A few specimens of *Ctenis kaneharai* and of *C. exilis* do show a slight suggestion of sinuosity, but this never approaches what is seen in the present fragment.

DISCUSSION. *C. stewartiana* is a rare species in the Lower Lias of Sweden and East Greenland. The present fragment is from the base of the Upper Deltaic at Fylingdales Upper Kirk Moor where it is associated with a peculiar flora of leaf cuticles, mostly of conifers. It is possible that the flora is of upland rather than Deltaic origin. The present fragment is alone and too small to identify fully. It does however indicate that *Ctenis* species resembling *C. stewartiana* in cuticle extend from the Lower Lias to the Lower Oolites.

[*Ctenis* sp., Seward]

- 1900 *Ctenis* sp., Seward, p. 231, text-figs. 42, 43.  
 1900a *Ctenis* sp., Seward, p. 21, pl. 2, figs. 3, 4.  
 1917 *Ctenis* sp., Seward, p. 579, text-figs. 624, 625.

The specimen called *Ctenis* sp. was mentioned by Nathorst (1880) as like *Anthrophyopsis nilssoni* (now *Ctenis nilssoni*) and described by Seward with its cuticle. Seward gave the same figure in 1917.

I am convinced the specimen is not a *Ctenis* pinna at all but a leaf of *Eretmophyllum pubescens* Thomas (1913b). The veins appear to anastomose but do not really do so, the leaf had rotted and the fibrous strands had shifted laterally. The veins as shown by the epidermis run normally without anastomoses.

## Genus PACHYPTERIS Brongniart

- 1828a *Pachypteris* Brongniart, p. 49. (Name only.)  
 1828 *Pachypteris* Brongniart, p. 166.

EMENDED DIAGNOSIS. Leaf as a whole elongated, once or twice pinnate, petiolate. Main rachis not forked, finely striated, bearing pinna rachises or lamina segments laterally

Fig. 51. *Ctenis* cf. *stewartiana* Harris, *C. exilis* sp. nov., *Pachypteris papillosa* (Thomas & Bose) A-C, *Ctenis* cf. *stewartiana*. A, lower cuticle,  $\times 200$ . B, upper cuticle,  $\times 200$ . C, a stoma,  $\times 400$ . All from V.45638. Fylingdales, Upper Kirk Moor. D-G, *Ctenis exilis*. D, V.45617,  $\times 8$ ; Flask Inn, roadside ditch. E, V.45618,  $\times 8$ ; Scalby Wyke, Black's drifted plant Bed. F, pinna, V.44855,  $\times 4$ ; Beast Cliff Bed A. G, pinna, V.44854,  $\times 4$ ; Beast Cliff Bed A. H, *Pachypteris papillosa*, details of specimen shown in I,  $\times 2$ . I, *Pachypteris papillosa*, abnormal form with lobed pinnae, V.45466,  $\times 1$ ; Hasty Bank.

or somewhat above the lateral margin, but leaving some of the upper surface exposed. In bipinnate leaves, lowest pinnae on basiscopic side at the very base of pinna or on main rachis between pinnae; in simply pinnate leaves lamina decurrent on to main rachis. Lamina segments more or less lanceolate or somewhat lobed; apex usually blunt, base somewhat contracted above, decurrent below. Substance of lamina very thick, margins flat (originally rounded and no thicker than the rest of the lamina). Veins inconspicuous, embedded in lamina, consisting of a midrib and forked laterals; but terminal lobe of lamina with a small number of diverging and branched main veins. Fibres and hypodermal cells absent.

Cuticles thick; stomata more numerous below or almost entirely below. On under side, stomata widely scattered but tending to avoid main veins and margins; on upper side any present more frequent near midrib. Epidermal cells nearly isodiametric but elongated over veins, straight walled, surface flat or bulging, or showing a median thin area. Stomata haplocheilic, not forming rows, variably orientated, surrounded by about five subsidiary cells. Subsidiary cells not clearly differentiated into polar and lateral cells but usually distinguished by surface markings from ordinary cells; size often uneven; at inner edge forming a definite pit; pit round or somewhat elongated. Guard cells sunken, thinly cutinised; aperture at a deeper level than poles; slightly thickened at sides and opposite the ends of aperture. Encircling cells often present but irregular in size and unspecialised.

TYPE SPECIES. *Pachypteris lanceolata* Brongniart (1828).

DISCUSSION. As defined above *Pachypteris* includes both *P. lanceolata* Brongn. and *Pachydermophyllum papillosum* Thomas & Bose. Thomas (1954) has summarised views on *Pachypteris* which was the first Mesozoic genus of coriaceous fern-like leaves described, but which remained very little known till recently. Later genera were thus made which were imperfectly distinguished from it and the number of these genera is considerable. We now know that the typical segments had one midrib with simple or forked laterals and are thus well distinguished from some of these other genera, such for example as *Dichopteris* Zigno which has several equal main veins. From *Thinnfeldia rhomboidalis* and several other species of *Thinnfeldia*, *Pachypteris* is distinguished by its stomata which have only slightly specialised and rather irregular subsidiary cells instead of a neat collar of small and even sized cells. *Cycadopteris* is very similar indeed, being only distinguished by its thickened margin which is sharply marked off from the under surface by a fold in the compressed fossil. As Townrow & Hancock (1961) made clear this character of *Cycadopteris* is not constant and a few of the present specimens do show a rudiment of such a margin. The generic distinction is, however, maintained here. *Lepidopteris* with similar branching and venation is at once distinguished by its blister-like swellings on the rachises. The stomata too differ in having small flat papillae, but neither feature is constant—see Townrow (1960). *Stenopteris* is mainly distinguished by its predominantly narrow, one-veined segments. Such segments do occur in *P. lanceolata* but they are not typical. *Scleropteris* Saporta (1873) may be very similar or indeed identical but is too little known to be discussed.

The simply pinnate leaf called *Pachydermophyllum papillosum* Thomas & Bose was included in *Pachypteris* as a result of new evidence. The differences between the two species which were supposed to be of generic value were:

- (1) *P. lanceolata* is bipinnate; *P. papillosum* is simply pinnate.

(2) *P. lanceolata* was said to be strictly hypostomatic, while *P. papillosum* always has some stomata above, chiefly near the midrib.

(3) In *P. lanceolata* the subsidiary cells are nearly flat, while in *P. papillosum* they bear prominent papillae.

The first of these differences is very obvious but it is one which is not normally used to separate genera. Many Recent fern genera include species with simple, once pinnate or repeatedly pinnate leaves. In fossils similar to *Pachypteris* we have both once and twice pinnate leaves in *Cycadopteris*, *Thinnfeldia*, *Dicroidium* and others. This very character, it is true, is the sole distinction between *Ptilozamites* and *Ctenozamites* but in my view these two would be better united. Large leaves of *P. papillosa* have slightly lobed pinnae and in an abnormal leaf they are deeply lobed, almost as in *P. lanceolata*.

The second difference would be impressive if it were strictly true. There is a real difference in frequency of stomata on the upper side between the two species, but one does not have to search *P. lanceolata* long before finding stomata above; and large pinnules seem always to have a few. Thirdly the papillae on the subsidiary cells of *P. papillosum* are usually obvious but by no means always present. Most of the stomata of the upper surface have flat subsidiary cells, and a small proportion of the stomata of the lower side have flat subsidiary cells, or some cells at least are flat. These flat subsidiary cells mostly show a thin strip, elongated in the direction parallel with the side of the pit.

In *P. lanceolatum*, no subsidiary cell with a well marked papilla has been seen, but the whole surface of the subsidiary cells does bulge somewhat, especially in specimens which are heavily cutinised. In many stomata the subsidiary cells show a thin strip, exactly as in the flatter stomata of *P. papillosa*. In both species there is much variety in stomata, even in a single leaf and the differences are of degree and the sort that distinguish two species of a genus. Though papillate stomata do not occur in the leaf of *P. lanceolata* a few are met in the 'berets' of that species.

It should be pointed out that when Thomas & Bose (1955) distinguished *Pachydermophyllum* there was no recent published account of *P. lanceolata* and none at all of the cuticle.

New evidence of agreement. (1) Venation: while we were uncertain about the venation of ordinary pinnules of *P. lanceolata* there might have been considerable difference between these and *P. papillosa* but we now know the venation of the two is similar. (2) The curious beret-like organs associated with the two species of leaf are extremely similar. We know how those of *P. papillosa* are attached, but not those of *P. lanceolata*, but even so they constitute a striking point of agreement, not shared by any other leaves.

CLASSIFICATION. *Pachypteris* is one of that rather vague group the 'Mesozoic Pteridosperms' of fern-like leaves with a leathery cuticle. Even without the reproductive organ *Pteroma* it would be treated as a Pteridosperm and *Pteroma* settles the matter. Admittedly though, its megasporophyll is unknown and the microsporophylls of these Pteridosperms are diverse; there is *Antevsia* (see Harris 1932; Townrow 1960), *Pteruchus* (see Thomas 1933; Townrow 1962), perhaps *Harrisothea* Lundblad 1961 (See Harris 1932 under *Hydropteridangium*) and now *Pteroma*. It is interesting that in 1900 people were already thinking that leaves like *Pachypteris* might be something between a fern and a Cycad (Seward 1900 : 171).

We still have no fruit of *Pachypteris* but the microsporophyll *Pteroma* which I attribute to

*P. papillosa* is so like *Pteruchus* that I think the two plants must be closely related and when its fruit is discovered *Pachypteris* may well go into the *Corystospermaceae*. This is not surprising for the leaves of the N. Hemisphere *Pachypteris*, *Thinnfeldia* and *Stenopteris* are sufficiently similar to the S. Hemisphere *Hoegia*, *Dicroidium* and *Xylopteris* to make clear generic separations between S. & N. Hemisphere genera troublesome to define. The forking of the S. Hemisphere leaves though prevalent does not always make a clear distinction from the Northern leaves.

The Yorkshire species of *Pachypteris* are: *Pachypteris lanceolata* Brongniart, the type species, and *P. papillosa* (Thomas & Bose).

Leaves looking like these two species are frequent in Jurassic floras, for example in Bornholm, but we have no details. The genus *Pachypteris* has been very little used and the following species are all unsatisfactorily known:

*P. dalmatica* Kerner 1895 (see also Halle 1913).

*P. brongniartiana* Zigno 1856-68 (*nomen nudum*).

*P. brevipinnata* Feistmantel 1876.

*P. microphylla* Brongniart which is *Stachypteris spicans* according to Saporta (1873).

The following species described by Zigno as species of *Dichopteris* were placed in *Pachypteris* by Schimper (1869):

*P. angustifolia*, *P. microphylla*, *P. paroliniana*, *P. rhomboidalis*, *P. visianica*.

The following S. Hemisphere leaves which have been included in *Pachypteris* are more probably allied to *Dicroidium*:

*P. acuta* du Toit 1927, *P. incisa* (Saporta) du Toit 1927 both from S. Africa and *P. stelzenana* Geinitz (see Frenguelli 1943) from Argentine.

Frenguelli (1943) has included in *Pachypteris* specimens described under the following names:

*P. lanceolata* = *P. phillipsi*, *P. ovata* and *P. laevigata*; Lower Oolites of Yorkshire.

*P. specifica* Feistmantel = *P. brevipinnata* Feistmantel 1876; Jurassic of Kach, India.

*P. dalmatica* Kerner = *P. dimorpha* Kerner 1895; Lower Cretaceous of Dalmatia.

*P. hallei* Frenguelli 1943 (= *P. dalmatica* Halle (non Kerner) 1913); Jurassic of Graham Land.

*P. incisa* (Saporta) Antevs (= *Thinnfeldia incisa* Saporta 1873, 1891); Lower Lias of France.

*P. bellhofensis* (Gothan) Antevs (= *Thinnfeldia bellhofensis* Gothan 1914); Lower Lias of Germany.

*P. obtusiloba* (Saporta) Frenguelli (= *Thinnfeldia obtusiloba* Saporta 1891); Kimmeridgian of France.

*P. speikernensis* Frenguelli (= *Thinnfeldia rhomboidalis* forma *speikernensis* Gothan 1914); Lower Lias of Germany.

I would merely remark that while several of these seem, on the present incomplete information, to be at least as well placed in *Pachypteris* as in *Thinnfeldia*, others, particularly the large *speikernensis* form of *T. rhomboidalis*, are only included in *Pachypteris* by disregarding the evidence of the cuticle.

Key to the Yorkshire species of *Pachypteris*

- Leaf once pinnate (Segments over 5 mm. broad; subsidiary cells papillate) . . . . . *P. papillosa*  
 Leaf twice pinnate (Segments under 5 mm. broad; subsidiary cells not papillate) . . . . . *P. lanceolata*

***Pachypteris pabillosa*** (Thomas & Bose) nov. comb.

Pl. 5, figs. 7, 10–13; Pl. 6, fig. 7; Pl. 7, figs. 2, 4, 8, 9; Text-figs. 51 H, I, 52–54

- ?1845 *Salicites longifolius* Buckman, p. 68, pl. 1, fig. 1. (Poor specimen badly figured and indeterminable. Bathonian, English Midlands.)  
 1904 cf. *Thinnfeldia speciosa* Ettingshausen: Seward, p. 95, pl. 10, figs. 1–3. (Bathonian, English Midlands.)  
 1913a '*Thinnfeldia* cf. *rhomboidalis*' Thomas, p. 199. (Name in list for Roseberry Topping, not Ettingshausen's *T. rhomboidalis*.)  
 1914 '*Thinnfeldia*', Gothan, p. 115. (Roseberry Topping specimen distinguished from *T. rhomboidalis*.)  
 1915 '*Thinnfeldia rhomboidalis*' Thomas, p. 9 (figure). (Leaves from Roseberry Topping.)  
 1955 *Pachydermophyllum papillosum* Thomas & Bose, p. 536, text-figs. 1–3. (Holotype and other leaves, cuticle.)  
 Note: References in the literature of 1913 onwards to Yorkshire specimens of *Thinnfeldia* mostly refer to this leaf.

DIAGNOSIS (from description of Thomas & Bose 1955). Leaf [once pinnate] typically  $30 \times 2.5$  cm., but occasionally longer or shorter. Range of width noted 0.5–7.5 cm. Petiole 3–7 cm. long, 2–4 mm. wide, base slightly expanded, upper surface showing a slight ridge continued on to the rachis, sometimes wrinkled in its middle part (Text-fig. 52 I). Pinnae ovate to lanceolate, margins entire or rarely showing a slight notch (Text-figs. 52 K, M); apex rounded, lower margin decurrent on the rachis, upper margin contracted. Pinnae 4–45 mm. long and 2–10 mm. broad, average 10 mm.  $\times$  4.7 mm., typically almost in contact, occasionally overlapping and occasionally separated by up to 3 mm., typically arising at an angle of about  $70^\circ$ . Near the leaf-apex, the division of the lamina into separate pinnae is incomplete and a series of short blunt segments decreasing in size towards the tip is usually present. Towards the base of the frond the pinnae become somewhat shorter than those in the central part of the leaf. The midrib of the pinnae is always visible but is not prominent; in the larger specimens it is decurrent but this is not seen in the smaller pinnae. Lateral veins are normally obscure (they are sometimes seen in partially decayed specimens and are visible when detached pinnae are viewed in strong transmitted red light), they were simple or forked, straight, and run out at an angle of about  $35^\circ$  to the midrib; near the margin about 13 veins per cm. are present (Text-fig. 52 K, L–P).

Cuticle typically  $6\mu$  thick above,  $4\mu$  below [ $10$ – $20\mu$  thick above, see later]. Stomata rather few on the upper surface, chiefly occurring near the midrib but seldom directly over it (Text-fig. 53 A); numerous and widespread on the lower surface, but seldom directly above the midrib or, in large pinnae above the lateral veins (Text-fig. 53 B). Stomatal structures on both surfaces similar in size and shape. Upper epidermal cells isodiametric or, in large pinnae, very slightly elongated parallel with lateral veins; cells along midrib distinctly elongated and sometimes pointed. Anticlinal walls very thick and very prominent. Both the inner and outer periclinal walls cutinised. Outer wall either flat or with an elongated slit (Text-fig. 53 G), rarely with a very obscure papilla. Lower cuticle showing similar cells but anticlinal walls more prominent. Outer wall sometimes flat but often showing a conspicuous thickened area over the whole middle region of the cell, sometimes raised as a papilla (Text-fig. 53 H), but often a thickened area divided by a thin strip. The positions of the secondary veins are usually invisible but occasionally indicated by a few elongated rounded cells.



Fig. 52. *Pachypteris papillosa* (Thomas & Bose)

A–J, all  $\times 1$ . The midrib is only shown where clearly seen. A, holotype, V.31551. B–J, specimens V.31552–60. K, L, specimens showing some of their secondary veins, V.31561–62,  $\times 2$ . M, lobed pinnae, V.31566,  $\times 1$ . N, veins of narrow pinna, V.31664,  $\times 2$ . O, veins in broader pinna, V.31663,  $\times 2$ . P, form and venation of a large pinna, V.31563,  $\times 2$ . The specimens are all from Roseberry Topping. The figures are from Thomas & Bose (1955).

Stomata evenly scattered and well isolated, irregularly orientated but in large pinnae tending to be parallel with lateral veins. Guard cells thinly cutinised, aperture  $46\mu$  long, situated at the bottom of a fairly deep pit formed by the subsidiary cells. Base of pit oval, but its opening typically constricted by overhanging subsidiary cells. Number of subsidiary cells commonly about 8, range noted 5–11. Subsidiary cells on lower surface mostly bearing large rounded papillae projecting over the edges of the stomatal pit (Text-fig. 53 E, F). Papillae solid except at their bases. Subsidiary cells on the upper surface less papillate but cuticle much thickened around the stomatal pit. Occasional stomata with undeveloped papillae and widely exposed (Text-fig. 53 C). Encircling cells seldom distinguished, never specialized. Trichomes absent.

HOLOTYPE. V.31551, figured Thomas & Bose (1955, text-fig. 1 A). Lower Deltaic; Roseberry Topping.

DISCUSSION. When unmacerated pinnae are examined with red transmitted light the mesophyll is seen to contain a very large number of dark particles of unknown nature (Text-fig. 52 O).

Reasons for transferring this leaf to *Pachypteris* are given above. I have checked the account of Thomas & Bose both against my own material and the numerous specimens in the Hamshaw Thomas Collection and have very little to add.

One of Thomas' specimens (V.45466) is unusual in its strongly lobed pinnae (Text-fig. 51 I) and this approaches *P. lanceolata* but its cuticle is as in *P. papillosa*. A general point not mentioned before is that the compressed margin of the pinna in this species is never scarious, nor locally thickened. The leaf must have been thick and rounded at the edge.

Thomas & Bose (1955) figure various forms of stomata but they do not include irregular ones, though these are common. In these one subsidiary cell has a strong papilla and the next may be flat or weakly papillate.

COMPARISON. *P. papillosa* is compared with *P. lanceolata* on pp.125 and 140. The leaves figured by Seward (1904, pl. 10 figs. 1–3) from the Stonesfield Slate look like typical specimens of *P. papillosa* and though ill-preserved are probably to be identified with it. Fortunately Seward refrained from giving them a new specific name. The leaf described by Buckman as *Salicites longifolius* from the Stonesfield Slate of another locality may also be the same (in which case its name would have priority) but I prefer to regard it as indeterminable.

Seward (1904) considered that his Stonesfield leaves were fragments of the pinnae of bipinnate leaves and considered that the specimens described by Brongniart (1828) as *Sphenopteris macrophylla* and by Saporta (1873) as *Stenopteris desmomera* were more complete leaves of the same species. The poorly figured fragments of Phillips (1871) called *Taxites polydioides* and 'Ramosé Plant' also represent a bipinnate leaf.

I consider that the specimens figured by Seward are different both from the various bipinnate leaf fragments mentioned above and also from Ettingshausen's *Thinnfeldia speciosa*. The bipinnate fragments have much narrower segments and the best of them show a single median vein and apparently no other veins. They may be identical with Saporta's much better specimens called *Stenopteris desmomera*. Ettingshausen's *T. speciosa* from the Lower Lias is a little known leaf with rather slender segments, though with midribs and lateral veins. I suspect his specimens do not represent whole leaves but detached pinnae of a large bipinnate leaf and I suspect also that *T. speciosa* may be just an extreme form of *T. rhomboidalis* which is abundant in the same flora.

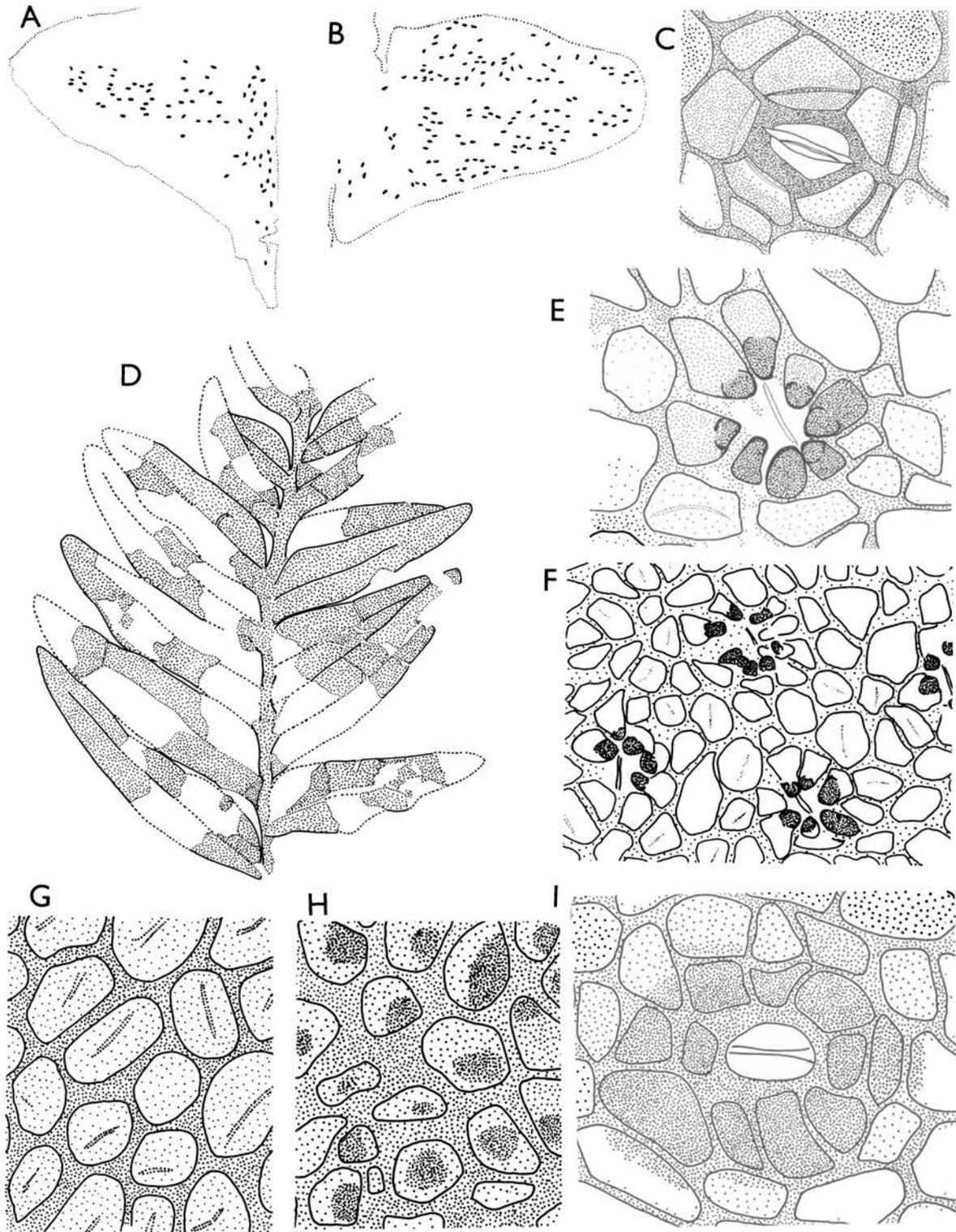


Fig. 53. *Pachypteris papillosa* (Thomas & Bose)

A, B, distribution and orientation of stomata in upper and lower cuticles of one leaf, V.31567-68,  $\times 10$ . C, stoma from lower surface near wound of D,  $\times 400$ . D, exceptionally broad leaf, V.31565,  $\times 1$ . E, one stoma from same leaf as F,  $\times 400$ . F, lower cuticle of V.31569,  $\times 200$ . G, upper epidermis, V.31567,  $\times 400$ . H, lower epidermis with obscure papillae, V.31570,  $\times 400$ . I, stoma of upper epidermis, V.31569,  $\times 400$ .

C, D are from Hasty Bank, the rest from Roseberry Topping. All the figures are from Thomas & Bose (1955).

Certain specimens of *Thinnfeldia rhomboidalis* Ettingshausen (see Gothan 1914) look very similar but are at once distinguished by the cuticle. The cells have no papillae and the stomata are surrounded by a neat ring of subsidiary cells as Gothan (1914 : 115) pointed out. I suspect that the simple forms of *T. rhomboidalis*, e.g., Gothan's pl. 20, fig. 2 may be isolated pinnae of a very large leaf and therefore not really similar to *P. papillosa* in shape.

This leaf is remarkable for its xeromorphy shown by its very thick cuticle. Thomas & Bose give its thickness as 4–6 $\mu$  but do not say how this was measured: it may well be the actual thickness in the fossil state as seen in section. Cuticles are much reduced in compression and the apparent thickness in folds produced at the time of compression gives a truer picture of original thickness. These folds indicate, though obscurely, a total thickness of between 10 $\mu$  and 20 $\mu$ , most of which is no doubt cutinised deep layers of wall and possibly some is the inward extension along the sides of cells. 10–20 $\mu$  is extremely thick.

It is probable that the lamina was thick and succulent, with a tough skin and soft interior. This is suggested by pinnae which have wrinkled in compression; (Pl. 5, figs. 7, 10, 11). Many specimens, particularly at Hasty Bank, show a crack along the midrib of the pinna, and occasionally other cracks which evidently result from a shrinkage in area after the leaf was buried. Succulent leaves do shrink greatly under some conditions: I found that a *Crassula* leaf shrank to about 88 % of its width after being dipped in boiling water and to 61 % after drying under gentle pressure. A mesophytic leaf (*Corylus*) treated in the same way at the same time still remained at about 85 % of its width when dried. The stomata are sunken and very well protected, those on the under side having heavily cutinised papillae. Their distribution is unusual. On the under epidermis they are indeed normal, there being none along the midrib but plenty on the lamina.

The upper epidermis shows frequent stomata at the sides of the midrib in large pinnae, or in small ones at its sides and over it as well (Text-fig. 53 A) but elsewhere there are only very few (in some pinnae) or none at all (in others). Every pinna examined showed this distribution. It appears that the midrib is scarcely prominent at all in small pinnae but in large ones it projects considerably below and rather slightly above; it never forms a sheltered groove above. A search was made of Recent leaves to find an analogous stomatal distribution in the hope that this might throw light on the original form of the leaf and possibly its ecology, cf. Townrow's (1960) investigation of a similar problem in *Lepidopteris stormbergensis*.

I limited myself to a moderate number of leaves only and merely those with fairly thick cuticles. All those laurel-like leaves I examined had plenty of stomata below and none at all above. Succulent leaves (both of plants from dry places and from salt marshes) have nearly equal numbers on the two sides. The closest I saw to *P. papillosa* is in *Ailanthus* (which is not xeromorphic), for in this Dicotyledonous tree some stomata occur on the upper side along the midrib, as they do in certain palms (I am indebted to Dr. C. R. Metcalfe for this information).

Among Gymnosperms such distribution may be commoner. In *Stangeria* I found no stomata above except along the midrib where they are frequent and well formed. Among Bennettitalean leaves I have repeatedly seen a few stomata above the rachis but not elsewhere on the upper surface of the lamina. No stomata are found on the under side of these Bennettitalean rachises nor below the midrib of a *Stangeria* segment. I presume this stomatal distribution is not related to any particular environment but is the result of some morphogenetic factors determining the development of epidermal cells.

OCCURRENCE. *P. papillosa* is unique among Yorkshire plants. Apart from one specimen in the Hamshaw Thomas collection, its 22 localities are all at the very base of the Lower Deltaic Series.

The best and longest known localities, Roseberry Topping and Hasty Bank, were once thought to be Uppermost Liassic (Thomas 1915) but later he gave up this idea. At these two places the bed with *P. papillosa* rests on the eroded top of the Alum Shale (*communis* Zone). But elsewhere, as at Ravenscar brickworks and in Rye Dale (Snilesworth), it rests on the Dogger, or at least its lower part, and at Rock Hole, Guisborough and at Esklets Crag, Westerdale the bed yielding it has been mapped as Dogger, no doubt rightly. So far as I know the 'Dogger' at these points cannot be precisely zoned, but it doubtless belongs to some part of the usual range of rocks of littoral facies included in the Dogger, mainly the *murchisonae* Zone, but it might include beds of the *jurensis* Zone in places.

(The reader is reminded that a different use of the word Dogger is widely current, for the whole of the Lower Oolites.) Nowhere does *P. papillosa* occur in typical Upper Liassic (*communis* Zone) rock. Where the bed containing *P. papillosa* is thick (as at Roseberry and at Hasty Bank), it may well extend beyond the limits of the Dogger, upwards or downwards.

Hand-specimens have been obtained from the following localities which are all from the base of the Lower Deltaic:

Roseberry Topping	Abundant
Little Roseberry	Abundant
Hasty Bank	Abundant
Baysdale Black Beck Leaf Bed	Abundant
Farndale Hillhouse Nab	Abundant
Westerdale, Esklets Crag	Common
Westerdale, Clough Gill	Abundant
Ravenscar, Peak Alum Quarry, (one specimen)	
Ravenscar or Blea Wyke; one specimen in Cardiff Museum (Jackson Coll.)	

Its relative abundance in the last two is unknown; the Ravenscar Peak Alum Quarry specimen was from a fallen block.

Cuticle fragments have been obtained by maceration from the following localities all of which are at the base of the plant-bearing series and in all of which it is the commonest species:

Bransdale, Hodge Beck 3  
 Rosedale, Hartoft Beck 2  
 Rosedale, Hartoft, Craven Farm, Old coal pit  
 Farndale, Spout House Black Shale  
 Snilesworth, R. Rye, Loc. 7  
 Snilesworth, Arnsgill *Pachypteris* Bed  
 Guisborough, Rock Hole Quarry  
 Bilsdale, Fangdale Waterfall  
 Bilsdale, Tripsdale  
 Bilsdale, Tarn Hole Beck 1  
 Bilsdale, Tarn Hole Beck 2  
 Bilsdale, Lincoln Slack Waterfall  
 Whorlton, Scugdale, Holiday House.

Thomas & Bose (1955) mention other localities but these are so near those given above that they can be considered the same locality.

In some of these localities *P. papillosa* is so abundant as to form a thin paper coal but in others there is very little and in Tarn Hole Beck 2 my maceration gave just two fragments of *P. papillosa* and one of an undetermined conifer. It happens that nowhere is it an uncommon species associated with a great deal of something else and this statement is reliable because it is easy to find and recognise fragments of *P. papillosa* cuticle.

Finally there is the exceptional specimen from Haiburn Wyke in the Hamshaw Thomas collection. The specimen was clearly labelled and there would be no reason to doubt the locality were it not exceptional. I met no fragment of this species in several macerations of rocks above and below the Haiburn plant bed, and it might be from a fallen block from still younger beds. No rocks belonging to the base of the Deltaic Series are exposed near Haiburn Wyke. Thomas & Bose (1955) mention this specimen in their paper on *P. papillosa*.

Another locality from just above the Eller Beck Bed at Goathland mentioned by Thomas & Bose must be ruled out; the specimens are *P. lanceolata*. The specimens of cf. *Thinnfeldia speciosa* in the Stonesfield Slate (Seward 1904) belong to the *Tulites* Zone of the Bathonian which corresponds to some part of the Yorkshire Upper Deltaic. Clearly if these later localities can be accepted the species has a fairly long range.

The associates of *P. papillosa* are remarkable. In the two rich localities, most of these associates are indeed the ordinary plants of the Lower Deltaics and nothing need be said about them, but there is one species of land plant which is characteristically found with it almost everywhere and not without it. This is a Conifer agreeing with *Brachyphyllum expansum* (see Kendall 1949), but this Yorkshire material still awaits study. Among microfossils there is the marked association with pollen of *Pteroma thomasi* which I think belongs to it (p. 171). There is also very marked association with two groups of marine microfossils, *Tasmanites* spp. and Hystrichospheres. *Tasmanites* is indeed found in almost every locality examined but Hystrichospheres in rather few, perhaps because my too drastic maceration destroyed them. I noted *Tasmanites* in twelve localities (all those that gave reasonably frequent spores and some where this is almost the only spore). Five of these twelve gave Hystrichospheres also. Mrs. Muir found *Pteroma* pollen in a fragment of the exceptional Haiburn specimen.

Thus we have the following outstanding facts:

(1) *P. papillosa* is characteristic of the base of the series. Here it is either the commonest species and dominant or entirely absent.

(2) *P. papillosa* is associated in most of its localities with *Brachyphyllum expansum*. So marked is this association that I think the same special ecological factor must have been necessary for both. The two species are perhaps also associated in the Stonesfield Slate, a local facies of the Bathonian in the English Midlands which, though marine, has many fossils of land origin.

(3) It is associated in Yorkshire with marine microfossils (as well as with much of land origin).

The occurrence of *P. papillosa* as fragments in the marine (Coastal) Dogger rocks is not itself significant, nor is its occurrence in the marine Stonesfield Slate since land plants are often carried by rivers to the sea. But the association of marine microfossils with it in localities

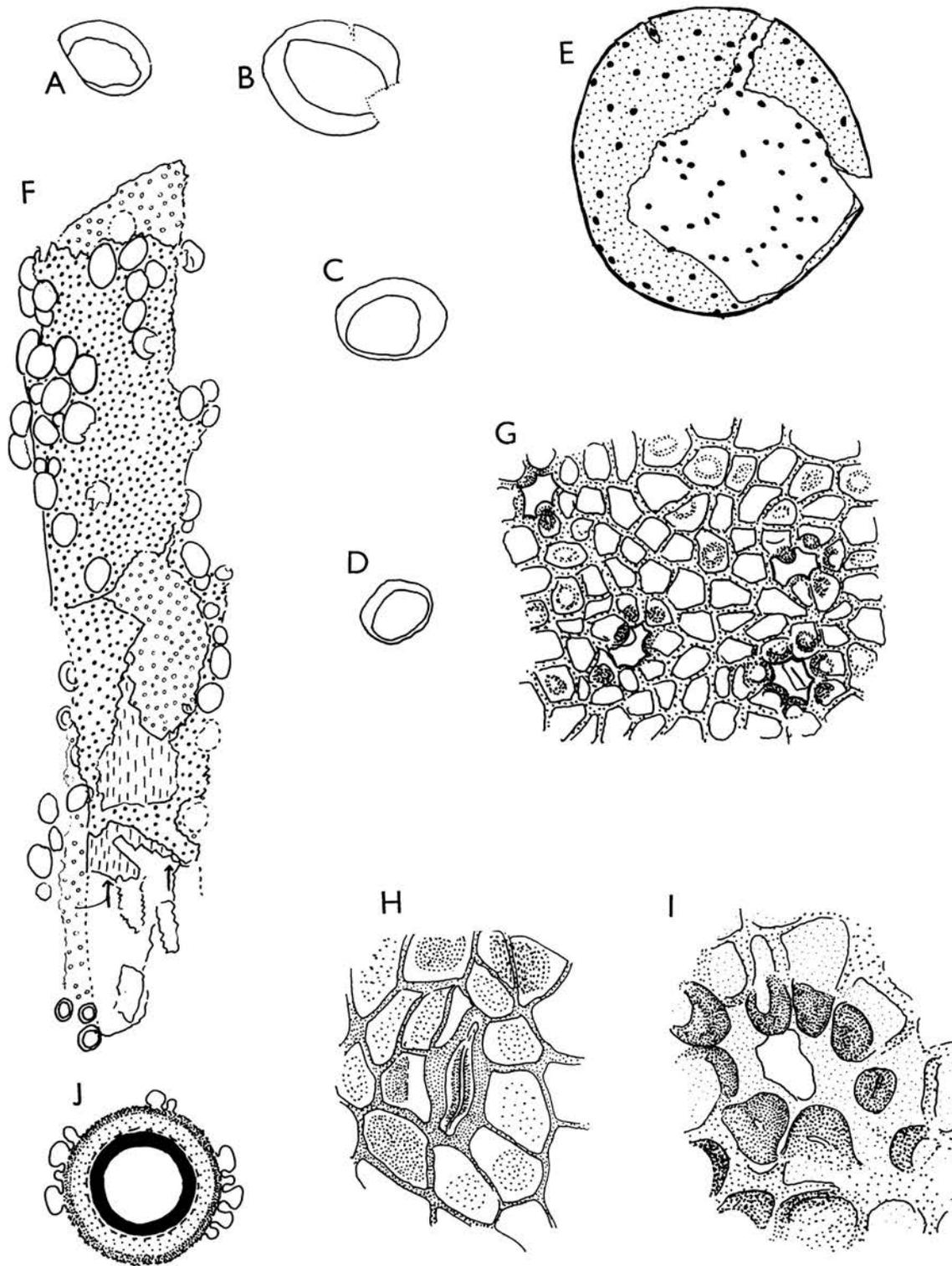


Fig. 54. *Pachypteris papillosa* (Thomas & Bose). Axis and 'berets'

A-D, detached berets, seen from inner side, V.45667,  $\times 10$ . E, beret showing stomata, V.45668,  $\times 20$ . F, diagram interpreting the specimen in Pl. 5, figs. 12, 13. Berets are shown as large ovals and their imprints as ovals with broken lines and with an inner oval marking their attachment. The outer cortex is marked with black dots and its imprint with small rings. The woody core is marked with vertical lines; it has fallen off below. Two arrows mark the extent of the innermost mud layer representing medulla. The unshaded part at the base may be phloem and inner cortex. G, cuticle of beret (outer part) showing four stomata V.45467,  $\times 200$ . H, stoma of beret with feeble papillae and a restricted pit, V.45670,  $\times 400$ . I, stoma of beret with strong papillae and a wide pit, V.45671,  $\times 400$ . J, Imaginary transverse section through F, shape restored. Solid black = xylem, broken line = phloem, inner and outer cortex stippled. The medulla and berets are left white, V.45467.

A-D, I, Farndale Hillhouse Nab. E, Rosedale Hartoft Bed 2. F, G, J, Hasty Bank. H, Westerdale, Baysdale Black Beck Leaf Bed.

where the beds look like ordinary river deposits is very significant, particularly as Mrs. Muir tells me that in the normal freshwater rocks *Tasmanites* and *Hystrichospheres* are very rarely seen (those few seen being perhaps derived).

The strangely local distribution at the base of the plant-bearing series which may be called 'dominant or absent' points to an ecological factor of overwhelming incidence, a presence or absence effect, rather than one of the more usual factors of graded effects. Frequent burning (as opposed to no burning at all) is such a factor but there is nothing to suggest that burning was frequent at this stage, and stages where fossil charcoal (fusain) are prevalent have no *P. papillosa*. I suggest that the factor concerned is flooding by salt water, and my hypothesis is that *P. papillosa* grew between the tide marks, either on mud flats (salt marshes) or along channels like the mangroves. The succulence of both leaf and axis are consistent with a salt habitat. A constant and peculiar associate (*Brachyphyllum expansum*) is explained by supposing that it shared the special habitat. This hypothesis receives its strongest support from the occurrence of marine microfossils sometimes in large numbers, in beds as at Roseberry which would otherwise have been regarded as of purely freshwater origin. No doubt most of the Roseberry species were brought down from the river banks or grew in fresh water; but *P. papillosa* and *B. expansum* grew in the region flooded by tidal waters and the marine microfossils were washed in from the open sea.

#### Axis of *Pachypteris papillosa*

There are a good many specimens, mostly collected by Hamshaw Thomas, which are here identified as an organ of *P. papillosa* though whether they are indeed the stem is more doubtful. They vary greatly in size, the smaller ones (Pl. 7, figs. 2, 3) look like stems of varying width, while the larger ones are merely sheets of tissue torn along their edges. Their common character is that they bear small oval cushion-shaped bodies with thick and characteristic cuticles which are here described under the name 'berets'. They resemble men's berets in shape and that term was selected because it is entirely without botanical implications.

The specimen shown in Pl. 5, figs. 12, 13 and Text-fig. 54 F is regarded as typical, the others as more or less diverging variants. The specimen is illustrated by photographs and a diagrammatic drawing (Text-fig 54 F) to help in the interpretation of the photograph as well as the purely imaginary transverse section (Text-fig. 54 J). This specimen makes a rather confusing fossil as it seems to have rotted and to have been abraded before deposition and also to have lost a certain amount when the rock cleaved. The counterpart is missing. Still it has the advantage of showing several different layers. A little mud penetrated between the tissue layers at an early stage in preservation and thanks to this the different layers are to be distinguished.

At the top of the specimen and to the left is the outermost layer, the cutinised berets, and at the very top is a small area on the rock where the whole fossil has fallen off and the same layer of the far side is represented as an imprint. Over most of the specimen, these berets have disappeared before deposition and no trace of them remains but a few have evidently been removed when the rock was cleaved. Towards the lower part of the figure, where mud has penetrated more considerably, the outer tissues were removed on the counterpart when the rock was cleaved and deep layers are now exposed. See Walton (1936) for the theory of compression of plant fossils.

The widths of the various layers are as follows:

External width including berets .	. 15 mm.
Cortex without berets	12 mm.
Woody core	. 8 mm.
Pith cavity .	. 5-6 mm.

The 'pith cavity' is merely a very thin layer of mud inside the woody core which stops short at about 1.0 or 1.5 mm. from its compressed edges. There is nothing to show whether the pith was originally an open tube or whether a parenchymatous pith had decayed to leave a cavity, but marks on its exposed surface suggest the presence of parenchyma cells about  $100 \times 40\mu$  next to the xylem.

The 'woody core' consists of two layers of compact coal, one above and the other below the 'pith cavity'. Each is compressed to a layer of coal about 0.1 mm. thick, but at the sides where the layers join its extent is at least 1.0 mm. and this may be its original thickness. Its outer surface shows fine striations  $25\mu$  apart perhaps representing tracheids. No leaf or branch traces exist in the part exposed. When this 'woody core' was macerated it dissolved completely, as expected.

Where the woody core has split off (near the bottom of the figure) there is a very thin layer of coal isolated by mud layers above and below it. It shows fine longitudinal cellular striations. This layer might represent phloem or perhaps pericycle fibres or even a fibrous inner cortex. It was not recognised above the woody core and may there be included with the cortex in an undivided coaly mass.

The 'cortex' forms a layer of crumbly coal compressed to about 0.1 mm. thick but extending 2 mm. beyond the woody core at its sides. In some parts this cortex tissue has itself been penetrated by a minute amount of mud, suggesting that its inner layers were partly soft, but its outer surface is compact and forms a good deal of the exposed fossil. This outer surface shows rather distinct bulges and pits about 0.5 mm. wide, not arranged in any order but covering the whole surface. There is no trace of cuticle over this layer. I imagine this to represent a sclerotic layer in the outer cortex but there is no direct evidence of fibres or any other cells. It is clear that this layer formed the outside of most of the fossil when it was deposited, the berets and any underlying soft tissue of the exterior having disappeared. At two points there are the bases of berets removed by rock cleavage and these show that there is yet another layer of crumbly coal outside the outer cortex forming the base of the beret. This outermost soft layer is exceedingly thin and is only preserved underneath a beret.

The berets are mostly oval bodies of very uneven size, but often about  $2 \times 1$  mm. and projecting about 1 mm. The largest are nearly twice this size, the smallest half and some are not elongated but round. At the top left of the figure they completely cover the cortex and this is assumed to be the original condition. No regular pattern of arrangement was recognised in this or any other specimen.

Where the beret has been split off, its scar is seen to be smaller than the beret, that is the beret overlaps its base. (This is always to be seen in detached berets also.)

Near the top of the specimen, to the right, are suggestions of what may be two moderate sized lateral organs of some sort, but no leaf prints were recognised.

The specimen shown in Pl. 7, fig. 7 is 10 mm. wide and most of its surface is formed by the

outer cortex, marked by pits and bulges. A few berets remain above. No leaf scar or other lateral organ is seen and this specimen shows nothing of the deeper layers but where the fossil has flaked off the cortex of the far side is seen. A similar but still narrower specimen is shown in Pl. 7, fig. 4. This which is 7 mm. wide is the narrowest seen.

The specimen shown in Pl. 7, fig. 2 is rather similar but its width varies from 10 mm. in the middle to 20 mm. at one end and nearly 20 mm. at the other. Again the outer cortex forms most of the surface except where berets remain but at a few points deeper layers are exposed, perhaps the 'phloem' and 'xylem'. No lateral organs or scars are seen, but as there are regions where the surface is damaged I cannot state for this specimen that none occurred.

Fragments of bark-like character (Pl. 6, fig. 7, Pl. 7, fig. 8) are numerous, but none of them show their margins with any certainty and some of them were certainly deposited as torn fragments of much larger pieces. Again the main layer seen is the finely lumpy outer cortex, and berets occur, rather thinly as a rule, at intervals of 5 mm. or more. Here and there deeper layers are visible which look like the 'xylem and phloem' of the smaller specimens. All these large fragments are merely a single isolated surface (just like ordinary loose pieces of bark), the tissue facing the rock being a deep layer of the same organ and not the far side. Clearly these fragments come from wide organs but I can see no way of estimating the original width, for they may originally have been curved round a stem of only moderate size and then flattened or they may be nearly flat pieces from very wide stems.

The berets are similar in all specimens and a considerable number of isolated berets were studied. They are remarkably irregular in arrangement in the first specimen (Pl. 5, figs. 12, 13) as indeed in all others and this fact, together with the absence of any disturbance in the deeper tissues of the cortex suggests that they are just superficial emergences formed of the outermost tissues alone.

One of the largest berets is 4 mm. long  $\times$  2 mm. broad and its attachment scar is  $2.0 \times 1.5$  mm. The whole outer surface and the edges are thickly cutinised, but the cuticle quickly becomes delicate towards the scar. Folds in the cuticle suggest an original total thickness of nearly  $20\mu$  on the outside but this is reduced to  $1\mu$  before the cuticle is torn at the scar. The epidermal cells are shown very clearly and stomata are numerous both on the outer surface and on the protected surface just beyond the edge.

DISCUSSION. *Morphology.* The large organ described here is regarded as a stem, although it is very imperfectly known: indeed I find it hard to see what else it could be. The main objection to this idea is that I have not seen one convincing leaf scar and I am by no means satisfied in explaining away this lack by poor preservation, though many specimens certainly are poor. Hamshaw Thomas found specimens many years ago which he thought to be the seed-bearing axis of *P. papillosa* and to which he gave the manuscript name of '*Sarcostrobus*', but this name was never published though used in exhibits of fossils to learned societies. The berets (which Hamshaw Thomas then considered seeds) though of seed-like size, have no structural character at all in common with true seeds and I feel sure that that is not their nature. He refers to them (without name) in a brief report (1930) when he considered the possibility that comparison with *Phyllocladus* might be possible both for the foliage and the 'cone'. He dropped the *Phyllocladus* idea later.

The stem appears to be a fleshy one which easily rotted and had only thin layers of xylem

and of firm tissues in the phloem and outer cortex. It is its berets alone which give it character. I regard them as emergences produced by the epidermis and subepidermal photosynthetic tissue of entirely superficial origin and without disturbing even the firm outer layer of the cortex. The evidence that they contained photosynthetic tissue is that their epidermis shows considerable numbers of well-developed stomata, nearly as frequent as on the leaf. It seems to be a rule that numerous and fully formed stomata are only found over photosynthetic tissue, or at least tissue which was photosynthetic at first. Organs whose only gas exchange is that of respiration have few or more usually none at all: if there are exceptions to this rule I do not know them. The tissue forming the interior of the berets must have been soft for very little remains whatever the plane of compression. It is wholly dissolved on maceration.

The possibility was considered that the berets (which seem easily detached) might serve as bulbils but no supporting evidence could be found.

ATTRIBUTION. This stem is attributed to *P. papillosa* on the evidence of (1) its association, (2) anatomical agreement and (3) anatomical disagreement with other fossils. The evidence of association is very strong. Hand-specimens of the stem have only been found in rock crowded with *P. papillosa* at the three best localities, Roseberry Topping, Hasty Bank and Farndale Hillhouse Nab. Isolated berets occur more widely and could probably be found wherever looked for in macerations of beds with *Pachypteris*, but until specifically looked for they are hard to notice. When searched for they were found in these three localities and in the following where *P. papillosa* is abundant:

Bilsdale, Fangdale Waterfall  
Farndale, Spout House  
Bransdale, Hodge Beck 3  
Rosedale, Hartoft Bed 2  
Westerdale, Baysdale Leaf Bed  
Westerdale, Esklets Crag  
Westerdale, Clough Gill.

Not one of these berets was found in the absence of *P. papillosa* leaves anywhere but a similar though distinguishable beret occurs with *P. lanceolata*.

*Agreement in structure.* The extremely thick cuticle of the *P. papillosa* leaf is easily distinguished from all other Yorkshire cuticles. The stomata are particularly characteristic. The cuticle of the beret is at least as thick as that of a typical *P. papillosa* leaf and sometimes thicker. Its cells are intermediate between those of typical upper and lower surfaces of the leaf.

The stomata are not only similar but show the same range of structure, each type seen on the leaf can be matched by a similar one on the beret. The figures given here might suggest that the beret stomata are less regular than those of the leaf, but as mentioned earlier plenty of irregular stomata occur on the leaf. In spite of the great development of cutinised epidermis, neither leaf nor beret shows any hypodermis.

No other Yorkshire leaf has a cuticle much like the beret and most are very different. The most similar perhaps is *P. lanceolata* which has a less thick cuticle (as a rule) and is not papillate.

*Pachypteris lanceolata* Brongniart

Pl. 5, figs. 1-5; Pl. 7, fig. 6; Text-figs. 55-58

The following are Yorkshire specimens:

- 1828a *Pachypteris lanceolata* Brongniart, p. 50. (Name only.)  
 1828a *Pachypteris ovata* Brongniart, p. 50. (Name only.)  
 1828 *Pachypteris lanceolata* Brongniart, p. 167, pl. 45, fig. 1. (Pinna.)  
 1828 *Pachypteris ovata* Brongniart, p. 168, pl. 45, fig. 2. (Pinna.)  
 1829 *Sphenopteris lanceolata* (Brongn.) Phillips, p. 153, pl. 10, fig. 6. (Pinna fragment; veins.)  
 1829 *Neuropteris laevigata* Phillips, p. 154, pl. 10, fig. 9. (Bipinnate fragment.)  
 1836 *Pachypteris lanceolata* Brongn.: Goeppert, p. 179, pl. 1, fig. 4. (Figure from Brongniart.)  
 1856 *Dichopteris lanceolata* (Brongn.) Zigno, p. 118, pl. 14, fig. 2. (As Brongniart but veins misinterpreted.)  
 1856 *Dichopteris laevigata* (Phillips) Zigno, p. 118, pl. 14, fig. 3. (Figure from Phillips.)  
 1873 *Scleropteris phillipsi* Saporta, p. 369, pl. 45, fig. 2. (Drawing by Phillips.)  
 1873 *Scleropteris laevigata* (Phillips) Saporta, p. 370, pl. 46, fig. 3. (Drawing by Williamson.)  
 1873 *Pachypteris lanceolata* Brongn.: Saporta, p. 366, pl. 45, fig. 1. (Figure from Brongniart.)  
 1873 *Pachypteris ovata* Brongn.: Saporta, p. 366, pl. 46, fig. 2. (Brongniart's figure.)  
 1875 *Dichopteris lanceolata* (Brongn.): Phillips, p. 200, pl. 10, fig. 6. (Figure as in 1829.)  
 1875 *Dichopteris laevigata* (Phillips): Phillips, p. 201, pl. 16, fig. 9. (Figure as in 1829.)  
 ?1877 *Sphenopteris* sp., Lebour, p. 57, pl. 28. (Large fragment, origin not secure.)  
 1900 *Pachypteris lanceolata* Brongn.: Seward, p. 171, text-figs. 27, 28. (Good pinnae, various forms united.)  
 1910 *Dichopteris lanceolata* (Brongn.): Seward, p. 550. (Change of genus.)  
 1913 *Pachypteris lanceolata* Brongn.: Halle, p. 39. (Discussion.)  
 1914 *Pachypteris lanceolata* Brongn.: Antevs, p. 62, pl. 1, fig. 1. (Comparison.)  
 1943 *Pachypteris lanceolata* Brongn.: Frenguelli, p. 241, text-fig. 3. (Figures from Brongniart and Zigno.)  
 1947 *Pachypteris lanceolata* Brongn.: Carpentier, pp. 2, 3. (Comparison.)  
 1954 *Pachypteris lanceolata* Brongn.: Thomas, p. 316, text-figs. 1-3. (New specimens. Discussion.)  
 1955 *Pachypteris lanceolata* Brongn.: Thomas & Bose, p. 542. (Comparison.)  
 1961 *Pachypteris lanceolata* Brongn.: Townrow & Hancock, p. 303. (Comparison.)

The following specimens are from other regions:

- ?1902 *Cycadopteris heterophylla* Zigno: Möller, p. 23, pl. 2, figs. 11-17. (Leaf fragments, Bornholm, see below.)  
 1958 *Pachypteris lanceolata* Brongn.: Vachrameev & Samylyna, p. 1611, pl. 1. (Leaf fragment, cuticle, U.S.S.R.)  
 1963 *Pachypteris lanceolata* Brongn.: Baranova, Burakova & Bekasova, p. 176, pl. 35, figs. 3, 7, 8; text-fig. 73. (Jurassic, Central Asia.)

The following is excluded:

- 1927 *Pachypteris lanceolata* Brongn.: du Toit, p. 346, text-fig. 70. (Similar in outline but most probably a fragment of a *Dicroidium*; Trias, South Africa.)

DIAGNOSIS: Leaf as a whole lanceolate; rather narrow; typical leaf possibly 20 × 7 cm. and with a rachis 7 mm. wide; but largest leaves possibly twice as wide. In lower part of leaf rachis longitudinally striated and also marked with transverse wrinkles, lamina of lowest pinnules continuing downwards as a marginal wing. Pinnae crowded, arising at an angle of less than 45° over most of leaf, typically 3-5 cm. long, but shorter in lower part of leaf; in largest leaves pinnae over 10 cm. long. Pinna rachis up to 2 mm. thick. Pinnules arising at 30° to the pinna rachis in middle and upper part of leaf, rather crowded and often overlapping. Pinnules typically lanceolate in middle region of leaf but (especially in small leaves) sometimes ovate. In large leaves pinnules from 15 mm. long × 4 mm. broad to 10 mm. × 5 mm. broad, sometimes with a lobed margin; in normal leaves 5-8 mm. × 2-3 mm., margins entire; in small leaves (or apical parts of leaves?) pinnules ovate, 2 × 1.5 mm. or even smaller. At end

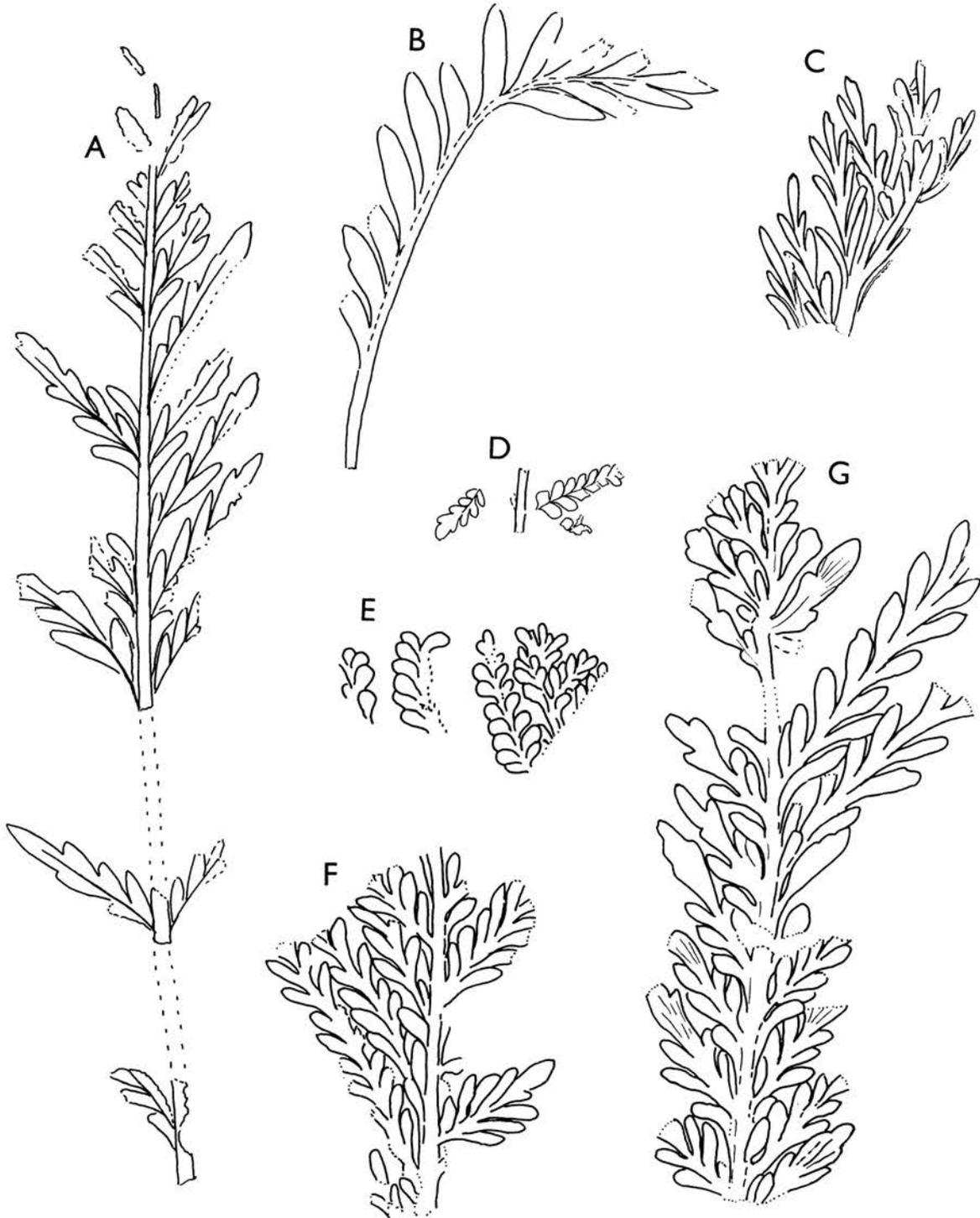


Fig. 55. *Pachypteris lanceolata* Brongniart

A, possibly a nearly complete leaf; dots represent parts of the rachis lost by breaking of rock and also parts of pinnae where the imprint is obscure, V.45475,  $\times 1$ . B, large pinna, V.45476,  $\times 1$ . C, leaf with small narrow pinnules, V.45477,  $\times 1$ . D, fragment with small oval pinnules, V.45478,  $\times 1$ . E-G, three specimens (V.45479-80) redrawn from Thomas (1954, text-figs. 1-3).

A, B, 'Station shale' 180 yds downstream from Goathland Railway Station. C-G, Roseberry Topping. Figs. E-G by permission of the publishers of *Svensk botanisk Tidskrift*.

of pinna, lamina incompletely divided and rather broader than other pinnules of same leaf. Lowest pinnule on basiscopic side situated very low on the pinna or on main rachis (especially in pinnae of lower part of leaf), sometimes rounded or lobed.

Basiscopic margins of pinnules distinctly decurrent, apex usually rounded or obtuse. Lamina coriaceous, margins of pinnules without any membranous wing; marginal region of pinnules normally not thicker than the rest, but exceptionally somewhat thicker and delimited but a slight fold in the lower epidermis. Veins concealed, and not projecting on either side of lamina, but position often shown on lower cuticle (and occasionally visible by transmitted light); in typical pinnules veins slender consisting of a midrib giving off a few forked laterals at a small angle, midrib and laterals ending before reaching the margin, small pinnules with a midrib and few or no laterals. Lamina showing coarse granules but containing no resin or other definite bodies. Hypodermal fibres absent.

Cuticles thick, upper up to  $10\mu$  (measured in folds) lower rather thinner. Stomata almost confined to lower side, avoiding margins and in moderate sized pinnules avoiding midrib, in largest pinnules avoiding lateral veins. Upper cuticle typically showing almost uniform cells, midrib and margin scarcely distinguished. Cells usually isodiametric polygons but tending to be square and to form longitudinal files. Cell walls very strongly marked by prominent ridges; walls broad, straight, not interrupted by pits. Cell surface flat, usually without fine markings but with a simple or branched thin strip in the middle. Trichomes absent but occasional cells thickened (? pathological). Stomata almost absent but larger pinnules showing a very few near midrib. Occasional specimens showing cells slightly elongated but others with cells slightly shorter than broad.

Lower cuticle showing irregular polygonal cells but with a tendency to form longitudinal files near midrib and margins. Cell walls straight, very prominent, uninterrupted by pits. Surface of cell flat, often showing a thin strip; rarely showing fine parallel striations. Stomata scattered and variably orientated, but in some leaves tending to be longitudinal and in others transverse. Stomata rather numerous (between 100 and 200 per sq. mm. but usually separated by ordinary epidermal cells. Subsidiary cells often 6, forming a rounded or elongated group, or transversely elongated. Subsidiary cells irregular in size, but usually smaller than other epidermal cells, surface usually thicker than in other epidermal cells, probably almost flat; usually with a conspicuous thin strip running parallel with the side of the stomatal pit; polar subsidiary cells not differentiated from others. Subsidiary cells occasionally marked with fine radiating striae. Stomatal pit usually showing a very thick margin, margin probably raised in some leaves. Encircling cells irregular in size, unspecialised. Stomatal pit shallow, polygonal or elongated, sometimes rounded. Guard cell surface rather thinly cutinised; aperture usually slightly longer than the pit in most cutinised specimens, surface of guard cells at sides of aperture thicker than poles; poles lying behind subsidiary cells.

LECTOTYPE. Specimen figured by Brongniart (1828, pl. 45, fig. 1).

DISCUSSION. The range of form of *Pachypteris lanceolata* is by no means fully known but there is intergradation between leaves with small oval pinnules, those with small narrow pinnules and others with larger lanceolate pinnules. In agreement with Seward (1900) and Thomas (1954) the *ovata* and *laevigata* forms are here included in *P. lanceolata*. Pinnules of the different shapes have just the same cuticle structures.

Thomas (1954) specially emphasised the pinnules borne on the main rachis (zwischenfiedern)

and suggested that they might be in the position of subtending bracts, but they are here regarded as merely the lowest of the pinnule series. Many Palaeozoic and some other Mesozoic leaves have similar *zwischenfiedern*.

*Venation.* Few specimens show their veins clearly and the earlier authors gave widely different figures. Brongniart (1828, pl. 45, fig. 1) shows a midrib but no laterals while Phillips (1829, pl. 10, fig. 6) shows the laterals but the midrib is stated to be absent (Neuropterid venation) while his pl. 10, fig. 9 shows Odontopterid venation. Thomas observed and drew a few slightly diverging veins in the large terminal pinnules but did not settle the ordinary pinnules. Most pinnules except the smallest show their midribs when macerated, as a tract without stomata and some large pinnules show their lateral veins as well. They are seen easily in a few specimens which seem to have been cleared by partial oxidation before they were preserved and here the veins form slender, dark strands and the laterals arise at a rather small angle to the midrib in ordinary pinnules or a very small angle in terminal pinnules. Even these cleared pinnules show no fibrous tissue or hypodermis.

*Margin.* In most specimens the pinnule margins although lacking stomata, are no thicker than the rest of the lamina. In a few pinnules which appear typical otherwise, the pinnule margin is slightly thickened and there is a distinct fold just at the edge of the stomatal region; this fold represents slight vertical crushing but no overhang. Slight though it is, this fold is of interest in relation to *Cycadopteris* where it is more strongly developed. The epidermal cells at the leaf margin pass gradually from upper to lower side in most specimens and the edge of the leaf was certainly rounded and not sharp.

Vachrameev & Samylina (1958) have given figures of the cuticle of a well preserved Russian specimen. The figures look just like the normal form and cuticle of Yorkshire specimens and they are the first published figures of the cuticle of this plant. The cuticle is easy to prepare, but sometimes so thick and with such strongly projecting anticlinal walls that details may be difficult to make out, especially of the stomata. It serves to group *Pachypteris* with *Cycadopteris*, *Thinnfeldia*, *Stenopteris* and other genera while also giving distinguishing points. Even when the cell walls are extensively cutinised there is no trace of hypodermis.

The small 'berets' associated with *Pachypteris lanceolata* are presumably of the same nature as the very similar ones with *P. papillosa* and again emphasise the close affinity between the two species.

COMPARISON. Although good specimens of *Pachypteris lanceolata* are at once distinguishable from all other Yorkshire leaves, fragments may be hard to distinguish from *P. papillosa* as their lamina segments may be of similar size and shape. Their cuticles distinguish them readily enough. In the Bornholm floras there are leaf fragments which look like this species (while others look more like *P. papillosa*), but they have not been studied closely. Some of the specimens described as *Cycadopteris* by various authors may also be similar as by no means all figures of *Cycadopteris* show the thickened margins.

The more finely divided forms of the Lower Liassic *Thinnfeldia rhomboidalis* look very like *P. lanceolata* while the coarser forms, or possibly fragments of large leaves, look like *P. papillosa*; compare for example the figures given here with those of Daber (1962) and Gothan (1914). The cuticles are moderately different, for the stomata of *T. rhomboidalis* tend more to avoid the veins and the ring of small subsidiary cells is better developed. The veins in *T. rhomboidalis* are more odontopteroid in that the lower ones seem to arise from the rachis while in *P.*

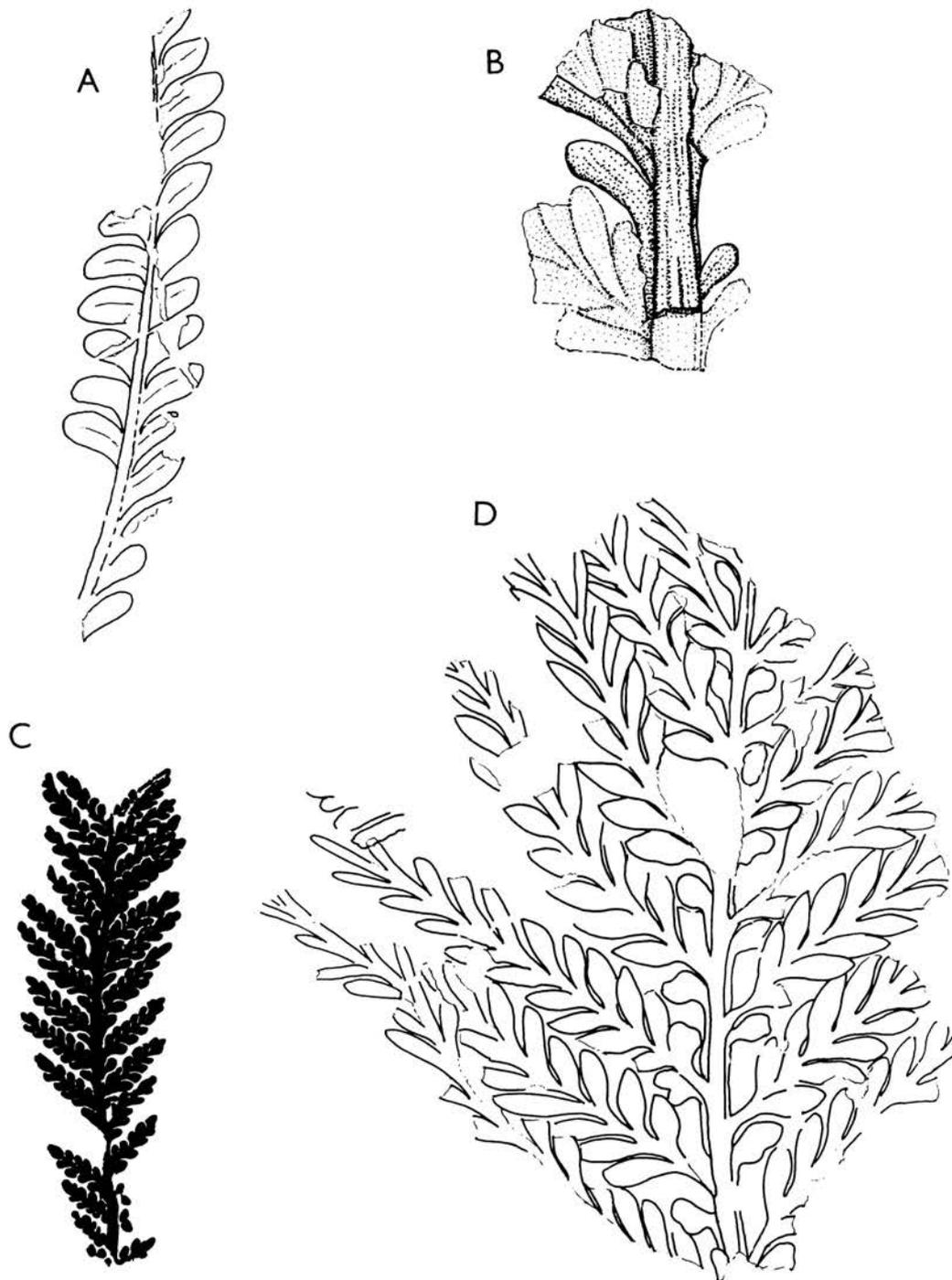


Fig. 56. *Pachypteris lanceolata* Brongniart

A, isolated pinna resembling *P. papillosa* leaf, V.45481,  $\times 1$ . B, broad rachis fragment showing decurrent bases of lower pinnules, V.45482,  $\times 2$ . C, small but nearly complete leaf, V.45483,  $\times 1$ . D, middle region of large leaf showing slender apical pinnules and irregularly lobed basal ones in rather varied positions, V.45484,  $\times 1$ .

A, 'Sewell's Colln. 1920, Goathland'. B-D, Roseberry Topping.

*lanceolata* they arise from the base of the midrib, but the difference is slight. Though placed in different genera, the two leaves may be very similar.

*P. dalmatica* Kerner 1895 (including *P. dimorpha*) is very similar in some of its forms, though too little known to be identified, particularly as it is of different age (Lower Cretaceous). *P. dalmatica* as interpreted by Halle (1913) is similar also, though without *zwischenfedern*.

**OCCURRENCE.** Thomas calls *Pachypteris lanceolata* 'a very rare plant' but this only describes the ordinary hand-specimens, not the small fragments which are widespread and abundant though not in the best plant beds. Their occurrence is interesting, they chiefly occur in sandstones along with driftwood and they are often found with certain other tough leaves like *Pagiophyllum*. It suggests that it was an abundant plant somewhere inland but that it only seldom grew in the delta itself where it could fill the sediment with intact leaves (that it did sometimes do so is shown by its occurrence at Roseberry Topping and at the Goathland locality where a number of leaves are found together). It is rare on the coast (except as fragments) and even fragments are seldom seen in the moorland coalfield centred around Castleton. It is almost equally common at all levels in the Deltaic series.

Hand-specimens are recorded by Phillips (1829) from Saltwick, Haiburn Wyke (both Lower Deltaic) and from Egton Moors (level unknown). Hamshaw Thomas and later Miss Kendall collected it from Roseberry Topping and Thomas states that he found one leaf at Hasty Bank (both Lower Deltaic). I collected it in two localities of the Sycarham Series both in sandstones; at just below Goathland Station where it is frequent in a bed above the Eller Beck Bed. I presume Sewell's specimens also came from here. I collected another specimen from Stoneygate Slack, Hawsker. There are good specimens in Stockholm from Goathland and 'between Saltwick and Hawsker'.

Cuticle fragments have been found as follows:

Upper Deltaic . . . . .	28 localities 24 %
Middle Deltaic Gristhorpe Series	10 localities 8 %
Millepore Bed (Marine) . . . . .	2 localities
Middle Deltaic Sycarham Series	15 localities 21 %
Lower Deltaic	45 localities 19 %
	—
Total	100 localities
	—

The percentage figures represent the number e.g., 28 for Upper Deltaic divided by the total number of Upper Deltaic fossil localities, 118 known to me at the time of writing (1961). This perhaps gives a truer figure of the frequency at each stage than the absolute frequency. (The Millepore Bed has two out of a possible four localities.) Even the percentage figures seem to do less than justice to its occurrence in the Sycarham Series for it is about the commonest plant in those relatively barren rocks. This distribution contrasts sharply with that of *P. papillosa*.

Seward (1903) included *Dichopteris ellorensis* Feistmantel and *Cycadopteris heterophylla* Möller in *P. lanceolata*.

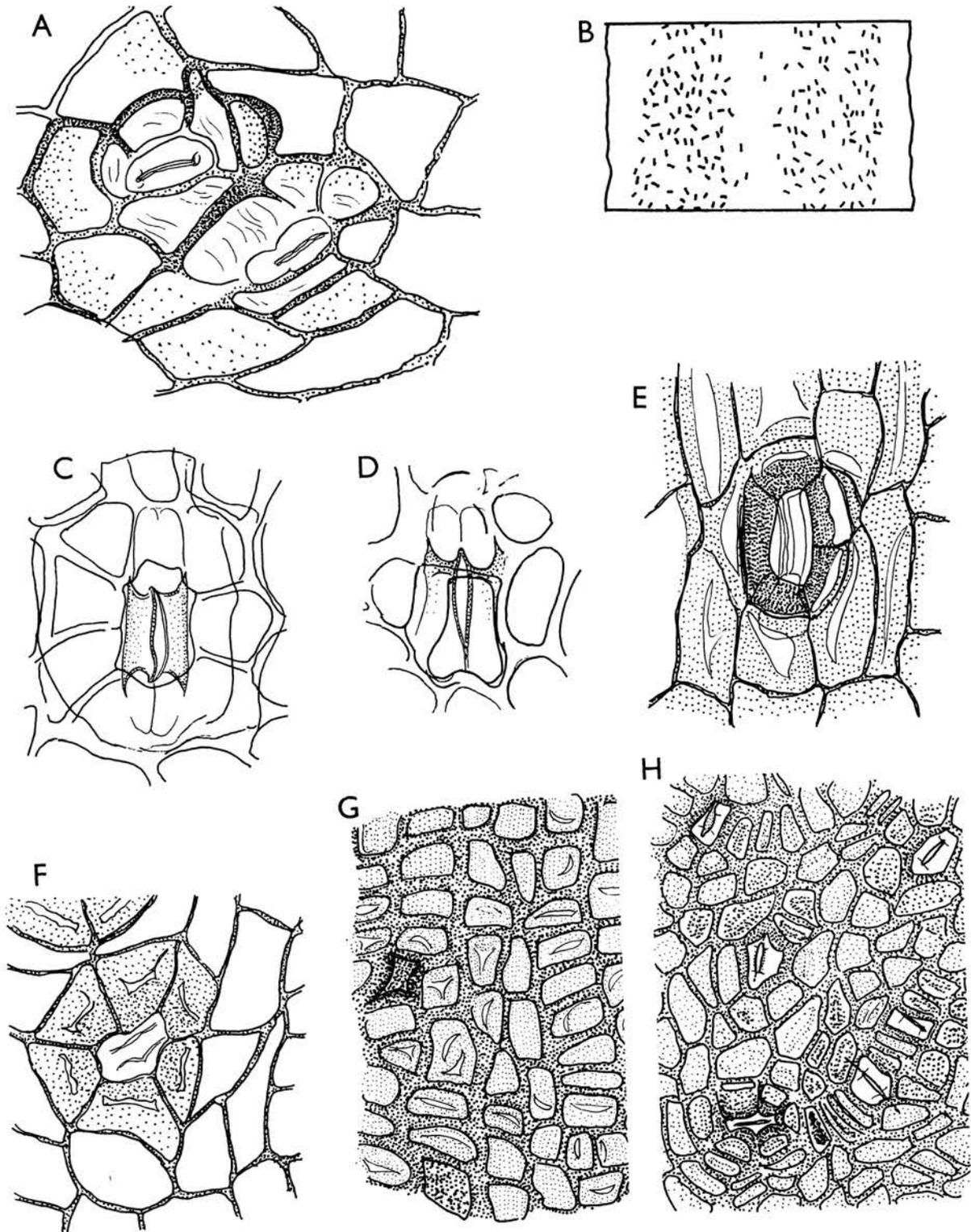


Fig. 57. *Pachypteris lanceolata* Brongniart

A, stomata with thin and striated subsidiary cells, V.45686,  $\times 500$ . B, distribution and orientation of stomata in a strip 1 mm. wide from a narrow segment, V.45687,  $\times 30$ . C, D, stomata from a very thickly cutinised leaf, seen from within. Guard cell thickenings alone stippled, V.45688,  $\times 800$ . E, stoma in which the inner part of the subsidiary cells is heavily thickened, V.45689,  $\times 500$ . F, stoma in which the subsidiary cells are more evenly thickened, apart from thin strips, V.45687,  $\times 50$ . G, H, upper and lower cuticles of the same segment, V.45687,  $\times 200$ .

A, Scarborough Brick Pit, top clay. B, F–H, Rosedale High Hollins. C, D, Fylingdales, Normanby Jet Dump. E, Bilsdale, Black Intake C, V.45689.

Beret-like organ of *P. lanceolata*

At a late stage in the present work I realised that cutinised 'berets' very like those of *P. papillosa* are to be found with *P. lanceolata*. They are smaller and much less conspicuous and I earlier dismissed some as small and poorly preserved leaves of *Brachyphyllum mamillare*; I only recognised them after becoming familiar with the berets of *P. papillosa*. No attached berets are known but they are so abundant in certain macerations that it is possible that the axis bearing them may have been present. All the specimens studied are isolated cuticles.

The berets are compressed in various planes which taken together suggest they were nearly hemispherical, the height being equal to the radius. Some show a basal constriction, but the cuticle in the constricted part rapidly becomes delicate near the torn edge. The exposed part is thick,  $10\mu$  or even more, measured in folds. The whole surface may be provided with stomata, at a concentration of about 100 per sq. mm.; but they are usually less, and in some specimens there are just a few round the sides and none on top. The width varies from 0.6–2.1 mm., most being just over 1 mm. wide and round.

The epidermal cells are not in rows and are isodiametric and usually have broad walls which project strongly inwards. The outer wall is distinctly convex and in extreme specimens is thickened in the middle part of the cell to form a large, ill-defined papilla. Cells in which the middle part forms a thin strip are met in occasional specimens, but are not typical. The vertical walls are not pitted and the surface wall is without fine sculpture. No trichomes occur.

The stomata are scattered, or may form a ring below the top. In most berets they show a prevailing orientation (Text-fig. 58 P) where they are transverse to the long axis, but in others they are parallel and I could see no way to relate them to the long axis of the organ bearing them. The stomata are of varied structure. Most have 6–8 rather small subsidiary cells; but ones with 5 and others with 9 were noticed. Occasional stomata may have subsidiary cells in contact, but they do not share subsidiary cells. The subsidiary cells are often of very uneven size and polar cells are not specialised.

In the less thickly cutinised berets the subsidiary cells are often conspicuously darker and thicker than other cells; but in the thickly cutinised ones they are usually no thicker than other cells, and occasionally are thinner. They tend to be smaller and their surface may bulge more distinctly to form a real papilla, such as is never seen on the leaf. In some berets the subsidiary cells show a thin strip in the middle of their bulging surface, as is often met in the leaf. The stomatal pit is round or oval and the rather thinly cutinised guard cells are just as in the leaf. Not only do various forms of stoma occur in one beret, but the subsidiary cells of one stoma may differ from one another, one having a central round papilla, another a flat one over the aperture, and others no papilla at all.

These berets are attributed to *P. lanceolata* on the evidence of repeated association and agreement in cell structure. They were, as mentioned, only found late and as a result of deliberate search for such organs and thus any that may have occurred have been missed in most localities. They have been found with *Pachypteris* leaf fragments at:

Newtondale, Ray Gate Slack	}	Both Upper Deltaic.
Pickering, Keys Beck Road		<i>P. lanceolata</i> the main species.
Cloughton Wyke <i>Pachypteris</i> Bed	—	Middle Deltaic Gristhorpe Series, <i>P. lanceolata</i> abundant and nearly pure.
Riccaldale, Bonfield, Botany Bay	—	Lower Deltaic. (Other species present.)

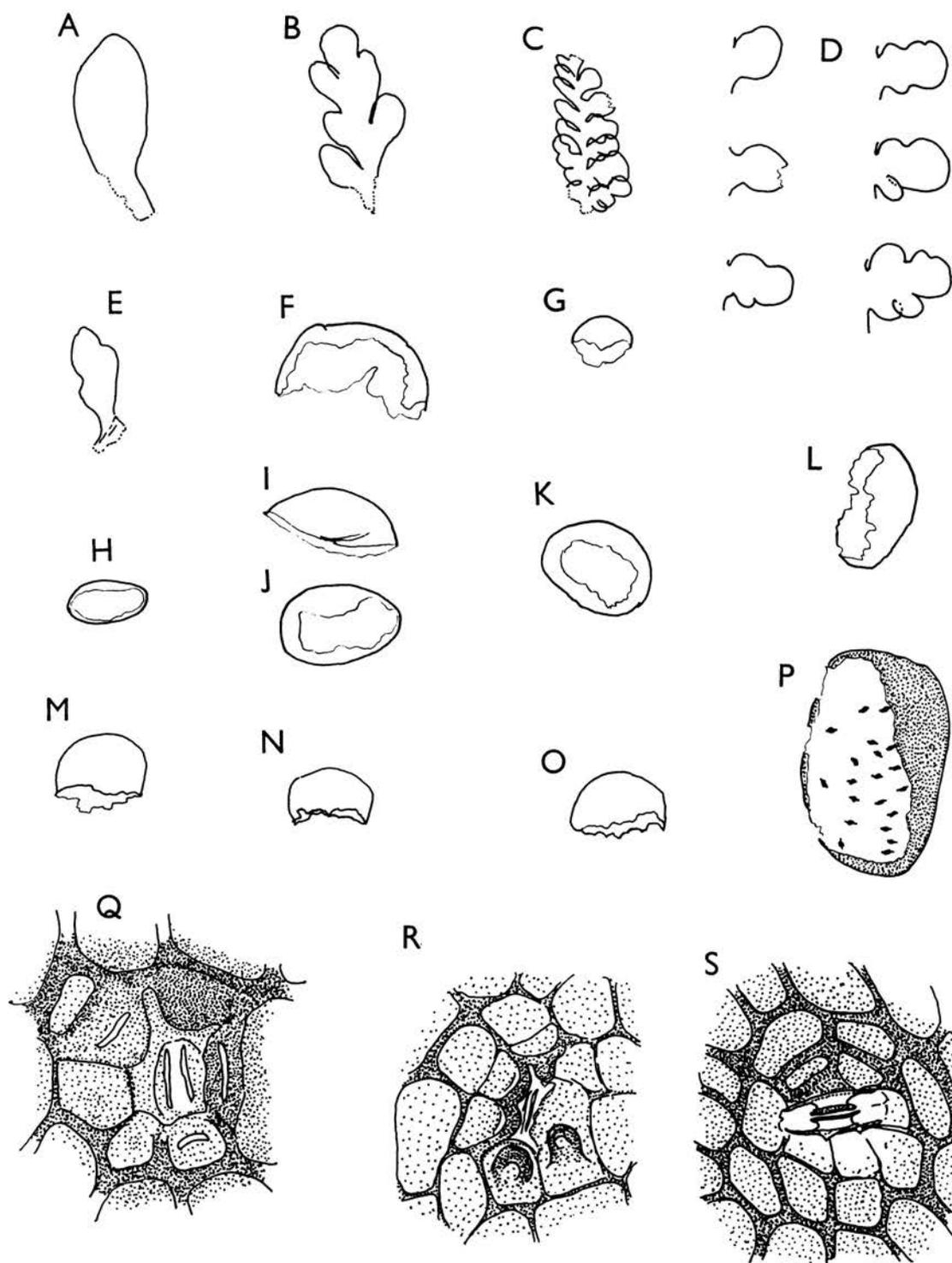


Fig. 58. *Pachypteris lanceolata* Brongniart

A, typical leaf segment, V.45690,  $\times 4$ . B, C, E, small leaf segments  $\times 4$ ; D, group of small segments from the right side of C,  $\times 8$ ; all V.45691. F-S, 'beret-like' organs. F-L, typical specimens in V.45692,  $\times 10$ . M, N, specimens in V.45693,  $\times 10$ . O, specimen in V.45694,  $\times 10$ . P, specimen showing distribution and orientation of stomata (some stomata partly concealed by the two layers on the right are omitted), V.45692,  $\times 20$ . Q, R, typical stomata, V.45692  $\times 400$ . S, stoma of specimen with small cells, V.45695,  $\times 400$ .

A-E, Haiburn Wyke *Zamites* Bed. F-L, P-S, Cloughton *Pachypteris* Bed. M, N, Newtondale Ray Gate Slack. O, Riccal Dale, Bonfield, Botany Bay.

The agreement in structure between leaves and berets is closest between well cutinised leaves and the more thinly cutinised berets. The thickly cutinised berets show features like papillose epidermal cells not shown by leaves. The most similar specimens indeed are so much alike that it would scarcely be possible to tell a fragment of the beret from a fragment of lower epidermis of a leaf.

The most striking difference between the berets of *P. lanceolata* and *P. papillosa* is in their size. Those of *P. lanceolata* are mostly a little over 1 mm. wide and scarcely exceed 2 mm., while those of *P. papillosa* are mostly over 2 mm. in at least one dimension. This difference is more obvious when a number of specimens of each are compared.

The cells of *P. lanceolata* berets are usually a good deal smaller, about half the size, and their papillae are much less strongly developed. It must be admitted that their characters overlap and it would be possible to miss a rather large papillose beret of *P. lanceolata* among a set of *P. papillosa*. As it happens, however, their localities are different.

### Genus STENOPTERIS Saporta 1873 : 290

EMENDED DIAGNOSIS. Leaf normally falling from its stem, coriaceous, shape of leaf as a whole lanceolate, branching one or more times pinnate, lamina deeply dissected into narrow segments. All parts of leaf (main rachis, pinnae segments) tending to be almost equally narrow. Rachis normally simple (occasionally forked); primary branches usually opposite. Lamina thick, continuing without interruption from sides of main rachis onto primary and secondary branches, margins never scarious (originally rounded). Main and branch segments typically with a single median vein or two below a point of branching, only exceptionally with more than two; ultimate segments always with a single median vein extending to the apex. Ducts and resin absent from leaf substance.

Cuticles well developed. Epidermal cells straight walled. Stomata usually equally numerous on the two sides, but typically sparsely scattered, longitudinally orientated. Subsidiary cells haplocheilic, about 6, size often uneven, some of them usually bearing a hollow papilla. Encircling cells if present, unspecialised. Guard cells at the bottom of a small rectangular pit, thinly cutinised. Trichomes usually present, formed as a conical extension of an ordinary epidermal cell. Hypodermal fibres absent.

TYPE SPECIES. *Stenopteris desmomera* Saporta.

DISCUSSION. Saporta's figures show fine large specimens of *S. desmomera* but we know nothing about their microscopic structure. I have therefore taken the microscopic characters of the five or six species where we do know it and have put them in the diagnosis, assuming that the type species is similar. These are *S. astartensis* and *S. dinosaurensis* from the Rhaetic and Lower Lias of Greenland (Harris 1932, 1937); *Stenopteris* sp. (Lundblad 1950) from Sweden and the three species described here.

I have excluded the S. Hemisphere *S. densifolia* which may also be placed in *Xylopteris* or *Dicroidium*. Its cuticle has been described by Thomas (1933). It differs from the Northern species in the constant dichotomy of the rachis, the sinuous walls of its epidermal cells and more irregular subsidiary cells. As dichotomy does occur in some Northern leaves, even if perhaps exceptionally, the distinction cannot be considered fully satisfactory, see also Jones & de Jersey (1947 : 22).

*Stenopteris* differs from *Pachypteris* in its narrower ultimate segments which have only one vein, while in *Pachypteris* 1-veined segments are unusual. The stomata are differently distributed; in *Stenopteris* they occur in a similar but low concentration on both sides, while in *Pachypteris* they are very numerous below but few above.

*Amdrupia stenodonta* Harris (1932) from the Greenland Rhaetic is also similar but its pinnae are rather broader though they do end in 1-veined segments and all the stomata occur below. The cell walls are slightly sinuous.

Most species of *Thinnfeldia* have ultimate segments with several veins but *T. schwarzi* (Gothan 1914) is exceptional in its narrow 1-veined segments which look very like those of *S. dinosaurensis*. Its stoma is, however, that of a typical *Thinnfeldia*, surrounded by a neat ring of small subsidiary cells which form a rampart round the circular pit. Very possibly it is better placed in *Thinnfeldia* than in *Stenopteris* in spite of its form.

The cuticle of *Stenopteris* is very like that of *Czekanowskia* and narrow leaves of *Baiera*. Usually the leaves of *Stenopteris* are easily distinguished by their pinnate branching, but *Czekanowskia microphylla* has branching which is so unequal that it could be described as pinnate and an isolated leaf of that species would be generically indistinguishable from *Stenopteris*. It happens that its leaves are retained permanently on a dwarf shoot, so the difficulty does not arise. The fact that *Stenopteris* leaves are shed is mentioned in the diagnosis.

#### Key to the Yorkshire species of *Stenopteris*

- |     |  |   |   |   |   |                        |
|-----|--|---|---|---|---|------------------------|
| (1) | Leaf over 10 cm. long, trichomes very numerous | . | . | . | . | <i>S. williamsonis</i> |
|     | Leaf under 10 cm. long, trichomes few          | . | . | . | . | 2                      |
| (2) | Leaf finely branched, cuticle rather thin      | . | . | . | . | <i>S. nitida</i>       |
|     | Leaf coarsely branched, cuticle robust         | . | . | . | . | <i>S. nana</i>         |

There are a good many cuticle fragments which may represent other Yorkshire species.

#### *Stenopteris williamsonis* (Brongniart) Harris

Text-figs. 59, 60

The following are all Yorkshire specimens:

- 1828a *Sphenopteris williamsonis* Brongniart, p. 50. (Name.)  
 1829 *Sphenopteris williamsonis* Brongniart, pl. 49, figs. 6-8. (Good figures.)  
 1829 *Sphenopteris digitata* Phillips, p. 147, pl. 8, figs. 6, 7. (Outline drawings.)  
 1834 *Sphenopteris williamsonis* Brongn.: Lindley & Hutton, pl. 131. (Good figures, specimen 619.39 in Scarborough Museum.)  
 1875 *Sphenopteris williamsonis* Brongn.: Phillips, p. 217, pl. 8, fig. 6. (Change of name, figure as 1829.)  
 1900 *Sphenopteris williamsoni* Brongn.: Seward, p. 154, pl. 17, figs. 1, 2. (Good figures.)  
 1944 *Stenopteris williamsonis* (Brongn.) Harris, p. 685, text-fig. 9 A-C (not 9 D which is *S. nitida*), text-fig. 10. (Change of name; leaf, cuticle.)

Note. Seward (1900) gives several additional references in the literature and mentions other name combinations, in particular, *Hymenophyllites williamsonis* due to Goepfert.

EMENDED DIAGNOSIS. Leaf up to about 15 × 6 cm., but often smaller; petiolate, leaf base expanded bearing stipular segments, lamina typically tripinnate. Rachis usually simple but occasionally forked in its upper part; slender, flanked by a narrow wing of lamina formed by decurrent bases of pinnae. Primary pinnae usually opposite, rather distant, the lower ones short, arising at a wide angle; upper ones at a small angle; longest pinnae in middle or upper

parts of leaf. In large and medium sized leaves, rachis bearing one or two small pinnae (zwischenfedern) on each side between large primary pinnae. Pinnae pinnately divided into narrow segments, segments themselves divided into ultimate branches the first branch being on the basiscopic side, ultimate branches making a very small angle with one another, short, about 1 mm. wide, acutely pointed.

Ultimate branches of lamina about 0.7 mm. wide and with a single median vein; in sparsely branched and elongated leaves ultimate branches up to 5 mm. long and with acute apices, but in densely branched leaves ultimate segments very short and rounded. In sparsely branched leaves lamina at its widest under 2 mm. and with only one or two veins, but in densely branched leaves, segments up to 4 mm. wide and with 4 veins at widest points.

Lowest basiscopic branch of a pinna situated at the base of the pinna or on main rachis below the pinna origin. Lamina substance moderately thick, segments with a single vein branching at an acute angle below the point of branching of the lamina. Mesophyll where preserved forming small rounded blocks, ducts, resin bodies absent. Cuticles of medium thickness ( $2\mu$ ), tough and easily prepared. Cuticle on one side very slightly thicker and with more prominent cell outlines but other details almost identically similar. Near apices of segments cells isodiametric but becoming elongated below and very elongated on main rachis. Cell outlines straight, formed by a prominent and fairly broad wall, not interrupted by pits. Surface of ordinary cells flat, finely and evenly mottled, rarely showing parallel striations. About a third of epidermal cells on both sides bearing a prominent median outgrowth, outgrowth varying from a low hollow papilla to a tapering trichome  $60\mu$  long, walls of trichome thickly cutinised. Trichome never divided by septa. Lower trichomes projecting stiffly at right angles to the surface.

Veins scarcely distinguished in ultimate segments, but recognisable below as tracts of narrower and more elongated cells, slightly fewer stomata and slightly longer trichomes. Margins of lamina scarcely specialised but resembling the region along a vein.

Stomata very sparse, equally numerous on the two sides but fewer on main rachis than on ultimate segments of lamina. Stomatal index very low, less than 1%. Stomata almost uniformly scattered, not forming longitudinal files, or if in files, files short and not clearly marked, orientation usually longitudinal. Subsidiary cells irregularly placed and often resembling ordinary cells or rather smaller; usually bearing a hollow papilla. Guard cells almost flush with the surface but region of aperture slightly overlapped by subsidiary cells to form an elongated, very shallow pit; guard cell poles usually concealed but occasionally exposed. Surface of guard cells very thinly cutinised except at sides of aperture. Encircling cells often present but irregular in distribution, often absent but occasionally forming a complete ring. Hypodermal fibres absent.

LECTOTYPE. Specimen figured by Brongniart (1829, pl. 49, fig. 7).

OCCURRENCE. All the larger specimens are from the Gristhorpe Bed. Here *S. williamsonis* is rare in general except very locally where several leaves may be found on the same bedding plane. Cuticle fragments agreeing with *S. williamsonis* are occasional in the Lower and Middle Deltaics, and at a few points they are abundant. The species is rare in the Upper Deltaic. Most of the fragments are in rich plant beds or in the coals and this species would seem to be an element of the flora of the delta itself though an uncommon one rather than drifted in from a long distance up river.



Fig. 59. *Stenopteris williamsonis* (Brongniart)

A-C, apical fragments of leaf from a maceration in bulk, V.45647,  $\times 5$ . D, E, similar fragments from another maceration, V.45648,  $\times 5$ . F, main rachis and pinna from counterpart of H,  $\times 5$ . G, two leaf fragments V.45485,  $\times 1$ . H, finely divided leaf, V.45482,  $\times 1$ . I, upper part of elongated leaf, the apical division being a dichotomy, V.45483,  $\times 1$ . J, leaf base, V.45484,  $\times 1$ .

A-C, J, Cloughton *Solenites* Bed. D, E, Haiburn Beck Plant Bed. F-I, Gristhorpe Bed.

The localities are distributed as follows:

Upper Deltaic	2 localities
Middle Deltaic Gristhorpe Series	4 localities
Middle Deltaic Sycarham Series	2 localities
Lower Deltaic	10 localities

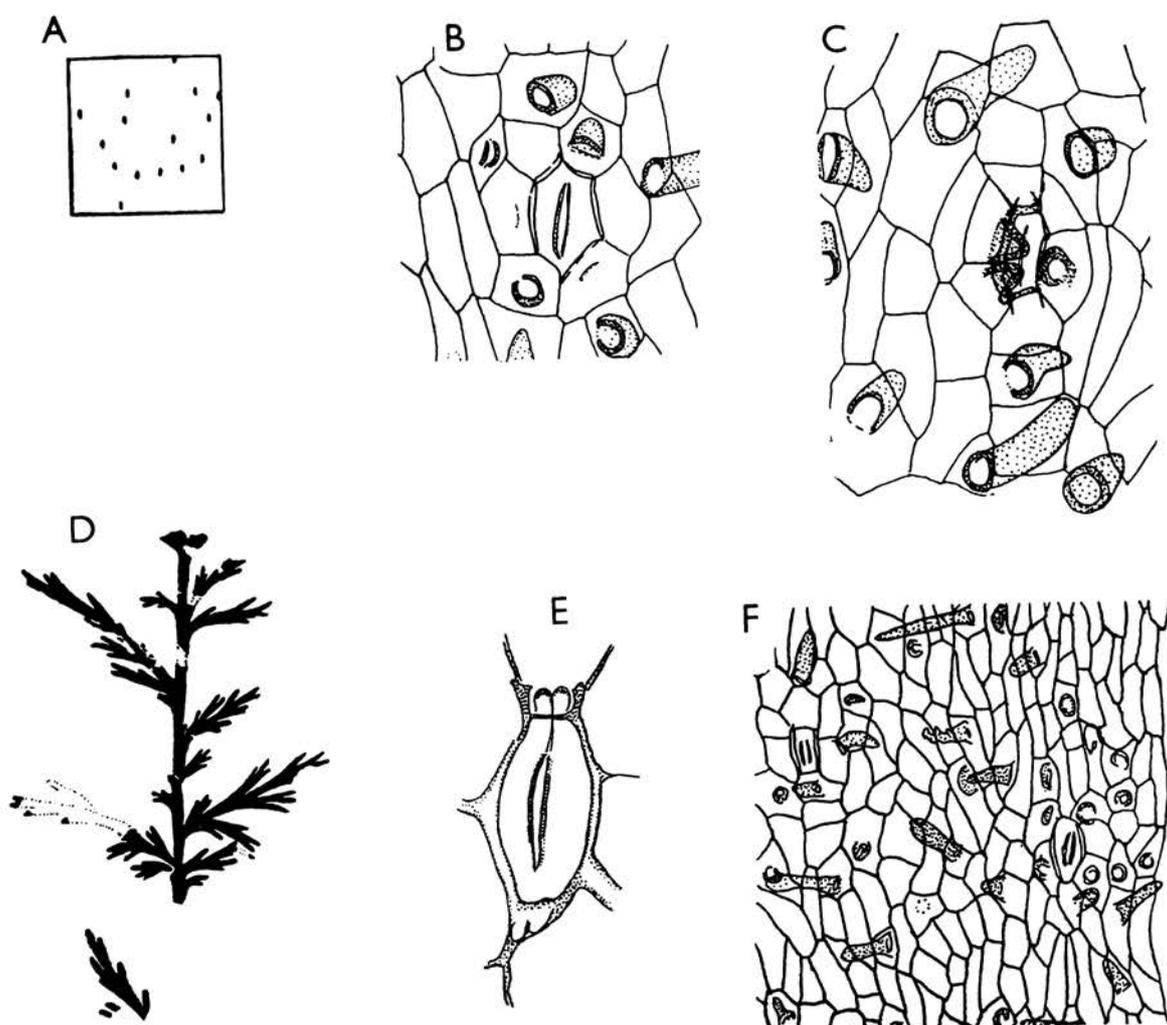


Fig. 60. *Stenopteris williamsonis* (Brongniart)

A, distribution and orientation of stomata in 1 sq. mm. B, moderately exposed stoma  $\times 400$ . C, strongly papillate and protected stoma,  $\times 400$ . D, middle region of a normal sized leaf, Yorkshire Museum,  $\times 1$ . E, stoma in which the poles are partly exposed,  $\times 800$ . F, general view of cuticle  $\times 200$ .

All the cuticle preparations are from the specimen shown in D; Gristhorpe Bed. All the figures are from Harris (1944, text-figs. 9, 10).

DISCUSSION. The specimens figured here seem to cover most of the range of variation seen in earlier figures except that one of Lindley & Hutton's (1834) figures represents even more sparse branching than in Text-fig. 60 D. The cuticle seems nearly constant, though some leaves are more richly provided with trichomes than others. The main variability indeed is seen between the rachis and ultimate segments of a single leaf.

In a previous account (1944) I commented on the irregular branching in the specimen shown in Text-fig. 60 D. The alternation of long and short pinnae is to be explained as main pinnae and zwischenfiedern which are merely basal pinnules decurrent on the main rachis. I was perplexed by the additional fact that the lateral segments were at different levels on the rachis, but it now seems that this is like what Townrow (1960) demonstrated in *Lepidopteris* where the small zwischenfiedern may be at varied levels. The rule determining this has not been worked out, but it has probably nothing to do with spiral phyllotaxis or the axillary branching of stems. In the three new specimens figured here the pinnae and zwischenfiedern all appear perfectly lateral.

Certain specimens which had undergone natural decay until little remains but the cuticle, appear delicate and may give the reason why Goeppert and some others suggested that it was like *Hymenophyllum* (see Seward 1900 for references). Certain leaves of this kind are useful in that they show the mesophyll by transmitted light and also satisfactorily demonstrate the absence of hypodermal fibres. Lightly macerated specimens suggest that the trichomes had thick walls for there is a dense brown mass enclosed by the lighter brown cuticle. They appear stiff and entangle rock fragments so that the surface of the fossil looks dirty.

### *Stenopteris nana* Harris

Text-fig. 61

1947 *Stenopteris nana* Harris, p. 407, text-figs. 7, 8. (Figures repeated here.)

DIAGNOSIS (slightly emended). Leaf typically 3–4 cm. long, 2 cm. broad. Leaf base slightly expanded, petiole varying from short to a third of the leaf length, not differentiated from the rachis of the branched region, rachis usually simple but sometimes forked. About four pairs of pinnae arising at an angle of 30°–60°, usually evenly spaced; secondary branches arising alternately on the pinnae, the lower ones forked, the upper simple; no small branches arising on or near the midrib.

Petiole and midrib 1.0–2.0 mm. broad, pinnae about 1.0 mm. broad near their base, gradually narrowed above, secondary and tertiary branches tapering to about 0.8–0.5 mm.; apices obtuse, simple. Leaf substance thick; vein not distinguished on the surface but recognisable as a broad dark strand; vein slightly over half the width of the midrib and petiole, slightly under half the width of the smaller branches; lamina at the sides of the vein continuous from the branches to the petiole. Resin absent, mesophyll structure not characteristic.

Cuticle of the two sides very similar, fairly thick (2–3 $\mu$ ), regions over vein and margins showing the same structure as elsewhere. Epidermal cells isodiametric or moderately elongated, forming more or less definite longitudinal files but irregularly placed near a branch base or apex. Lateral and end walls moderately broad, distinctly marked, almost straight. Cell surface sometimes showing one or two longitudinal striae; surface of most cells flat, but occasional cells bulging and thickly cutinised in the middle to form a conspicuous hollow papilla. Papillae conical, typically 30 $\mu$  long, 20 $\mu$  broad, often smaller; rarely as much as 40 $\mu$  long. Stomata not very numerous (20–40 per sq. mm.), longitudinally orientated, some scattered, but most unevenly spaced in short longitudinal files; epidermal cells of stomatal files not distinguished in any way. Subsidiary cells nearly as large as ordinary cells, forming an elongated, rather irregular group. Surface of subsidiary cells usually thicker than that of ordinary cells; surface

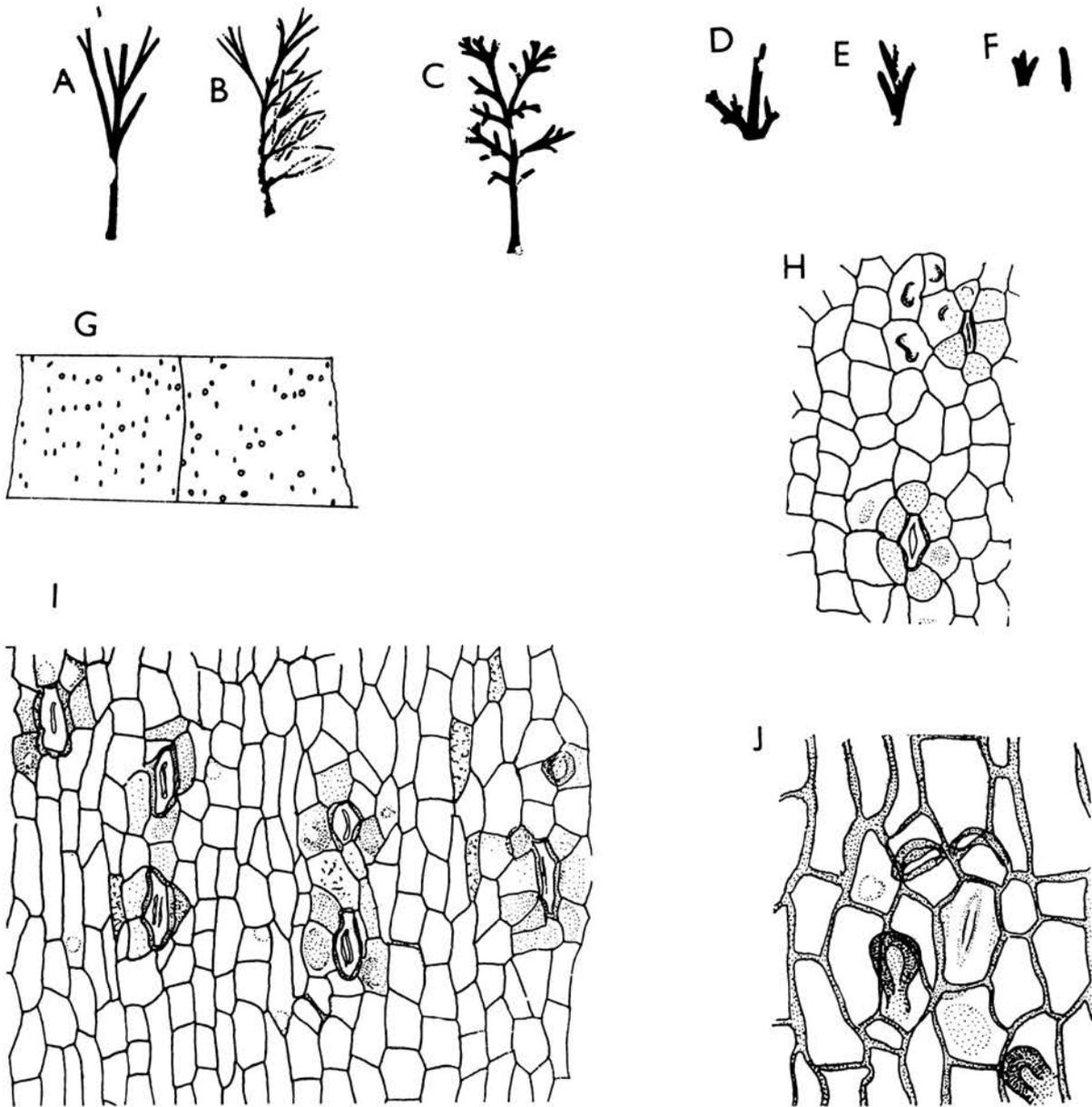


Fig. 61. *Stenopteris nana* Harris

A, specimen with broken branches, K.645, Sedgwick Museum, Cambridge,  $\times 1$ . B, holotype, K.644, Sedgwick Museum, Cambridge,  $\times 1$ . C, V.45563,  $\times 1$ . D, E, two fragments associated with the holotype,  $\times 2$ . F, isolated apices, V.27057,  $\times 2$ . G, cuticles from the middle of specimen in A,  $\times 20$ . Stomata are shown by black ovals, the larger papillae by rings. H, cuticle of holotype,  $\times 200$ . I, cuticle of specimen shown in A,  $\times 200$ . J, cuticle of holotype,  $\times 400$ .

A, B, D, E, G–J, Black's Drifted Plant Bed, Scalby Wyke. C, ?nr. Saltwick. F, Hawsker, Jack Ass Trod. All the figures, except C, are from Harris (1947, text-figs. 7, 8).

often bulging to form a small papilla. Stomatal pit shallow, elongated but usually fairly broad, and unstricted by ingrowths from the subsidiary cells. Encircling cells occasionally present. Trichomes (apart from papillate cells) absent.

HOLOTYPE. Specimen no. K.644, Sedgwick Museum, Cambridge. Figured Harris (1947, text-figs. 7 B, 8). Upper Deltaic, Black's 'Drifted Plant Bed', Scalby Wyke.

OCCURRENCE. *S. nana* is known from Black's 'Drifted Plant Bed' at Scalby Wyke (Upper Deltaic) where it may be moderately frequent. Cuticle fragments resembling it occur in the Lower Deltaic at Hawsker, Jack Ass Trod. There is a moderately good specimen in Middlesbrough Museum (named *Baiera lindleyana*) and collected by the Rev. George Lane from Carlton Quarry (Lower Deltaic).

The specimen collected by Hamshaw Thomas is imperfectly localised as 'Near Saltwick?' which would indicate Lower Deltaic. The matrix is a sandy shale which is widespread. The associated spores rather suggest an Upper Deltaic age as they include Couper's *Tsugae-pollinites mesozoicus* and *Parvisaccites enigmaticus*.

The fact that no additional cuticle fragments have been discovered is striking as nearly 600 localities now yield determinable cuticles. It is true that if an occasional specimen occurred with much *Solenites* or *Baiera furcata* it would probably be missed but even so some should be found if it were reasonably common.

DISCUSSION. Only two additional hand-specimens of *S. nana* have come to light since 1947, and one was collected many years ago by Dr. Hamshaw Thomas, the other by the Rev. G. Lane.

The hand-specimens differ considerably from one another, but their cuticles agree closely. All show the characteristic hollow conical papillae in small numbers. The new specimen collected by Thomas shows definite forking in the upper part of the rachis. It also shows the slightly expanded leaf base.

*S. nana* is a robust leaf of thick substance. The even distribution of stomata and papillae over both surfaces, across the midrib and apparently the margins also suggests that it was originally rounded in section. The vein is not shown at all by the cuticle but is sometimes visible as a central darker strand by transmitted light.

COMPARISON. *S. nana* is similar to *S. nitida* and the large, but incompletely known range of variation in both makes it difficult to compare them. *S. nana* is, however, always more coarsely branched and tends to have a much shorter petiole. *S. nitida* has a thinner cuticle and lacks conical papillae and has apparently no stomata above.

### *Stenopteris nitida* Harris

Text-fig. 62

1900 *Ruffordia Goepperti* (Dunker): Seward (in part), p. 133; reference to specimen 144, Leckenby Colln., Cambridge, only.

1944 *Stenopteris williamsonis* (Brongn.): Harris (in part), fig. 9 D and description of that specimen only. (Other figures and the rest of the description refer to true *S. williamsonis*.)

1946a *Stenopteris nitida* Harris, p. 820 text-figs. 1, 2. (Figures and description repeated here.)

DIAGNOSIS. Leaf small, petiole slender, about 3 cm. long; lamina as a whole oval, about 3-4 cm. long, 2 cm. wide. Rachis at base of lamina simple or once forked. Leaf branched pinnately two to three times. Primary branches opposite, secondary branches usually alternate,

ultimate branches almost dichotomous, apices acute. Rachis near base of lamina about 1.5 mm. broad, main branches about 1 mm. broad, gradually narrowing to ultimate pointed branches 2 mm. long, 0.5 mm. broad. Branches crowded, overlapping to a considerable extent. Lowest secondary branch on basiscopic side arising at the very base of the primary branch, or even on the main rachis. Petiole and main rachis largely composed of the vascular tissues, but with a slight wing of lamina, vascular strand narrowing above and lamina becoming broader in main branches and continuing without interruption into the final branches, where there is only a slender mid-vein which extends to the apex of the branch. Substance of lamina fairly thick, showing no characteristic mesophyll structure.

Cuticle of both sides thin (barely  $1\mu$ ) but fairly tough; stomata confined to underside, as far as is known.

Upper cuticle showing elongated cells with almost straight, moderately conspicuous walls. Cells along veins narrowed. Trichomes absent.

Lower cuticle showing stomata at a rather low concentration, about 24 per sq. mm.; stomata absent near veins. Cells along veins narrow, longitudinal walls strongly marked, end walls scarcely visible; cells between veins varied, usually about two to three times as long as broad and sometimes (especially near stomata) isodiametric. Walls rather finely marked but usually distinct, almost straight, but sometimes appearing discontinuous or with very slight sinuous folds. Cell surface on both sides obscurely and evenly mottled with small thickenings or pits.

Stomata longitudinally orientated, irregularly spaced and not forming definite rows. Guard cells thinly cutinised except round aperture, only slightly sunken, most of surface usually exposed. Subsidiary cells forming a very indefinite ring, but usually small; sometimes thicker than rest of cuticle. Lateral subsidiary cells usually overhanging margins of guard cells, but poles of guard cells probably at the surface.

Petiole slightly more thickly cutinised; cells nearly all elongated, but with a few short ones near stomata. Cell surface mottled, or with fine parallel ridges running in any direction. Stomata less frequent and more overhung by subsidiary cells than on the lamina.

**HOLOTYPE.** Specimen figured Harris (1944, text-fig. 1 D). Yorkshire Museum. Probably Middle Deltaic Gristhorpe Bed.

**OCCURRENCE.** The localities are imperfectly known but it is possible that the two specimens concerned come from the Middle Deltaic Gristhorpe Bed. *S. nitida* is not represented by any cuticle fragments from macerations but this may well be the result of my failure to recognise them.

**DISCUSSION.** This leaf has not been found in recent times and the only two specimens known are in old collections, one in the Yorkshire Museum and the other in the Leckenby Collection at Cambridge. Fragments of a third leaf occur on the same block as the Leckenby specimen. Neither specimen is fully localised, but it is possible that both are from the Gristhorpe Bed. Both have been coated with varnish which has damaged their cuticles but the associated fragments on the Leckenby specimen yielded fair preparations though in very small pieces. It is for this reason that I cannot state with confidence that no stomata at all occur on the upper side. The Yorkshire Museum specimen seems to have roused no interest, but the specimen in the Leckenby Collection at Cambridge was labelled by Nathorst as 'Possibly the young leaf of *Sphenopteris Williamsonis* or perhaps the same as *Sphenopt. Jugleri* Leck A.N.' Seward took up the *S. Jugleri* suggestion and called it *Ruffordia goepperti* which he considered

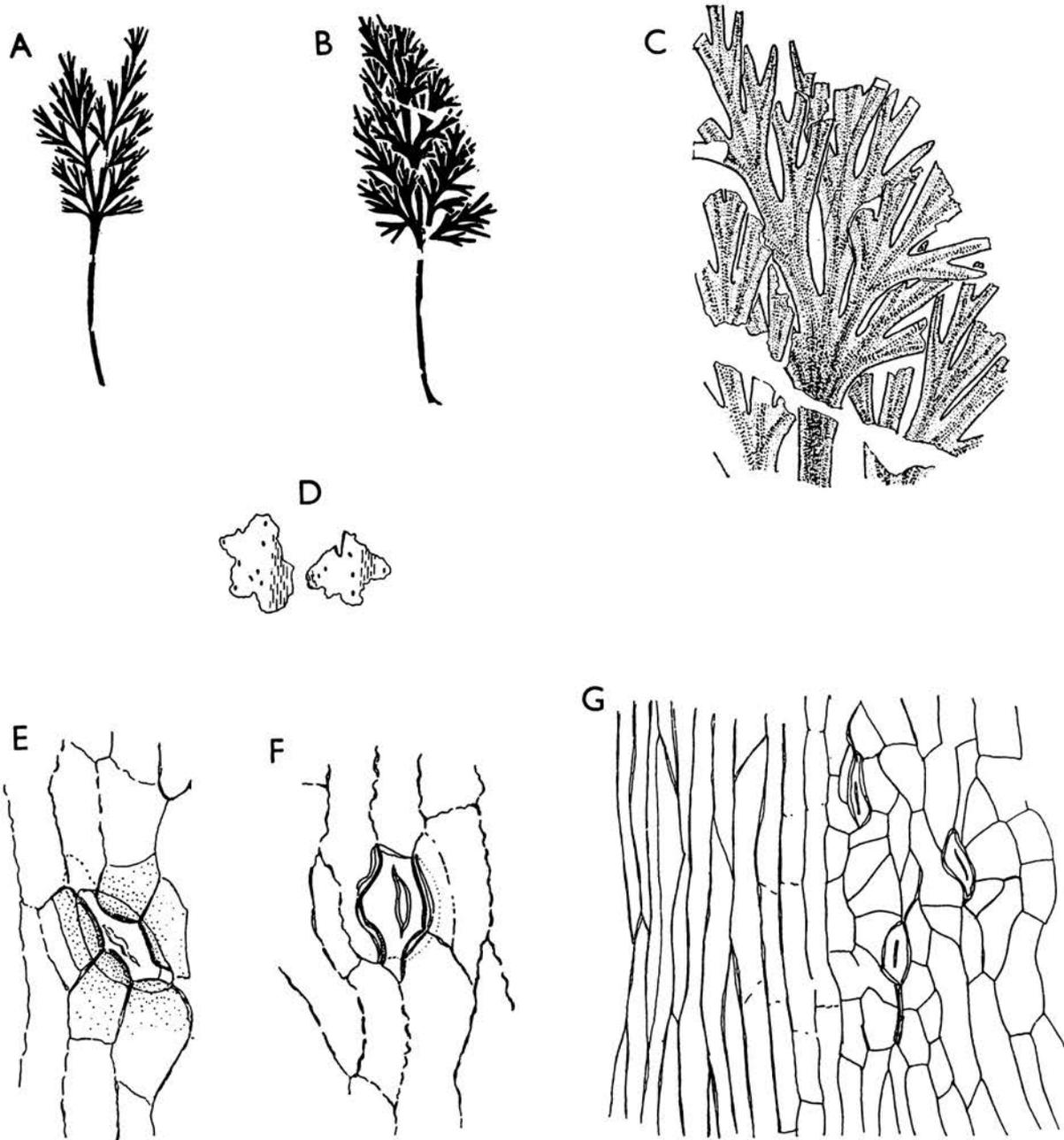


Fig. 62. *Stenopteris nitida* Harris

A, holotype, Yorkshire Museum,  $\times 1$ . B, Leckenby Colln. 144, Cambridge,  $\times 1$ . C, part of B,  $\times 4$ . D, two fragments of lower cuticle from B showing distribution and orientation of stomata in relation to veins,  $\times 20$ . E, F, two stomata from B,  $\times 400$ . G, lower cuticle from B,  $\times 200$ .

Both specimens are probably from the Gristhorpe Bed. All the figures are from Harris (1946a, text-figs. 1, 2).

the correct name. The specimen was at the same time confused with the fern which was later described as *Sphenopteris metzgerioides* Harris (1946a).

COMPARISON. *S. nitida* differs from *S. nana* in its longer petiole and much denser branching. Its cuticle is thinner and it lacks conical papillae and the stomata are limited to the under side. It is a much smaller leaf than *S. williamsonis* and is distinguished by its cuticle which in *S. nitida* is thinner, has narrower cells, no papillae and stomata on one side only. The two Greenland species *S. dinosaurensis* and *S. astartensis* are leaves of very different form and both have much thicker cuticles. *S. nitida* is at once distinguished, even in fragments, from *Sphenopteris metzgerioides* and indeed all Yorkshire ferns by possessing a cuticle.

## Unnamed Pteridosperms or Cycads

Many cuticle fragments obtained by macerating Yorkshire rocks in bulk more or less resemble the species of *Stenopteris*, *Pachypteris* and *Ctenozamites* described here but are distinguished by some difference which suggests that they belong to an undescribed species. The number of these species is considerable, between ten and twenty, but some of them may prove to be Ginkgoalean, for cuticle fragments of *Stenopteris* are often very like those of some Ginkgoales. They are mentioned as a pointer to the fact that the Yorkshire flora is far from exhausted.

It is interesting that no leaf or cuticle fragment is met in Yorkshire which resembles one of the typical *Thinnfeldia* species of the Franconian Lower Lias.

### *Cycad-like reproductive organs*

Genus ANDROSTROBUS Schimper 1872 : 199

Schimper's diagnosis is as follows:

'Amenta cycadacea antherifera cylindrica, e squamis imbricatis latere postico anthera sessiles ferentibus efformata.'

This diagnosis is satisfactory but for the word 'cycadacea' which I presume means 'Cycadaceous' rather than 'like that of a cycad'. The objection is to a word in a diagnosis which insists that a fossil belongs to a certain family, for classification is not a diagnostic character but an inference. The case for supposing that the species described here do belong to the Cycadaceae is very strong, stronger indeed than for the type species. It is not only true that the Cycadaceae alone have sporophylls constructed in this way, but we have some additional points of agreement. The pollen sacs form small sorus-like groups and their dehiscence lines radiate from the centre of the group. Their rather thick walls show similar cells and similar internal and external cuticles. The pollen grains are oval and monosulcate. The epidermis of the sporophyll has a cuticle showing straight-walled cells and haplocheilic stomata, like those of Cycads. It is rather interesting that two species *A. manis* and *A. wonnacotti* probably differ from modern Cycad cones in being sessile and I have argued that they may have been produced rather

differently, that is hanging on the branches of some kind of tree rather than erect among the leaves on a palm-like trunk. We have no reason to suppose that other species such as *A. prisma* were sessile and it could well be that differences of generic value will one day be recognised, but no such differences are yet proved.

Besides the type species, *A. zamioides* Schimper, from the Bathonian of France, which was renamed *A. baldwini* by Saporta (1875), there are the following species in which there is at least some reason to suppose that they truly resemble Cycad male cones:

- A. cycadiformis* Roselt 1960 (Keuper, Germany).
- A. guerangeri* (Brongn.) Saporta 1875 (Cretaceous, France).
- A. jamnitschenkoi* Stanislavski 1957 (Jurassic, Russia).

In addition there are the following which have been described as Cycad male cones but the evidence is less clear:

- Androstrobus siberica* Heer 1877 (Jurassic, Siberia)
- Androstrobus borealis* Nathorst 1878 (Rhaetic, Sweden)
- Zamites familiaris* Corda 1846 (Lower Cretaceous, Bohemia)
- Fricia nobilis* Velenovsky 1885 (Lower Cretaceous, Bohemia)
- Androstrobus nathorsti* Seward 1895 (Lower Cretaceous, England).

The following has been removed from *Androstrobus*:

- A. scotti* Nathorst 1902 to *Lycostrobus scotti* (Nathorst 1908).

### *Androstrobus manis* Harris

Pl. 6, figs. 1, 4, 12; Text-fig. 63 A-D, J-L

The specimens are all from Yorkshire.

- 1941a *Androstrobus manis* Harris, p. 76, pl. 5, figs. 6-9; text-figs. 1, 3 C, D, E. (General description.)
- 1958 *Androstrobus manis* Harris: Couper, p. 122, pl. 26, figs. 15, 16. (Pollen.)
- 1960 *Androstrobus manis* Harris: Thomas & Harris, p. 141, pl. 1, fig. 1. (Pollen in micropyle of *Beania*.)

EMENDED DIAGNOSIS. Cone 2 cm. broad, length at least 5 cm., shape cylindrical in middle region, apex rounded, base tapered and then rounded. Stalk absent. Substance crumbly, resin bodies absent. Cone axis up to 3 mm. thick. Outer edges of microsporophylls imbricate and considerably overlapping scale in front. In middle region, microsporophylls short and broad, length barely 1 cm., width 1.0-1.5 cm. Distal exposed part smooth, overlapping the scales above, roughly rhomboidal, about twice as broad as high; upper margin of thin substance gently rounded but produced to a slight median point. Upper edge becoming scarious. Upper (protected) surface of microsporophyll marked with short, longitudinal ridges, lower surface covered with sporangia. Sporangia rounded in end view, about 1.2 mm. long  $\times$  0.7 mm. broad. Pollen grains monosulcate, oval, typically  $36 \times 26\mu$  (extremes of length  $40\mu$  and  $26\mu$ ); wall almost perfectly smooth but appearing faintly and very finely mottled.

Epidermal cells of distal part of microsporophyll rather thinly cutinised. Stomata occurring in middle region and just below the middle, absent elsewhere. Epidermal cells roughly isodiametric or slightly elongated, outlines distinct, straight or very slightly sinuous, surface

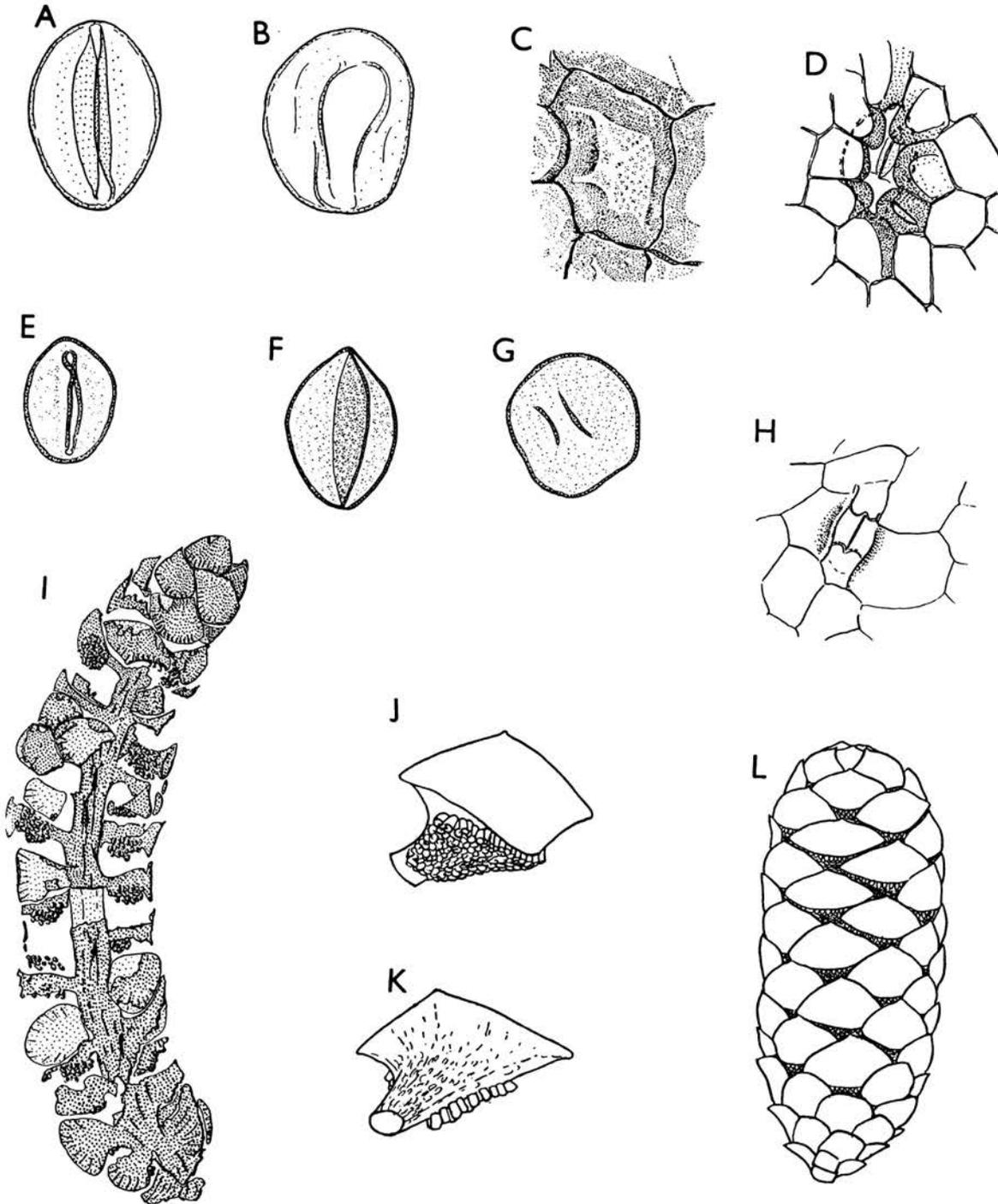


Fig. 63. *Androstrobus manis* Harris, *A. wonnacotti* Harris

A, B, pollen grains of *A. manis*, V.25899d,  $\times 800$ . C, *A. manis*, epidermal cell from one of the lower scales of the holotype, V.25900c,  $\times 800$ . D, typical stoma of sporophyll of *A. manis*, V.25899d,  $\times 400$ . E-G, pollen grains of *A. wonnacotti*, V.25850a,  $\times 800$ . H, stoma of sporophyll of *A. wonnacotti*, V.25850b,  $\times 400$ . I, *A. wonnacotti*, holotype, V.25850,  $\times 2$ . J, K, *A. manis*, restorations of sporophyll,  $\times$  about 2. L, *A. manis*, restoration of cone, about nat. size.

The specimens are all from the Gristhorpe Bed. All the figures are from Harris (1941a) by permission of the Royal Society of London.

faintly mottled with thicker and thinner patches. Trichomes absent apart from bulging cells near the top margin. Stomata distinctly sunken. Guard cells very thinly cutinised, at the bottom of a small pit, surrounded by an elongated, irregular or rounded group of subsidiary cells. Inner edge of subsidiary cells thickened and somewhat overhanging the stomatal pit or forming a definite hollow papilla which is directed inwards. Trichomes absent except possibly near the upper edge where occasional bulging cells occur. Inner surfaces of microsporophylls more thinly cutinised, showing elongated straight-walled epidermal cells.

Lower microsporophylls of cone smaller than those of middle region; basal scale leaves sterile, small, obtusely pointed; epidermal cells similar to those of microsporophyll but with a greater tendency for the cell surface to show a broad thickened border parallel with the cell outline.

HOLOTYPE. V.25900, figured Harris (1941a, pl. 5, fig. 9).

DESCRIPTION. No additional specimens have been found beyond the original seven collected by F. M. Wonnacott from the Gristhorpe Bed and described by Harris (1941a). A certain amount of information then given in the description has been included in the diagnosis to help to distinguish *A. manis* from other species; a few descriptive points which appear to have no general significance are here omitted. The name was suggested by the rather similar looking scales of *Manis* the pangolin.

DISCUSSION. The reasons for attributing this male cone to the same plant as *Nilssonia compta* and *Beania gracilis* still stand. These depend on close association and agreement in structure and it is convenient to discuss the structural links at one point, namely under *Beania gracilis*. It may here be noted that all seven specimens of *A. manis* are associated with *Nilssonia compta* but no other leaf of very similar structure.

### *Androstrobus wonnacotti* Harris

Pl. 5, fig. 8; Text-fig. 63 E-I

The specimens are all from Yorkshire.

- 1941a *Androstrobus wonnacotti* Harris, p. 79, pl. 5, figs. 11, 15; text-fig. 2. (General description.)  
 1958 *Androstrobus wonnacotti* Harris: Couper, p. 122, pl. 26, figs. 17, 18. (Pollen and comparison with that of Recent Cycads, and with dispersed grain *Monosulcites minimus* Cookson.)  
 1960 *Androstrobus wonnacotti* Harris: Thomas & Harris, p. 144, pl. 2, figs. 8-14. (Further specimens and pollen grains, attribution to *Nilssonia tenuinervis* and *Beania mamayi*.)  
 1961 *Androstrobus wonnacotti* Harris: Harris, p. 321, text-fig. 2. (Restoration of a stem bearing *N. tenuinervis* and *A. wonnacotti*.)

EMENDED DIAGNOSIS. Ripe cone 3.5-7.5 cm. long, about 1 cm. wide, shape cylindrical with rounded apex and base, not tapering below. Stalk absent. Substance of cone thick and fibrous but crumbly, containing frequent round bodies of resin 100 $\mu$  wide. Microsporophyll nearly 5 mm. long, wedge-shaped, expanding from a narrow base to an expanded outer part nearly 5 mm. broad. Distal exposed region rhomboidal, smooth apart from slight radiating striae, height about two thirds of width, upper margin of exposed surface thick. Microsporophylls in ripe cone loosely arranged, scarcely overlapping. Cone axis about 2 mm. thick, apparently flexible. Under surface of microsporophyll covered with sporangia, sporangia round in end view, about 0.5 mm. broad, pollen grains monosulcate, oval, typically 29  $\times$  21 $\mu$ , occasionally rather smaller. Wall smooth, or very obscurely mottled.

Epidermis thinly cutinised on exposed part. Epidermal cells isodiametric with finely marked but distinct outlines, surface flat, finely mottled or striated. Stomata only slightly sunken in a very shallow pit, subsidiary cell group elongated, subsidiary cells scarcely specialised. Guard cell aperture nearly  $20\mu$  long.

HOLOTYPE. V.25850, figured Harris (1941a, pl. 5, figs. 11, 15; text-fig. 2 A).

OCCURRENCE.

Middle Deltaic Gristhorpe Series:

Cloughton *Solenites* Bed.  
Gristhorpe Bed.

Lower Deltaic:

Hasty Bank.  
Whitby *N. tenuinervis* Bed.

DESCRIPTION AND DISCUSSION. The original specimen of *A. wonnacotti* found by F. M. Wonnacott has been supplemented by about a dozen others, some figured by Thomas & Harris (1960). Its attribution was at first uncertain, but there is now a strong case for attributing it to the same plant as the leaf *Nilssonia tenuinervis*, the female cone *Beania mamayi* and the bud scale *Deltolepis calyptra*; the evidence is discussed under *Beania mamayi*. The absence of a peduncle from any of the specimens showing the cone base is an interesting difference from the male cone of a modern Cycad and this fact, and the apparent flexibility of this cone was used in a restoration (Harris 1961) which shows the cone as pendulous from a moderately slender shoot.

*Androstrobus prisma* Thomas & Harris

Pl. 1, fig. 21; Pl. 6, figs. 5, 8

1960 *Androstrobus prisma* Thomas & Harris, p. 148, pl. 3, figs. 18-21; pl. 4, figs. 23, 24, 26, 27; text-fig. 2. (Cone, cuticle, pollen; attribution to *Pseudoctenis lanei*.)

DIAGNOSIS (slightly altered from Thomas & Harris 1960). Cone large, massive, compact. Microsporophylls rhomboidal in end view, about 18 mm. wide, 6-11 mm. high; forming oblique rows inclined at  $30^{\circ}$ - $40^{\circ}$  to the horizontal. Outer surface of microsporophyll convex, upper edge slightly depressed. Microsporophyll wedge-shaped in surface view, outer edge rounded, lateral margins approaching at  $45^{\circ}$  to one another but basal parts unknown. Outermost 5 mm. sterile but inner parts thickly covered with microsporangia; microsporangia in groups of 2-3 with apertures pointing inwards; width of microsporangia about 0.4 mm., outer ones short but inner ones up to 1.5 mm. long. Shape of microsporangium a prism and usually 4-6 angular but sometimes rounded, sides parallel; line of dehiscence conspicuous, running from the middle of the end across the surface and down the whole length. Surface of microsporangia glossy, but surface of sterile parts of microsporophyll dull with slightly projecting cells.

Cuticle of exposed part moderately thick, showing isodiametric or slightly elongated cells with broad but not very prominent lateral walls. Lateral walls straight, uninterrupted. Surface of cell often showing a broad thickening along each side, leaving a thin, median strip, or showing two or three longitudinal ridges and thin strips. Stomata moderately frequent,

scattered; variably orientated but often longitudinal. Guard cells sunken in a round, oval or rectangular pit; sides of pit strongly thickened but not raised. Subsidiary cells of the same size as other epidermal cells, often 4 lateral and 2 terminal. Lateral subsidiary cells often somewhat thickened near the pit, but surface flat; terminal subsidiary cells unthickened, flat. Encircling cells absent. Inner parts of scale with thinner cuticle; epidermal cells elongated, with thinner but more distinct walls; surface not ornamented. Stomata absent. Microsporangia with thin but coherent external cuticle, showing elongated cells with finely marked but distinct walls. Surface flat and not sculptured. Inner cuticle (next pollen) also thin; granular, showing broad but ill-defined outlines of cells, often of two sets, one rectangular and the other isodiametric polygons. Pollen grains very uniform, round; about  $35\mu$  wide, surface minutely granular with granules  $1\mu$  apart. Wall  $1\mu$  thick, but sometimes showing an ill-defined thinner area on one side. Grain probably originally almost spherical.

HOLOTYPE. V.42380, figured by Thomas & Harris (1960, pl. 3, fig. 21; text-fig. 2).

OCCURRENCE. Lower Deltaic: Roseberry Topping, Hasty Bank and Marske Quarry.

DESCRIPTION. There are two large specimens, the holotype (from Hasty Bank) a coaly compression of the cone surface about 7 cm. long and 8 cm. wide, which perhaps represents a sheet of microsporophylls separated from the cone axis. There are a few detached microsporophylls with the holotype and others from Roseberry Topping which are compressed to show the surface of the protected inner part. Then there is an almost uncompressed cast, 5 cm. wide, of the surface of the cone in ironstone from Marske. This may show nearly the full width. The specimens do not indicate the full length of the cone, nor do we know the shape of its apex and base, nor whether it was stalked.

DISCUSSION. *A. prisma* stands apart from *A. manis* and *A. wonnacotti*; it is more massive, more thickly cutinised and its pollen grains are more nearly round.

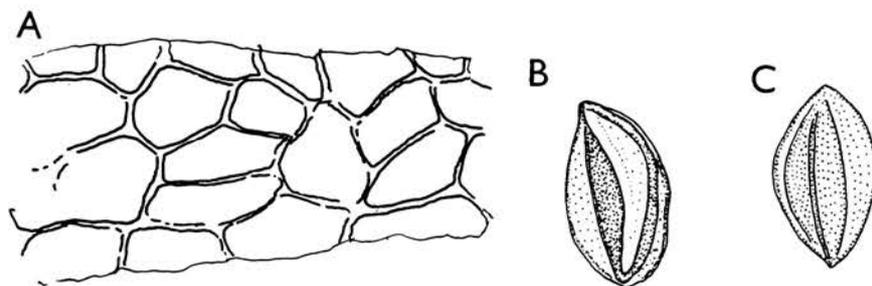
The evidence strongly suggests it belongs to the same plant as the leaf *Pseudoctenis lanei* (see Thomas & Harris 1960 : 151). This leaf is not at all a common one but it does occur with some frequency in all three localities and at Hasty Bank and Roseberry at least it is present on the same blocks of rock as the cone fragments. The small Marske block shows no other fossils. Other Cycad-like leaves include various Lower Deltaic *Nilssonia* species, *Ctenozamites cycadea*, *Ctenis kaneharai* and *Stenopteris williamsonis* none of which shows any very specially close association, nor specially close similarity in structure. There is marked agreement between the cuticle of the exposed part of the microsporophyll and of the leaf; it is intermediate in character between the upper and lower leaf cuticles. The epidermal cells are similar in size and shape, with broad rather inconspicuously marked walls and the cell surface shows two or three thick areas separated by thin strips. The stomata which are about half as numerous as on the leaf agree in being scattered, mostly longitudinally orientated and the guard cells are at the bottom of a round or oval pit with heavily cutinised sides but less cutinised ends. There are usually unspecialised terminal subsidiary cells and two pairs of lateral ones which are thickened near the pit. Their surface is nearly flat.

No associated fossil has a particularly similar epidermis, and the most similar occurring in different localities is perhaps *Pseudoctenis herriesi*, which is, however, distinctly different. If the cone and leaf do indeed belong to one plant, they are both very like the corresponding organs of such Recent Cycads as *Zamia* or *Encephalartos* and it may well be that the whole plant was closely similar to these genera.

*Androstrobus szei* sp. nov.

Pl. 6, figs. 9, 11, 13; Text-fig. 64 A-C

**DIAGNOSIS.** Cone nearly 5 cm. wide, cylindrical (length unknown but exceeding 10 cm., apex and base unknown). Sporophylls attached spirally, parastichies possibly 5+8. Free parts imbricate, each overlapping 2 sporophylls in front, free edges rather thin, straight, apex forming an angle of about  $120^\circ$ . Substance of microsporophyll thick, containing numerous fibres, individual fibres mostly separate, ends pointed, width about  $70\mu$ ; resin bodies absent. Sporangia entirely concealed by ends of microsporophylls, oval, about 0.6 mm. long. Pollen masses from undehisced sporangia  $150\mu \times 50-60\mu$ . Cuticle of exposed part of microsporophyll moderately thick ( $1-2\mu$  in folds) showing polygonal cells about  $35\mu$  wide. Lateral walls straight, fairly broad, cell surface flat. Cuticle of inner parts of microsporophyll delicate, inner cuticle of pollen sac granular. Pollen grains oval, monosulcate, walls thin, smooth; typical size  $26-28\mu \times 15-20\mu$  but often shrivelled and smaller. Largest grain seen  $36 \times 23\mu$ .

Fig. 64. *Androstrobus szei* sp. nov.

A, fragment of cuticle of holotype, V.45487,  $\times 400$ . B, C, typical views of pollen grains, V.45487,  $\times 800$ . Gristhorpe Bed.

**HOLOTYPE.** The only specimen, V.45487. Middle Deltaic, Gristhorpe Bed.

**DESCRIPTION.** The specimen was collected by Dr. Sze while a member of an international Botanical excursion. Dr. Sze generously gave it to Hamshaw Thomas who eventually passed it to me for description. The cone has been named after him. The preservation is not very satisfactory. Although the general matrix is the soft Gristhorpe shale, just around the cone the matrix is hard and lumpy, apparently forming a kind of concretion. A good deal of matrix has entered the substance of the cone, and it looks as if the cone had rotted and some of the epidermis had disappeared and mud had penetrated the soft tissues between the fibres.

Several attempts were made to prepare cuticles but the results were poor, for although the cuticle is not particularly thin it broke into very tiny fragments, so small indeed that they had to be treated like dispersed spores. Every preparation gave plenty of pollen which was adhering to the inner parts of the microsporophylls and to opened pollen sacs. Some thousands of these grains must have been seen and many were well preserved. All but a few were similar to one another. The macerations also yielded a few small cylindrical masses of pollen representing unopened sporangia. A few sporangia were seen on the surface of the fossil but I was unsuccessful in my effort to expose others by dissecting away a scale, as the deeper part of the fossil just forms a thick solid layer of crumbly coal. The intact pollen masses are a good deal smaller than the sporangia exposed on the surface and may well be from small and poorly formed ones.

The most clearly seen structures are the fibres which are conspicuous at points where the epidermis has disappeared, that is rather widely; and their imprints are seen on a displaced microsporophyll lying to the left of the cone.

It is likely enough that if this cone could be linked with its leaf the result would be of considerable taxonomic value but the vital evidence which the stomata should provide is lacking. Several stoma-like patterns were seen, but none was recognised as a stoma with any confidence and all may have been blemishes caused by bad preservation. It looks as though the cuticle were potentially good but that this specimen has been unfortunate in preservation.

ATTRIBUTION. The evidence is not sufficient to suggest the species of leaf corresponding to this cone. In the Gristhorpe Bed there are the following plants of presumed or possible Cycad affinity: *Ctenis sulcicaulis* (locally common), *Nilssonia compta* (abundant), *N. tenuicaulis* (rare), *N. tenuinervis* (abundant), *Pseudoctenis lanei* (rare and local), *Ctenozamites leckenbyi* (local), *Stenopteris williamsonis* (local). In addition the two rare species *Ctenis reedi* and *Stenopteris nitida* were probably obtained from this bed.

If previously suggested attributions are right, *Nilssonia compta*, *N. tenuinervis* and *Pseudoctenis lanei* have different male cones and are thus not involved. This directs attention to *Ctenis sulcicaulis* as the commonest remaining leaf. Unfortunately I do not know if it occurs in the same region of the Gristhorpe Bed as *A. szei*; the only species on this block are *N. tenuinervis* and a seed of *Caytonia nathorsti*. We have only the epidermal cells and fibres of *A. szei* to compare. The epidermal cells do look rather like those of *Ctenis* but there is nothing specific in their agreement. The fibres are just like those seen in suitably preserved *Ctenis sulcicaulis* leaves but they are of a kind which are seen also in the organs of *Nilssonia* species and may be widespread in Cycads. There is no particular reason to link this cone with any of the other leaves mentioned above. The most that can be said is that it is worth bearing the possibility in mind that it may belong to *Ctenis* when doing further work.

### *Androstrobus* sp. A

Pl. 6, fig. 2

Isolated sporophyll fragments; width about 8 mm., length about 15 mm., distal part sterile conspicuously marked with longitudinal striae. Sporangia oval in surface view, about  $1.2 \times 0.8$  mm. Pollen grains monosulcate, oval, smooth, about  $30 \times 24 \mu$ . (Cuticle of microsporophyll not satisfactorily known.)

The specimens are a few sporophyll fragments collected by Dr. Hamshaw Thomas from Hasty Bank and from Little Roseberry close to Roseberry Topping. They seem nearest *A. szei* with which they agree in the fibrous texture of the sterile outer part of the sporophyll but they differ in having larger sporangia.

There is no structural evidence for suggesting to what species of leaf these microsporophylls should be linked.

### Genus BEANIA Carruthers 1869: 98

EMENDED DIAGNOSIS. Female cone, axis bearing megasporophylls in a loose spiral; sporophyll consisting of a stalk expanding into a broad head; head bearing two inward pointing seeds at the sides of the stalk. Seed sessile, orthotropous, integument thickly cutinised enclosing

a flesh and a stone; nucellus only free in upper third of seed, forming a beak projecting into the micropyle. Megaspore membrane cutinised.

This diagnosis chiefly adds some characters of the seeds to Carruthers' diagnosis.

TYPE SPECIES. *Beania gracilis* Carruthers.

The validity of the generic name *Beania* is not quite clear; possibly the genus *Sphaereda* has priority, though Carruthers' account was the first satisfactory one.

Lindley & Hutton's pl. 159, fig. 1, which they called *Sphaereda paradoxa* is possibly a cone of what I called *Beania mamayi* but I cannot feel sure and according to Seward (1900 : 273) the specimen is lost. Their fig. 2 which is different is no doubt what we call *Beania gracilis*. Endlicher's genus *Zamiostrobus* is also earlier than *Beania* but unsuitable. In 1836 he gave the name *Zamiostrobus* to Lindley & Hutton's '*Zamia macrocephala*' (1835, pl. 125) a large petrified cone, which as Seward (1917 : 503) says, is doubtless coniferous. Endlicher's diagnosis, however, refers to a *Zamia* female cone rather than to characters observed in the fossil and since the *Zamia* cone is like *Beania*, his diagnosis is close to that of *Beania*.

*Stenorachis* Saporta (1875) includes *S. scanicus* Nathorst which Nathorst himself thought belonged to *Nilssonia* and later (1909) likened to *Beania*.

*Beania* proves to be a genus in which it is hard to distinguish the species, even when there is information about cuticles. The difficulty is mainly caused by the strong tendency for the cones—at least in *B. gracilis* which is the best known, to drop off at early stages of growth, so that there is a graduated series from very small to full sized cones. It is difficult to distinguish between these small aborted cones and what may be full grown ones of another species, for *Beania* cuticles are often poorly preserved and it is seldom possible to prove that the ovules had reached the pollination stage by finding pollen in them.

Isolated *Beania* seeds are not recognisable generically unless one can identify them specifically with seeds of the same sort still attached. Their cuticles conform to a common Gymnosperm type, shared by the living Cycads and *Ginkgo* as well as some Conifers; this type has been given the name *Allicospermum* Harris (1935). *Allicospermum* seeds are frequent in Yorkshire and are of a good many species and although sometimes strikingly associated with *Nilssonia* are not to be referred to *Beania*. Thus there is the unsatisfactory position that there is in Yorkshire a series of specimens of *Beania* and many seeds which may belong to *Beania* but which I am not prepared to describe under a specific name.

Attribution of *Beania* to *Nilssonia*. The recognition of *Beania* as the female cone of *Nilssonia* species was the result of a long series of small steps made by different workers, but the first few were made by Nathorst. Nathorst (1902) noted the association of certain seeds with *Nilssonia pterophylloides* (but he then thought them microsporophylls and called them *Antherangiopsis rediviva*) and at the same time he suggested that *Stenorachis scanicus*, a *Beania*-like cone might belong to *Nilssonia*. In 1909 he investigated the bodies with *N. pterophylloides* and showed they were seeds and he made the further suggestion that *Beania carruthersi* was the ripe cone of *Nilssonia*; but apart from the presence of round resin bodies in both leaf and seed, he gave no structural evidence. In the same paper he noted the association of bodies like his *Nilssonia* seeds with *Nilssonia polymorpha* and *N. brevis* in different Swedish localities. Other workers called attention to similar association: Thomas (1911) in Kamenka, Russia; Krasser (1913, 1920) in Sardinia; Harris (1932) in East Greenland; Sahni & Rao (1933) in India; Carpentier (1947) in France; Stanislavski (1957) in Russia. Unfortunately,

however, some of these seed-like bodies have not been studied in detail and we cannot be sure they are all of the same nature and the one described by Thomas which has numerous stomata seems different.

Harris (1932) found the '*Nilssonia*' seeds attached to *Beania* megasporophylls. Long before this, however, Thomas had realised that the seeds of *Beania gracilis* were like Nathorst's *Nilssonia* seeds and he noted the similarity between the stomata of *Nilssonia* and *Beania gracilis*. He seems not to have published this but Seward (1917 : 503) mentioned it, though he inclined to regard *Beania* as Ginkgoalean. In about 1924 Thomas must have told me his views, so I had them in mind when working in Greenland and later on the Yorkshire flora. Harris (1941a) published an account of the structure of *Beania gracilis* and gave a full statement of the agreement between the epidermis of the sporophyll and the leaf *Nilssonia compta* (together with the male cone and scale leaf). Later Thomas & Harris (1960) noted the presence of pollen grains like those of *A. manis* inside the nucellus of the seed of *B. gracilis*. They also furnished evidence that *Beania mamayi* belongs to the series *Nilssonia tenuinervis* and *Androstrobos wonnaccotti*. *B. mamayi* has two localities, both rich in *N. tenuinervis* and specific points of agreement were noted in the structure of their cuticles.

Several authors have described under the name *Beania*, isolated seeds more or less like those which Nathorst called *Nilssonia* seeds. The identifications may be correct but the name *Beania* should be restricted to the cone, and isolated seeds should only be described under this name when they can be specifically identified with seeds still attached to *Beania* cones. *Beania* seeds have no general distinguishing character which would separate them from isolated seeds of a *Ginkgo*, for example.

### *Beania gracilis* Carruthers

Pl. 6, figs. 3, 6, 10; Text-fig. 65 A-C, F, G

The following specimens are all from Yorkshire :

- 1829 'Winged seed', Phillips, pl. 8, fig. 2. (Sketch of seed.)
- 1835 *Sphaereda paradoxa* Lindley & Hutton (in part), pl. 159, fig. 2 only. (Williamson's description on p. 19 which according to Carruthers (1869) refers to this specimen alone.)
- 1869 *Beania gracilis* Carruthers, p. 97, pl. 4, fig. 1. (Good specimen.)
- 1875 *Beania gracilis* Carruthers: Saporta, p. 63, pl. 77, fig. 3. (Copy of Carruthers' figure.)
- 1875 *Sphaereda paradoxa* L. & H.: Phillips, p. 233, pl. 8, fig. 2; text-fig. 68. ('Winged seed' also said to belong to it. Text-fig. 68 is a sketch of Carruthers' specimen but there is no mention of Carruthers' work.)
- 1900 *Beania gracilis* Carruthers: Seward, p. 272, pl. 9, fig. 11. (Discussion, Carruthers' holotype redrawn, identification of Phillips' 'winged seed'.)
- 1917 *Beania gracilis* Carruthers: Seward, p. 502, text-fig. 586. (Discussion; figure from Seward 1900.)
- 1941a *Beania gracilis* Carruthers: Harris, p. 83. (Redescription, cuticles of seed and sporophyll, reference to *Nilssonia compta*.)
- 1960 *Beania gracilis* Carruthers: Thomas & Harris, p. 140, pl. 1, figs. 1-7; pl. 3, fig. 16. (Pollen in nucellus, discussion of young cones.)

Numerous authors have referred to *Beania gracilis* in discussing the fossil Cycads or sometimes in discussing the Ginkgoales.

EMENDED DIAGNOSIS. Cone when ripe at least 11 cm. long (base not known), width about 6 cm. but tapering to the apex. Axis about 5 mm. wide, strongly striated, appearing fibrous and flexible. Sporophylls borne at right angles in a very loose spiral, stalk 1.5 cm. wide, longitudinally striated; head broadly rhomboidal or oval, about 18 mm. wide, 6 mm. high, stalk attached

near basal angle. Ripe seed nearly round but hilum oval, typically 16 mm. long  $\times$  13 mm. broad, but seeds at cone apex smaller, flesh about 0.25 mm. thick usually without large resin bodies, stone 0.25 mm. thick. Cuticle of outside of megasporophyll head showing epidermal cells with clearly marked walls, surface wall sometimes showing a broad border round side walls. Stomata sunken in a pit, usually surrounded and overhung by six or more subsidiary cells; subsidiary cells often forming a cone with an apical hole, inner edges strongly thickened. Unicellular trichome bases present near upper margin of sporophyll. Seed integument thickly cutinised, cells isodiametric, lateral walls very prominent, surface wall showing a broad, thick border to the lateral walls.

LECTOTYPE. Specimen figured by Lindley & Hutton (1835, pl. 159, fig. 2).

DESCRIPTION. (Condensed from the accounts of Harris (1941a) and of Thomas & Harris 1960). *Beania gracilis* is moderately frequent in the Gristhorpe Bed as cone fragments, while identifiable isolated seeds are common. Half the specimens are small and range from examples with sporophyll stalks only 5 mm. long and seeds 3 mm. wide upwards to the full size mentioned in the diagnosis. The series is interpreted as one which illustrates stages of development and even the smallest cones are loosely constructed, though they look less fibrous and their cuticles are very thin. Cones where the sporophylls are 20 mm. or more long are ripe enough to have shed most of their seeds and loose seeds are 10–15 mm. wide, while seeds smaller than this are still attached. Pollen was found in certain ovules of 10 mm. or more wide and in one of these the pollen grains had penetrated deeply into the nucellus and had there burst widely. Presumably they had germinated in the Cycad manner in a Cycad-like pollen chamber.

#### Attribution to the same plant as

#### *Nilssonia compta*, *Androstrobus manis*, *Deltolepis crepidota*

The evidence has already been given by Harris (1941a, 1942). It consists in their striking association (the Gristhorpe Bed is the main locality for the leaf and the only one for the other organs), and in the agreement of their epidermal cells and stomata.

Such specimens of *Beania gracilis* as I have collected were certainly associated with *N. compta* and Hamshaw Thomas, who collected much more systematically in the Gristhorpe Bed, tells me that all of the numerous specimens he found were associated with it. So too, most of the blocks in the Wonnacott collection with *B. gracilis* have *N. compta* too. As Thomas has said, the species of the Gristhorpe Bed are restricted horizontally.

The epidermal cells on the exposed side of the sporophyll have rather thin straight walls flanked by thickened borders and a flat, finely mottled surface (periclinal) wall. Such cells are seen on the upper epidermis of the leaf, on the scale leaf *Deltolepis crepidota* and on the microsporophylls and basal scales of *Androstrobus manis*. They are not quite confined to this set of organs, for *Sagenopteris phillipsi* has similar cells, but no other common leaf in the Gristhorpe Bed has such cells and *S. phillipsi* has very different stomata. Then the stomata of this series of organs are rather characteristic. The guard cells are sunken and surrounded by a group of subsidiary cells forming a little cone with a truncated and open top. Other kinds of stomata occur, including irregular ones, but this is the most noteworthy. Certain other species, for instance *Nilssonia syllis*, have rather similar stomata but none of these occurs in the Gristhorpe Bed. *Ginkgo digitata* has less similar stomata for in it the subsidiary cells have separate papillae.

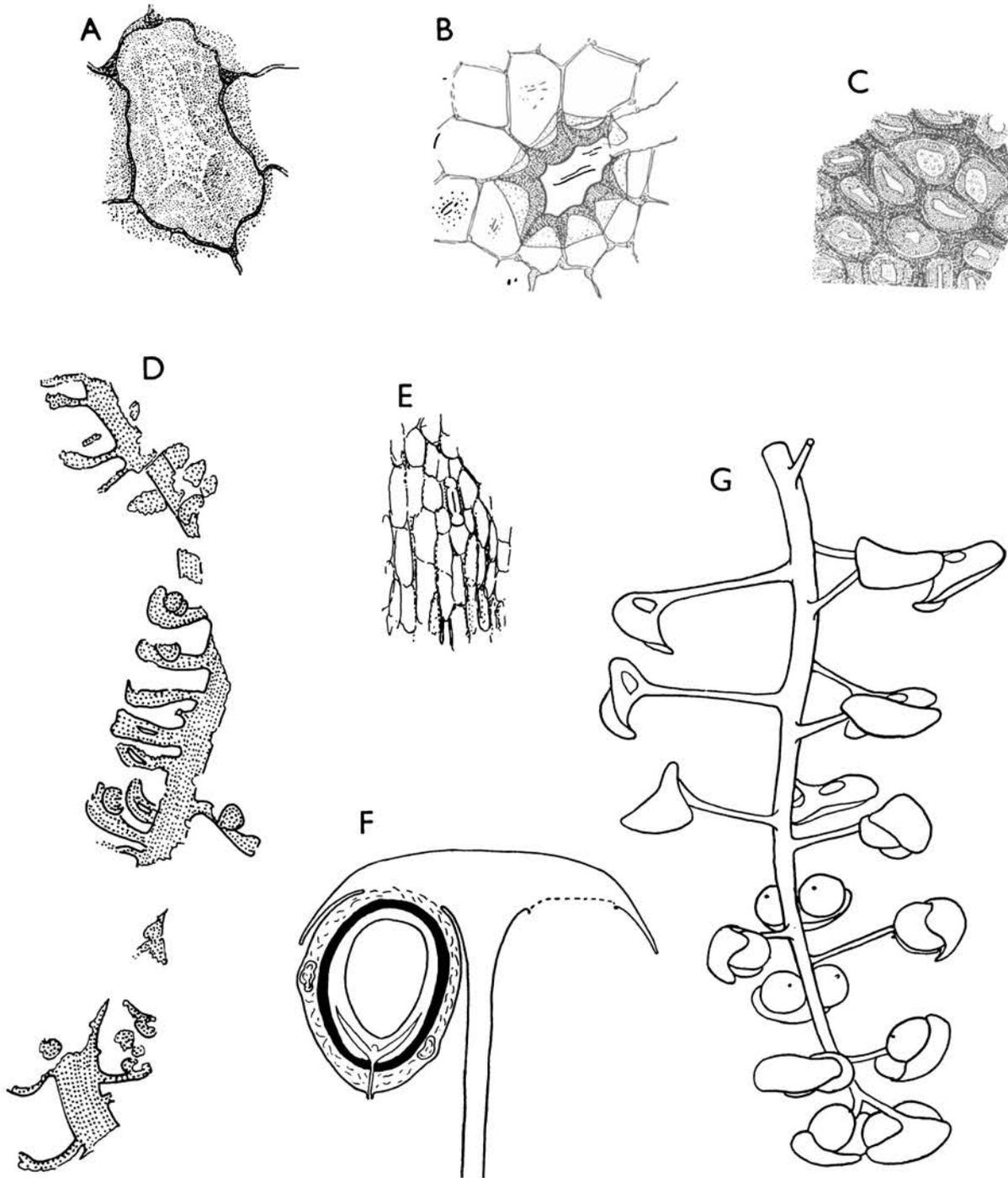


Fig. 65. *Beania gracilis* Carruthers, *B. mamayi* Thomas & Harris

A, *B. gracilis*, cell from outer surface of megasporophyll, V.26780,  $\times 800$ . B, *B. gracilis*, stoma from outer surface of megasporophyll (torn), V.23929a,  $\times 400$ . C, *B. gracilis*, outer cuticle of integument of ripe seed, V.26778,  $\times 400$ . D, *B. mamayi*, cone; the breaks were caused in collecting, V.41827,  $\times 1$ . E, *B. mamayi*, cuticle of megasporophyll stalk showing a stoma, V.42378,  $\times 200$ . F, *B. gracilis*, restoration of megasporophyll and seed in L.S. Two resin bodies are shown in the flesh; the stone is black and inside it is the nucellus and megaspore membrane,  $\times$  about 2. G, *B. gracilis*, restoration of cone (here shown as pendulous), about nat. size.

A-C, Gristhorpe Bed. D, E, Cloughton (*Solenites* and *Nilssonia* Beds). Figs. A-C, F, G are from Harris (1941) by permission of the Royal Society of London. Figs. D, E are from Thomas & Harris (1960) by permission of the publishers of *Senckenbergiana*.

*B. gracilis* was once favoured by Seward (1900) as a reproductive organ of *G. digitata* but this has long been abandoned: though both occur in the Gristhorpe Bed they are not closely associated.

***Beania mamayi* Thomas & Harris**

Text-fig. 65 D, E

The specimens are all from Yorkshire.

1835 *Sphaereda paradoxa* Lindley & Hutton (in part), pl. 159, fig. 1 only.

1960 *Beania mamayi* Thomas & Harris, p. 143, pl. 2, fig. 15; pl. 3, figs. 17, 22; text-fig. 1.

1961 *Beania mamayi* Thomas & Harris: Harris, text-fig. 2. (Restoration.)

DIAGNOSIS. Cone at least 180 mm. long, axis about 10 mm. thick below, fibrous, flexible. Sporophylls widely spaced, arising at right angles to the axis, about 16 mm. long; stalk 3 mm. thick, seeds borne at about 10 mm. from cone axis, seed-bearing part scarcely expanded. Sporophyll continuing for about 3–5 mm. beyond seeds, terminal part expanding to about 5 mm. wide, becoming dorsiventrally flattened but substance still fairly thick to the edge. Seed scars 2.5 × 1.0 mm., elongated in the direction of the sporophyll stalk, sporophyll stalk covered with fine hairs 1 mm. long, distal end without hairs but surface marked by ridges caused by internal fibres. Seed rounded, 4 mm. wide, with a thin flesh containing many small resin bodies and a stone 3 mm. wide; stone rounded but slightly flattened below and pointed above, substance thin but firm.

Cuticles of axis and sporophyll stalk delicate and fragile; showing elongated straight-walled cells. Sporophyll stalk with a few stomata and numerous trichome bases consisting of a small oval cell with a ring-shaped scar. Cuticle of head of sporophyll also thin, cells more nearly isodiametric, cell walls straight, finely marked, not interrupted by pits. Cell surface flat, not conspicuously sculptured. Stomata present, scattered; guard cells exposed but margins somewhat overhung by lateral subsidiary cells to form a wide, shallow, rectangular pit; poles of guard cells completely exposed.

Seed integument moderately thickly cutinised, cells isodiametric with faintly marked lateral walls. Stomata and trichomes absent. (Inner cuticles of seed not studied.)

HOLOTYPE. V.41826, figured by Thomas & Harris (1960, pl. 2, fig. 15).

OCCURRENCE. Middle Deltaic Sycharham and Gristhorpe Series: Cloughton, *Nilssonia* Bed and *Solenites* Bed.

DISCUSSION. The two best specimens (which were rather poor) were figured by Thomas & Harris (1960) and one of their figures is reproduced here. The possibility that one of the Lindley & Hutton specimens called *Sphaereda paradoxa* might belong to this species was not previously considered. Their specimen comes from Cloughton, like mine. I have not seen their specimen and Seward (1900) thought it had been lost so this cannot be settled. If their specimen does belong to it, it would follow that this cone reached a large size, with an axis 15 mm. thick which is twice as thick as in *B. gracilis*. Harris (1962) gave a restoration of the plant bearing *Nilssonia tenuinervis* and *B. mamayi* cones. Some modification would be needed if the Lindley & Hutton specimen belongs to it.

COMPARISON. *B. mamayi* has a thicker axis than *B. gracilis*, the sporophyll head is less expanded and the seed is smaller at the stage when it falls off. Its sporophyll stalk is hairy, its cuticle is thin, its stomata more exposed, and the sporophyll head contains resin bodies.

## Attribution to the same plant as

*N. tenuinervis*, *Androstrobus wonnacotti* and *Deltolepis calyptra*

The evidence from association is rather stronger than for the series including *Beania gracilis* since there are a number of different localities, but the evidence from agreement in structure is perhaps less because the cuticles are thin and poorly known.

*N. tenuinervis* has several Yorkshire localities and it is common in some of them. The reproductive organs (one, the other or both) are found only in these localities where it is common and in a matrix full of the leaf. *B. mamayi* has two localities, the Cloughton Wyke *Solenites* Bed (the main Cloughton plant bed) and the Cloughton Wyke *Nilssonina tenuinervis* Bed from the rather older Sycharham Series. The scale leaf *Deltolepis calyptra* is found in the Cloughton *N. tenuinervis* Bed and at Whitby probably in the *N. tenuinervis* Bed.

*A. wonnacotti* is associated with *N. tenuinervis* in the following localities:

Gristhorpe Bed (Middle Deltaic Gristhorpe Series)  
Cloughton Wyke *Solenites* Bed, also Gristhorpe Series  
Hasty Bank (Lower Deltaic)  
Whitby *N. tenuinervis* Bed (Lower Deltaic).

The first three contain certain other potential Cycads though none with a very similar cuticle, but the last one has scarcely any fossil besides *N. tenuinervis*.

All the organs of this suite have very thin cuticles and the stomata are only slightly sunken in a shallow rectangular pit. The other Cycads associated in one or more of these localities have much thicker cuticles and more protected stomata, except *Nilssonina tenuicaulis* which is found in the Gristhorpe Bed alone and has a thin cuticle and equally exposed stomata.

A second structural point of agreement is in the presence of spherical resin bodies about 100–200 $\mu$  wide which are found in the leaf, the microsporophyll and the megasporophyll. The only other Yorkshire species of *Nilssonina* with resin bodies of this sort are *Nilssonina* sp. A and *N. tenuicaulis*.

Undescribed species of *Beania*

Pl. 5, fig. 9

Small *Beania* cones are moderately frequent at Roseberry Topping and at Hasty Bank where they are associated with *Nilssonina kendalli*. They are not described because they show no distinguishing character from cones regarded as immature specimens of *Beania gracilis*. They are poorly preserved (Pl. 5, fig. 9) and although some gave moderately good cuticle preparations from the axis and from the seed integument, these showed no specific character. It is probable that these cones are distinct from *B. gracilis* as no specimen is of the normal mature size of *B. gracilis* while at Gristhorpe at least half the specimens are of full size, and it is thus probable that better material makes it possible to distinguish another species satisfactorily.

Specimen K334, Sedgewick Museum, Cambridge shows a similar small *Beania* cone. It is labelled '*Sphaereda parvula* Bean', and merely localised as 'Lower Shale Scarborough'; the matrix looks like the Lower Deltaic ironstone of Haiburn Wyke. It is ill preserved and has no determinable associates.

At Hasty Bank and at Roseberry Topping also there are a few fairly large seeds looking like mature ones of *B. gracilis*, but well distinguished by a surface covered with marked bulges 1 mm. wide. There is nothing to suggest that the small cones mentioned above bore these seeds and it has not been proved that the seeds are those of *Beania* at all. Their cuticles are poorly preserved but they seem to be of the *Allicospermum* type (which includes *Beania* seeds and others).

Macerations of certain coals have yielded numbers of well preserved seeds of the *Allicospermum* group associated with *Nilssonia* sp. B, but again while it is probable that they represent an undescribed *Beania* it would be wrong to ascribe such seeds to the genus.

### Pteridosperm-like reproductive organ

#### Genus PTEROMA nov.

DIAGNOSIS. Microsporophyll, rachis slender, simply pinnate, about 3 cm. long. Pinnae short, filiform, mostly simple terminating in oval or round fertile heads. Head bare on one side, fertile on other side (assumed to be the lower), on fertile side pollen sacs in two rows on either side of mid line; pollen sacs somewhat elongated transversely to axis of head, immersed and opening by an elongated split; sacs unilocular. Microsporophyll rather delicate but epidermis cutinised, heads showing elongated to isodiametric polygonal cells with straight walls and prominent papillae. Pollen grains disaccate, typically  $88\mu$  wide; anacolpate, colpus large and widely open; corpus of grain at least as high and as deep as wide (but outline of body often ill-defined). Roots of sacchi obscurely bounded, slightly offset distally (but free ends pointing laterally), height of sacchi a third or slightly over a third of the width of the whole grain. Cappa distinctly thickened, cappula (at opposite end of corpus) very delicate. Sacchi ornamented with minute pits, corpus more obscurely ornamented with pits.

TYPE SPECIES. *Pteroma thomasi* sp. nov.

The name is from *Pteroma*, a winged thing, and refers to the saccate grains.

COMPARISON. *Pteroma* is like *Pteruchus* (S. Hemisphere Mid-Trias) but also resembles *Harrisotheicum*. It looks particularly like *P. simmondsi* (see Townrow 1962) in its radiating pollen sacs, but while these point outwards freely in *Pteruchus* they are embedded in *Pteroma* and only look similar because cleavage passes through them. The pollen is very similar indeed. Even *P. simmondsi* differs in having pollen sacs arising in a crowded group while those of *Pteroma* could either be described as in two rows or as an elongated ring of radiating sacs. The other species of *Pteruchus* are more different, *P. africanus* has its numerous pollen sacs borne along diverging veins while *P. dubius* has very numerous sacs crowded beneath an elongated head.

*Harrisotheicum* Lundblad (1961) from the Rhaetic of Greenland (described as *Hydropterangium* by Harris (1932) and now known to be different from Halle's *Hydropterangium*) has fertile 'capsules' which if opened out would be very like the 'heads' of *Pteroma*, but in fact they are folded lengthwise and the two halves are almost in contact. The pollen grains, though disaccate are less similar (see Townrow 1962a) for the two sacs cover nearly the whole corpus and their roots are scarcely offset distally. Townrow considers that the grain has a leptoma and not a sulcus.

There is an important difference between *Pteruchus* and *Harrisotheicum* in that the branching is pinnate (in one plane) in *Pteruchus* but on all sides in *Harrisotheicum*. In *Pteroma* the primary branching is probably in one plane also but the facts are not quite secure. Two or perhaps three rachises which gave no sign of twisting show them as lateral, another shows them as arising above and below as well as lateral, but this specimen may be discounted because it is twisted. Better material is needed for a firm decision.

*Pramelreuthia* Krasser from the Upper Trias of Austria (see Kraüsel 1949) is somewhat less similar. Here the lateral branches arise very irregularly but are described as being in one plane. The fertile heads look solid and they enclose numerous long pollen sacs which are embedded except for their apices where presumably they open. The pollen grains (Townrow 1962b) look rather different having sacci strongly offset distally and a leptoma rather than a colpus.

DISCUSSION. *Pteroma* owes its interest (a) to the probability it belongs to the same plant as *Pachypteris papillosa* and (b) to its resemblance to *Pteruchus* and to a less extent *Harrisotheicum*. These microsporophylls have been linked with *Dicroidium* and *Ptilozamites* respectively. Though our knowledge of *Pteroma* is unsatisfactory there is a good hope that search will yield more and better specimens, now we know what to look for. We can hardly as yet assess the morphological value of two of the differentiating characters between *Pteruchus* and *Harrisotheicum*; 2- or 3-dimensional primary branching and the possession of a leptoma or a sulcus. (I only feel confident in recognising a sulcus in the most favourably placed grains and better preserved material is needed to establish the plane of branching without doubt.) Conceivably progress in knowledge may lessen the apparent importance of these differences, and it may be that the 'Mesozoic Pteridosperms' will show sufficient links combining the features of the present very diverse genera to make the whole group coherent even if a wide group. The present suggestions from *Pteroma*, uncertain as they are, do help to link *Pachypteris* with the others. This is not surprising for *Pachypteris* as well as *Dicroidium* have from time to time been included in *Thinnfeldia*, and though almost everyone now separates them, the plants may still have fairly close affinity.

*Pteroma thomasi* sp. nov.

Pl. 7, figs. 1, 3, 5, 7, 10, 11; Text-figs. 66, 67

DIAGNOSIS. Rachis at least 3 cm. long, up to 1.3 mm. wide, bearing short lateral branches at irregular intervals averaging 5 mm. on each side. Branches mostly simple, some forked. Middle region of rachis thicker than margins. Branches filiform but expanding slightly distally and then enlarging abruptly into a flattened oval head about 5 mm. long  $\times$  3-4 mm. wide. Middle region of head forming a ridge about 2 mm. long and nearly 1 mm. wide. Pollen sacs near stalk broad, those further forward narrower and curving outwards. Wider pollen sacs broadly wedge-shaped, 1.5 mm. long  $\times$  1 mm. at the outer end. Rachis and its branches glabrous, rachis showing elongated cells, back of fertile head showing short bulging cells. Cuticles rather thin, cell walls straight. Cells of back of head with finely marked outlines, cell surface not sculptured but each with one large hollow papilla. Pollen grains averaging  $88\mu$  wide ( $\sigma$   $13\mu$ ) and  $55\mu$  high ( $\sigma$   $5\mu$ ). (In the sample of 22 measured, extremes were width  $107\mu$  and  $53\mu$ , height  $61\mu$  and  $46\mu$ .) Sacchi marked with minute pits, pits often rather distant, size ranging from less than  $1\mu$  to  $2\mu$ . Boundary between sacchi and corpus obscurely marked.

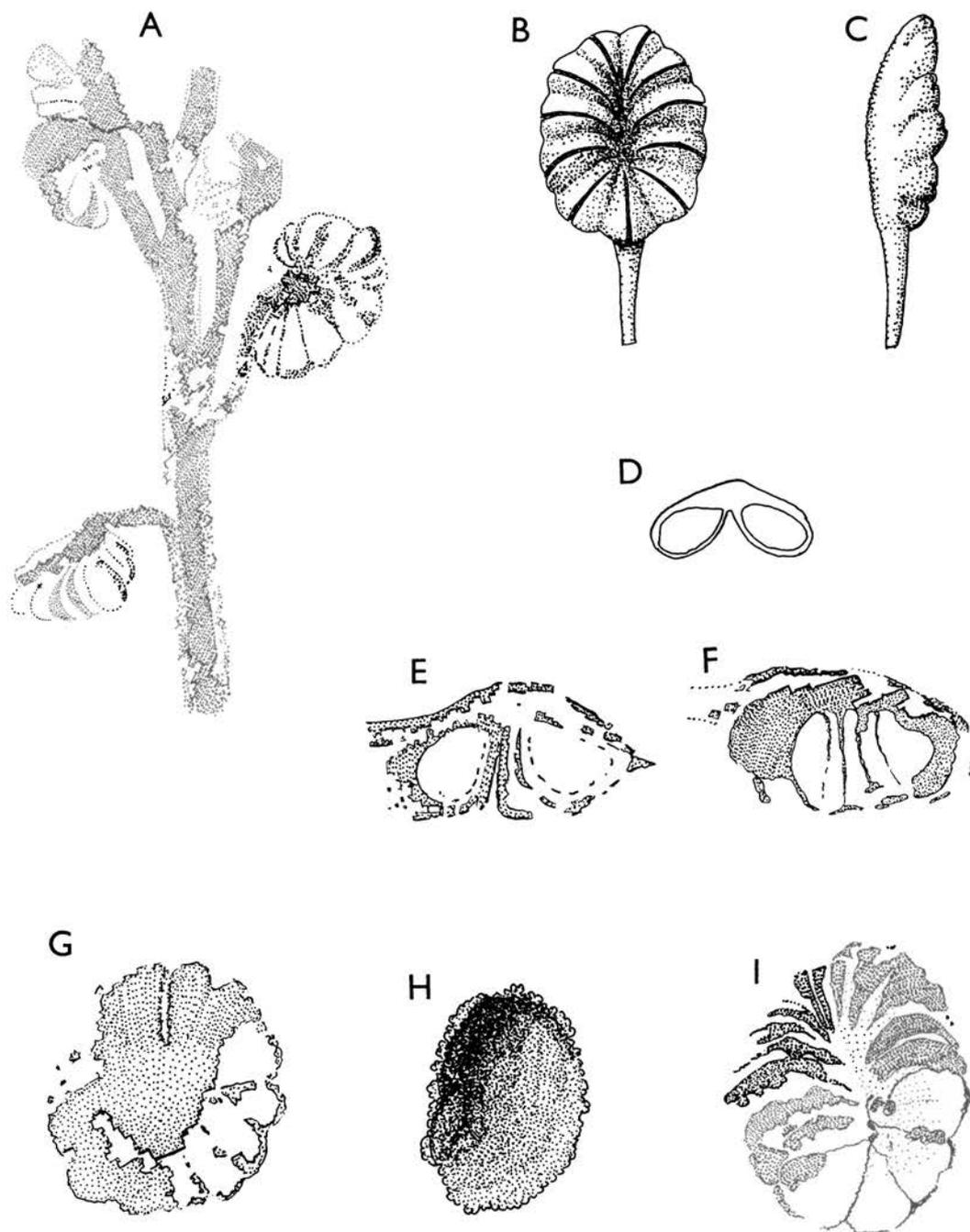


Fig. 66. *Pteroma thomasi* sp. nov.

A, middle region of holotype (see also Pl. 7, figs. 10, 11), V.45493,  $\times 10$ . B–D, restorations of fertile head,  $\times$  about 5. B, from below, C, from the side and D, in section. E, fruiting head in what amounts to transverse section, V.45492,  $\times 10$ . F, fruiting head in what amounts to oblique longitudinal section, V.45490,  $\times 10$ . G, fruiting head from above (the substance has crumbled away on the right to expose a deeper layer), V.45493,  $\times 10$ . H, mass of nearly ripe pollen grains macerated out of a fruiting head, V.45676,  $\times 20$ . I, under surface of fruiting head (towards the bottom right the plane of cleavage goes through the pollen sacs), V.45490,  $\times 10$ . Specimens in Figs. A, E–G, I were drawn under oil.

All specimens are from Hasty Bank.

HOLOTYPE. V.45493 (Pl. 7, figs. 10, 11; Text-fig. 66 A, G). Lower Deltaic; Hasty Bank.

The species is named after Hamshaw Thomas who collected the material.

DESCRIPTION. The material consists of two small blocks (each with part and counterpart) and three very small fragments. Each of the larger blocks shows a number of specimens of *Pteroma* while the small ones each have a single one. The blocks look as though they represent one bedding plane (on which *Pteroma* fragments must be locally abundant) but they do not fit together. The specimens of *Pteroma* are inconspicuous when dry, though various robust leaves with them are clear. Like many of the delicate specimens at Hasty Bank they look slightly weathered, the plant substance is crossed by innumerable parallel cracks, breaking it into rectangles  $0.2 \times 0.1$  mm. or even smaller. (This is therefore the largest size of my cuticle preparations.) For this reason also balsam transfers proved useless. The plane of cleavage passes through the fossil, half of the little coaly blocks being on one face, half on the other and from both faces the substance readily crumbles away and is lost.

The larger block (with the holotype) has five or six other rachises of *Pteroma*, all broken below but mostly at the edge of the block. Since they happen to radiate inwards they were no doubt separately deposited microsporophylls or microsporophyll fragments. There is nothing to suggest that these specimens are pieces of a large and more complex organ. As mentioned earlier I examined the branching carefully but I could not decide with certainty that it is truly lateral though it may well be so. The branches arise at very uneven intervals and even if they were, for example, spiral and compressed into the horizontal plane their original spacing must still have been uneven.

The different fertile heads were probably all similar except in size, but they present different aspects. The main ones are: (1) The upper surface (Text-fig. 66 G) of fairly uniform epidermis. The margins are lobed and the surface slightly grooved in relation to the pollen sacs. (2) The under surface showing the gaping pollen sac walls, or where these have flaked off, the interiors of the pollen sacs. This aspect is seen repeatedly in the photos and in Text-fig. 66 I. (3) Various sectional views caused, presumably, by the head being compressed in a tilted position (Text-fig. 66 E, F). Many heads show intermediate or combined views.

Fairly complicated organs like these would have been most satisfactorily studied by extraction whole from the rock, or failing that by balsam transfers, but neither was possible. All that could be done was to examine the various views presented and then to make a comprehensive hypothesis (Text-fig. 66 B-D) which fitted everything seen. The only confirmation possible was to scrape away one surface and then the underlying mud which fills the sporangia until the other surface was reached, and with the limited material this could not be done as many times as I would have wished.

Although most of the pollen sacs have dehisced and contain fine mud and a very few pollen grains on their inner walls one of those macerated proved to be full of ripe pollen (Text-fig. 66 H). This specimen has far more pollen at one side than the other, probably because the sac was originally wedge-shaped. It is a single mass, and gives evidence that the sac is unilocular, as indeed all the empty ones look to be. Another pollen sac on maceration yielded a hundred or more grains which readily separated from one another but were all shrivelled, the sulcus often being closed and there are strong folds in the sacci and often in the corpus also. Apart from this sac which I regard as abnormal, all the sacs gave well developed grains. Pollen was obtained from numerous sacs (even the dehisced ones always show a few grains) and all

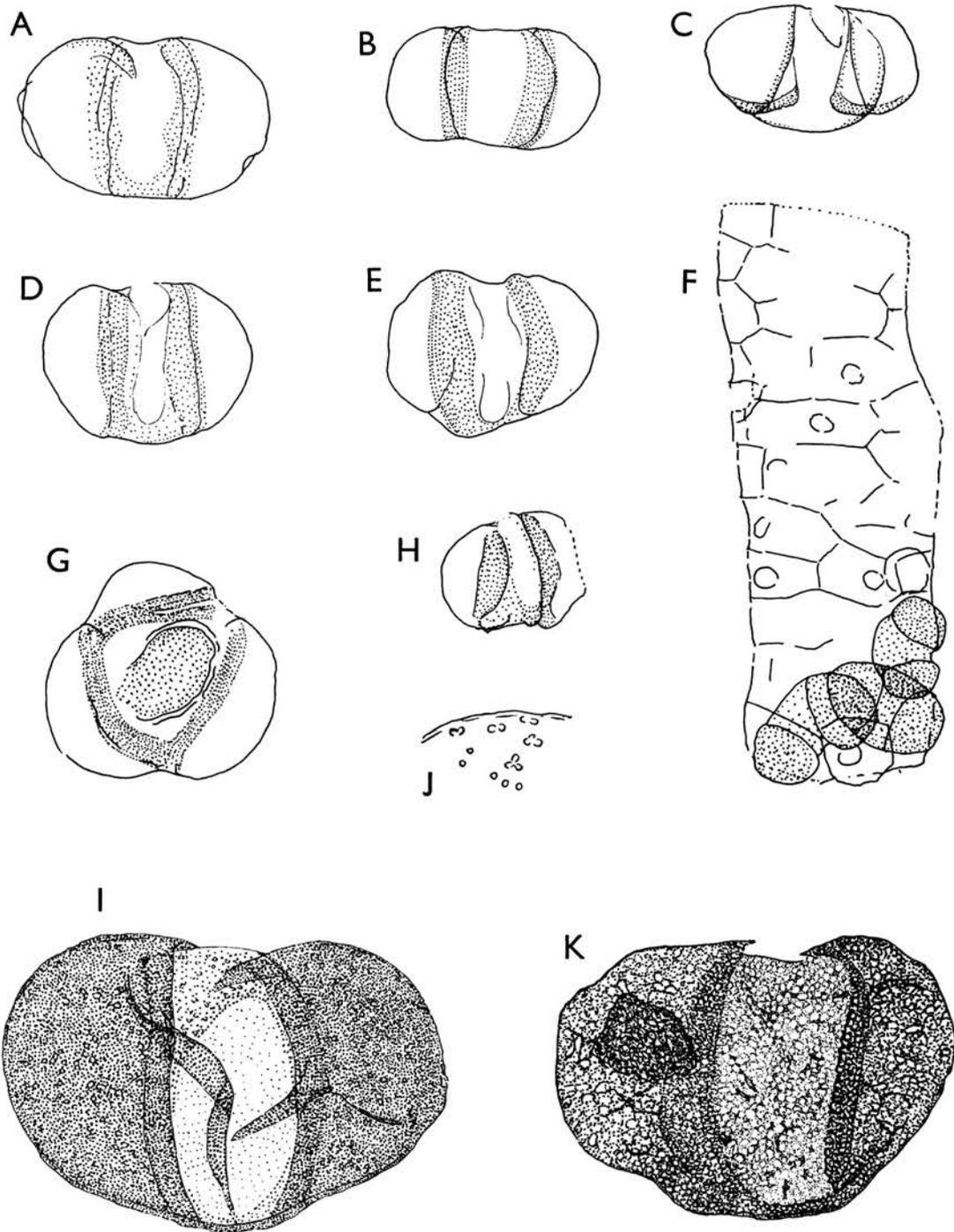


Fig. 67. *Pteroma thomasi* sp. nov. (Pollen)

A-E, normal grains, B is in polar view, V.45677,  $\times 400$ . F, fragment of cuticle of upper side of fertile head, three pollen grains are sticking to it, V.45678,  $\times 200$ . G, abnormal pollen grain with three sacci, V.45679,  $\times 400$ . H, abnormally small pollen grain, V.45677,  $\times 400$ . I, pollen grain showing the colpus. The sacci are very finely pitted, V.45680,  $\times 800$ . J, pits of the saccus of I (upper surface only),  $\times 2000$ . K, pollen grain with coarser pitting. The dark body is extraneous. V.45681,  $\times 800$ .

All the specimens are from Hasty Bank.

of it is of the one type, so there is no risk that the pollen is a contaminant. The drawings illustrate the whole range noticed, apart from the shrivelled grains of the one sac. One 3-winged grain was seen (Text-fig. 67 G) and one very small one (Text-fig. 67 H).

I have not given the mean width of the body and of the sacchi in the diagnosis because in a good proportion of the 22 grains measured I could not see the boundary clearly and I made arbitrary decisions: errors in such decisions are likely to remain uncorrected in arithmetic means. However the figures are:

Mean length of body . . . . .	51 $\mu$
Mean width of body (unreliable) . . . . .	31 $\mu$
Mean length of sacchi . . . . .	51 $\mu$
Mean width of sacchi (unreliable) . . . . .	26 $\mu$

Folds in the wall of the sacchi suggest a cuticle thickness of 2 $\mu$ . The various dimensions of the pollen grain vary independently, for example, one very wide grain is also very high but the next wide one is rather low.

These measurements agree closely with the pollen of *Pteruchus dubius*, but although the walls have small pits, they are distinctly smaller in *Pteroma* and the thick part between them forms no definite reticulum. *Pteruchus simmondsi*, also with pollen of similar size, has a considerably coarser reticulum and *P. africanus* with a smaller grain also has a reticulum. The present pollen resembles Couper's *Pteruchipollinites thomasi*, now *Alisporites thomasi*; that species was not found in Yorkshire but from the coal of Brora in N.E. Scotland. The Brora coal is of about the same age as some parts of the Yorkshire Deltaic Series.

I believe, however, they are distinct. Couper (1958) states that the reticulate thickenings of the sacchi are 1–2 $\mu$  wide which is about the same as in *Pteroma* but his figures suggest a coarser and more obvious reticulum. In *Pteroma* it is natural to describe the sacchi as having irregularly crowded pits rather than as being reticulate. Then in his figures the corpus appears almost smooth but in *Pteroma* the markings (on one surface) are nearly as well marked as on the sacchi. The lines of attachment of the sacchi are a good deal more clearly seen than in most specimens of *Pteroma*, where it is seldom possible to see the line at all.

These differences might seem negligible were it not that pollen grains have been found in Yorkshire which agree better with Couper's *Alisporites thomasi* than with *Pteroma* pollen. The pollen grains were found by Mrs. M. Muir at White Nab, Scarborough in a sandstone without determinable leaves. In this rock pollen like *A. thomasi* (Couper) is the commonest kind and I assume the grains are all of the same species. The pollen has the characters mentioned above, and in addition most of the grains show the sacchi pointing strongly distally, much as in *Pinus*. In *Pteroma* pollen the sacchi point almost transversely in nearly all grains and the only ones in which they point strongly distally are some of the shrivelled grains in one pollen sac already mentioned.

#### Attribution to *Pachypteris papillosa*

The evidence as usual depends on repeated association (here very strong) and on agreement in structure (here slight). The hand-specimens which are all from Hasty Bank and very probably a single layer are associated with:

*Pachypteris papillosa*  
*Nilssonina kendalli*  
*Elatides williamsonis*  
*Ptilophyllum pectinoides*

Unless there are errors in our views it cannot belong to any of the last three. The microsporophyll of *N. kendalli* is unknown but presumably it is an *Androstrobus* scale as in other species of *Nilssonina*. The male cone of *E. williamsonis* is known as is the male flower (*Williamsonia*) of *P. pectinoides*. The only one whose reproductive organs are unknown is *P. papillosa*. The Hasty Bank Plant Bed is one of those in which the specimens were often undamaged before deposition and *P. papillosa* must have lived near where it was deposited. Since leaves in general are far more numerous than reproductive organs, it is to be expected in such a bed that where a number of new reproductive organs are found, the corresponding leaf will be already known as a comparatively common fossil. This directs attention strongly on *Pachypteris papillosa*, the commonest leaf at Hasty Bank and the only common one with unknown reproductive organs.

We do not know which layer of the thick Hasty Bank provided the present specimens and this is unfortunate as certain of the species are restricted. The bed as a whole has the following Gymnosperms in addition to those on the *Pteroma* blocks.

A. Species to which male reproductive organs are already attributed with confidence:

*Sagenopteris colpodes*; *Nilssonina tenuinervis*; *Pseudocetenis lanei*; *Nilssoniopteris vittata*; *Ginkgo huttoni*.

B. Species whose male reproductive organs are unknown:

*Ctenis kaneharai* (frequent); *Ctenozamites cycadea* (rare); *Nilssonina thomasi* and *N. syllis* (both rare); *Pachypteris lanceolata* (rare); *Stenopteris williamsonis* (rare); *Brachyphyllum expansum* (common); *Otozamites gramineus* (rare); *Anomozamites nilssoni* (occasional).

Of these we may at once cut out the two *Nilssonina* species, *Brachyphyllum* and the two Bennettitalean leaves as exceedingly unlikely to have a microsporophyll resembling *Pteroma*.

*Structure.* The character of the epidermal cells suggests *Pachypteris papillosa* or *Stenopteris williamsonis*, the features of agreement being the straight walls, unsculptured surface and strong papilla. It is unfortunate that I have not yet observed a stoma on *Pteroma*.

*Further association.* Although *Pteroma* is restricted to one locality (and perhaps one bedding plane) pollen agreeing with it though far from general is more widespread. Such pollen (including *Alisporites thomasi*) is known from a moderate number of localities where it occurs in different kinds of associations with other fossils.

With regard to this association we can group our Yorkshire localities as follows:

- (1) The total examined for pollen.
- (2) Localities with both *P. papillosa* and *Pteroma*-like pollen.
- (3) Localities with *P. papillosa* but no *Pteroma*-like pollen.
- (4) Localities with *Pteroma*-like pollen but no *P. papillosa* though with leaves of other kinds.
- (5) Localities with no leaves at all but with *Pteroma*-like pollen.

Clearly the case for association depends on group 2 in relation to group 1. Group 5 does not matter, but groups 3 and 4 give weight against any case for regarding the association as significant.

With a view to obtaining evidence I collected fresh material in 1963 and my results (together with those of Mrs. Muir) are as follows:

(1) The total number of localities successfully examined for pollen is now considerable, it was 69 by Couper (none with *Pteroma*-like grains) and a considerably larger number by Mrs. Muir in which such pollen is absent, save as mentioned below under groups 2, 3, 4 and 5. Pollen of this type is very local in Yorkshire.

(2) The leaf and the pollen occur together at Roseberry Topping; in the Little Roseberry Leaf Bed; at Hasty Bank; Rosedale Hartoft Bed 2; Farndale Hillhouse Nab; Farndale Spout House Upper Black Clay; Snilesworth R. Rye location 7; Snilesworth Arnsgill *Pachypteris* Bed; Bilsdale Fangdale; Bilsdale Tripsdale; Guisborough Rock Hole Dogger and in the Deltaic Beds above; Westerdale Baysdale Black Beck Leaf Bed; Westerdale Esklets Crag; Ravenscar Brickworks (matrix of the specimen); Haiburn Wyke (matrix of the specimen). This is 15 localities. The pollen frequency is greatest in the best leaf localities namely Roseberry Topping, Little Roseberry and Hasty Bank.

(3) For various reasons a few localities of *P. papillosa* were not examined for pollen. Of those which were examined but in which I failed to find *Pteroma*-like pollen are:

Westerdale Clough Gill. Here land plant spores do occur but they could not be separated from an enormous bulk of wood fragments of similar size, density and resistance to maceration. Since I could not separate the pollen I did not devote the labour needed for an adequate search to this locality.

Bilsdale Tarn Hole Beck 1 and 2. Here *P. papillosa* is rare and spores of all sorts are very rare and mixed with great quantities of powdered fusain. No long search for *Pteroma* pollen was attempted.

The failure to establish association in these localities is thus not significant, since it results from my unwillingness to give the effort needed with difficult material.

(4) The only localities are: The Whitby Plant Bed, base of Lower Deltaic (Muir); Birk Brow Coal, Middle Deltaic (Muir); Beast Cliff Coal C (below Eller Beck) (Muir). These are discussed below.

(5) The only localities are Whitby, Top of Lias (Muir); Whitby Dogger (Muir); White Nab, Upper Deltaic Moor Grit (Muir). Until leaves of some sort are found here the failure of association is not significant. The White Nab pollen probably belongs to another plant.

The group which militates most seriously against the significance I would attribute to the association is Group 4. The flora of the Whitby plant bed is very well known and *P. papillosa* is certainly absent; the flora of Birk Brow is only known from cuticles macerated out of coal and here no cuticle of the leaf was found but no special search for it has been made. The Beast Cliff coal sample is less serious as we know nothing about its flora except that it has some *Equisetum*.

What weight then is to be attributed to these three cases of contrary evidence? As far as I know this is the first time such a search has been made and we have no experience to guide us when searching the rocks containing a particular leaf in the hope of recognising pollen

appropriate to it. I cannot say what weight is to be given to the contrary evidence of these three localities where the pollen occurs without the leaf. Various lines of enquiry would be possible and if pursued should make such assessment possible. For instance a general survey of the pollen of the plant beds at the base of the Deltaic Series, both beds with *P. papillosa* and without, and then the relative percentage frequency of *Pteroma*-like pollen could be correlated with the presence or absence of *P. papillosa*. No study has been made because it would involve labour disproportionate to the value of the results.

Surely though, some examples of plant beds (like the Whitby bed) are to be expected where the pollen is found without the leaf? Many pollen workers base their work on the supposition that pollen is far more widely dispersed than the leaf of the parent plant and might regard the number of associations of pollen and leaf in these two extremely local species as remarkably high. To me at least it seems so high as to be overwhelming.

I think Hamshaw Thomas must have collected the specimens of *Pteroma* on the same visit to Hasty Bank as when he collected Cycad cones. This was around 1950 when he had largely given up laboratory work on Yorkshire fossils. It is to be regretted that he did not investigate and describe these specimens for he would have loved to compare them with his own *Pteruchus*. To name them after him is the least I can do.

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*Zamites*, 71, 72  
   *buchianus*, 82  
   *eathiensis*, 71, 72  
   *familiaris*, 157  
   *gigas*, 82  
   *proximus*, 72

# PLATES

## PLATE I

### *Caytonia nathorsti* (Thomas)

Gristhorpe Bed

- FIG. 1. Fruit showing the lip, V.45494. × 16.  
FIG. 4. Small abortive fruit, from below. The lip projects beyond the stalk, V.45496. × 16.  
FIG. 5. Small and abortive fruit, from above, V.45497. × 16.  
FIGS. 6, 7. Seeds, V.45498. × 20.

### *Caytonia seawardi* Thomas

Gristhorpe Bed

- FIG. 2. Fruit showing bulges caused by seeds. The broken top of the stalk is near the bottom and conceals the lip. V.45495. × 16.  
FIG. 3. Fruit broken in maceration and exposing seeds (pitted), V.45495. × 16.  
FIGS. 8, 9. Seeds, V.45499. × 20.

### *Nilssonia tenuinervis* Seward

Cloughton *Nilssonia* Bed

- FIG. 10. Base of rachis showing vascular imprints, V.41107. × 5.

### *Caytonanthus arberi* (Thomas)

Gristhorpe Bed

- FIGS. 11, 12. Two sides of a 5-locular anther, V.45500. × 16.  
FIGS. 16, 17. Two sides of a trilocular anther, V.45500. × 16.  
FIGS. 18, 19. Two sides of a 5-locular anther, V.45500. × 16.

### *Nilssonia revoluta* sp. nov.

South Cliff, Scarborough

- FIG. 13. Specimen thought to have been preserved with the upper surface facing upwards, V.23968. × 4.  
FIG. 20. Holotype, thought to be preserved with upper surface facing downwards, V.23967. × 4.

### *Deltolepis mitra* sp. nov.

Beast Cliff *Otozamites* Bed

- FIG. 14. Holotype, V.42424. × 1.

### *Nilssonia syllis* sp. nov.

Beast Cliff *Otozamites* Bed

- FIG. 15. Part of a leaf segment and the edge of another in balsam transfer, showing prominent veins and down-turned margins. Specimen destroyed. × 10.

### *Androstrobos prisma* Thomas & Harris

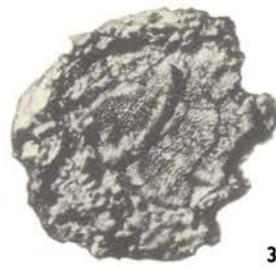
- FIG. 21. Specimen in Stockholm Riksmuseum, × 1. Labelled in Nathorst's writing as Marske Quarry, collected by Professor Percy Kendall of Leeds, and dated 28.7.1909.



1



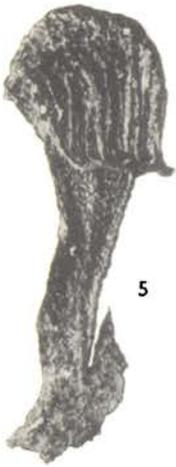
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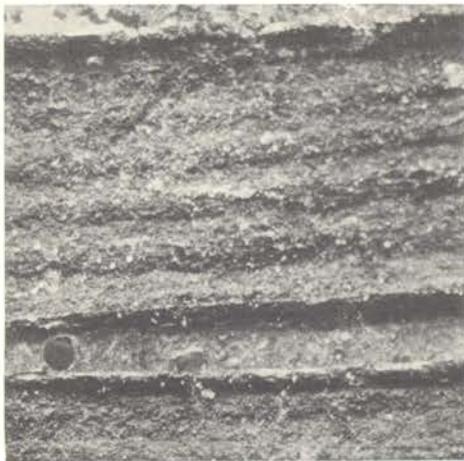
12



13



14



15



16



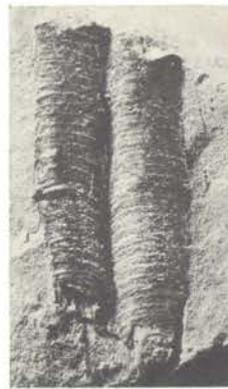
17



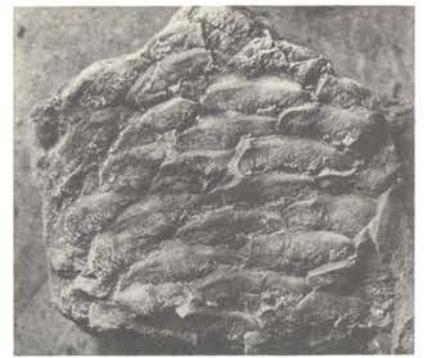
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20



21

## PLATE 2

### *Caytonia sewardi* Thomas

#### Gristhorpe Bed

- FIG. 1. Rachis by transmitted light, showing a single vascular strand giving off branches to the pedicel bases, V.45501.  $\times 10$ .  
FIG. 4. Apex of seed, V.45503.  $\times 200$ .

### *Caytonanthus arberi* (Thomas)

- FIGS. 2, 3. Ultimate branches, V.45504.  $\times 12$ . Gristhorpe Bed.

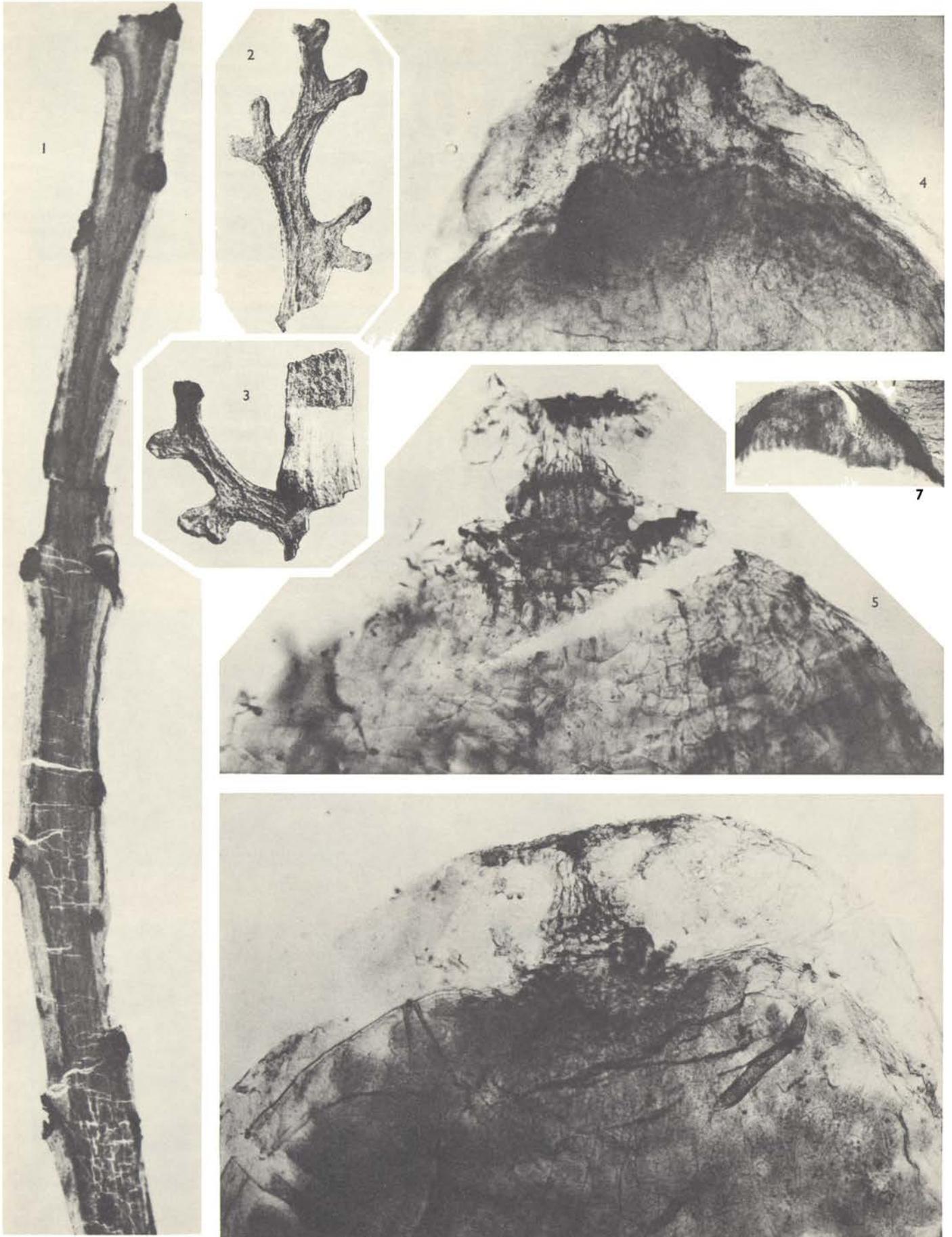
### *Caytonia kendalli* sp. nov.

#### Roseberry Topping

- FIG. 5. Apex of seed, V.45505.  $\times 200$ .  
FIG. 7. Lip of fruit showing obscure transverse bars, V.45507.  $\times 20$ .

### *Caytonia nathorsti* (Thomas)

- FIG. 6. Apex of seed, V.45502.  $\times 200$ . Gristhorpe Bed.



## PLATE 3

### Cuticles of Cycads

The upper cuticle is on the left, the lower cuticle of the same pinna on the right. The veins run vertically except in Fig. 2. All  $\times 200$ .

#### *Ctenozamites* sp. A

FIGS. 1, 2. Specimen V.45509, Flask Inn, Roadside ditch.

#### *Ctenozamites megalostoma* sp. nov.

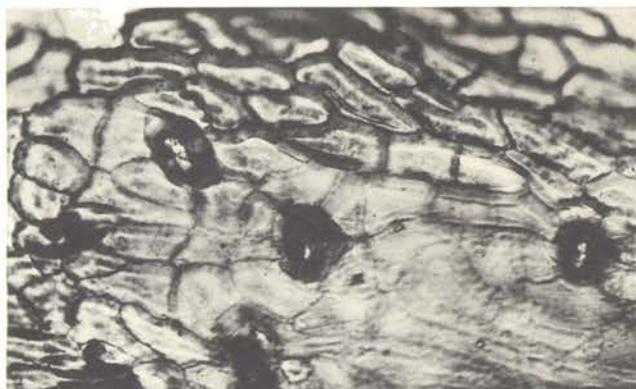
FIGS. 3, 4. A few cells in Fig. 3 show faint papillae and others a striation due to a hypodermal cell, V. 45510, Snilesworth Wheat Beck 3.

#### *Pseudoctenis* sp. A

FIGS. 5, 6. Specimen V.44877, Beast Cliff *Otozamites* Bed.

#### *Pseudoctenis* sp. B

FIGS. 7, 8. Specimen V.45512. Snilesworth R. Rye Old coal pit.



## PLATE 4

### *Amphorispermum pullum* Harris

Gristhorpe Bed

- FIG. 1. Micropylar end of fully macerated seed, V.45515.  $\times 50$ .  
FIG. 2. Chalazal end of lightly macerated seed, V.45516.  $\times 50$ .  
FIGS. 4, 5. Unmacerated seeds; in Fig. 4 compression is parallel to the narrow axis and in Fig. 5 parallel to the broad axis, V.45517.  $\times 16$ .

### *Ctenozamites cycadea* (Berger)

Roseberry Topping

- FIG. 3. Pinnules, V.44868.  $\times 3$ .  
FIG. 7. Pinna, V.44867.  $\times 3$ .

### *Ctenozamites leckenbyi* (Leckenby)

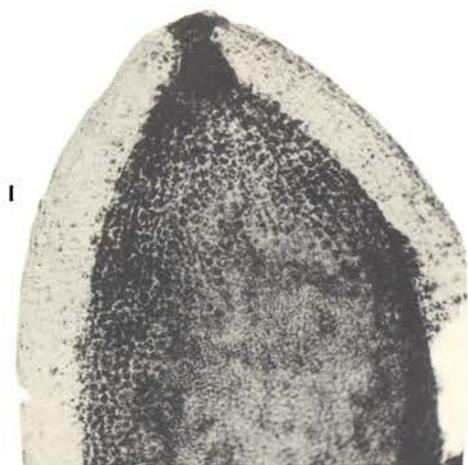
- FIG. 6. Pinnules, V.21875.  $\times 3$ . Gristhorpe Bed.  
FIG. 10. Lightly macerated upper cuticle showing conspicuous outlines of palisade mesophyll cells, each cell containing a round body, V.45511.  $\times 200$ . Beast Cliff *Ctenozamites* Bed.

### *Pseudoctenis lanei* Thomas

Gristhorpe Bed

- FIG. 8. Lower part of rachis, V.44874.  $\times 1$ .  
FIG. 9. Base of petiole, V.44875.  $\times 1$ .

All the figures are untouched photographs.



1



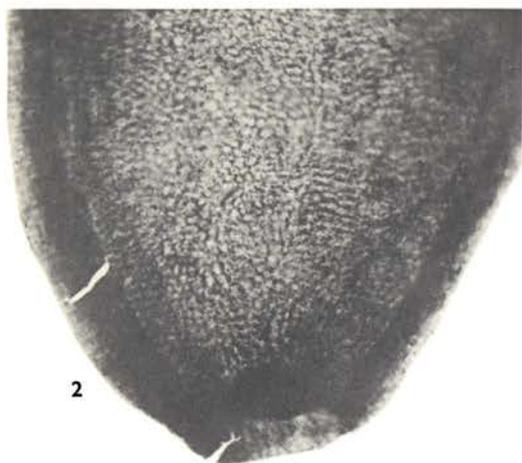
3



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7



8



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10

## PLATE 5

### *Pachypteris lanceolata* Brongniart

- FIGS. 1, 2, 4. Naturally cleared pinnules showing the veins by transmitted light, V.45696.  
× 10. Fylingdales Upper Kirk Moor.
- FIGS. 3, 5. Isolated pinnules in which the thick margin is sharply delimited from the lower cuticle, V.45697. × 10. Snilesworth Wheat Beck 3.

### *Nilssonia thomasi* sp. nov.

- FIG. 6. Specimen coated with  $\text{NH}_4\text{Cl}$ , V.45460. × 1. Hasty Bank.

### *Pachypteris papillosa* (Thomas & Bose)

- FIG. 7. Leaf in which compression has caused wrinkling, V.45468. × 2. Roseberry Topping.
- FIGS. 10, 11. Distorted leaf. Fig. 10 under oil, Fig. 11 coated with  $\text{NH}_4\text{Cl}$ . Note splitting along midribs and wrinkles in Fig. 11, V.45469. × 2. Roseberry Topping.
- FIG. 12. Axis, part of the specimen seen in Fig. 13, × 2. Showing also in Text-fig. 54 F.
- FIG. 13. Axis, V.45467. × 1. Hasty Bank.

### *Androstrobus wonnacotti* Harris

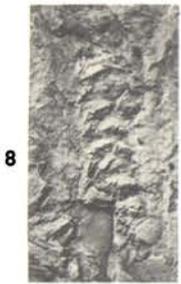
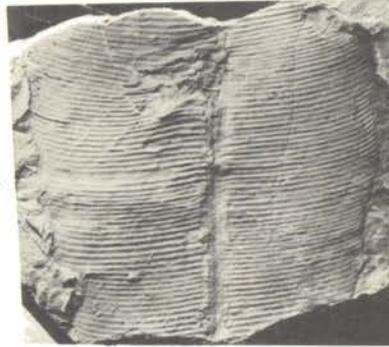
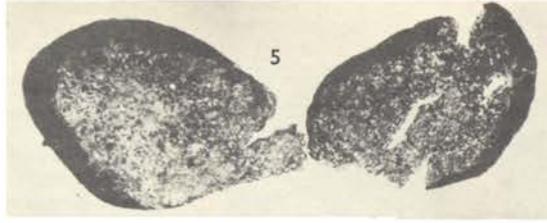
- FIG. 8. Cone in which the sporophylls are still in contact ( $\text{NH}_4\text{Cl}$  coated), V.45486.  
× 1. Hasty Bank.

### *Beania* sp., *Pachypteris papillosa* (Thomas & Bose)

- FIG. 9. *Beania* sp., small cone on left; *P. papillosa* axis and berets on right, V.45488.  
× 1. Hasty Bank.

### *Caytonia kendalli* sp. nov.

- FIG. 14. Nucellar cuticle of seed showing characteristic dark spots, V.45508. × 200.  
Ryston Nab.



## PLATE 6

### *Androstrobos manis* Harris

#### Gristhorpe Bed

- FIG. 1. Holotype, V.25900. × 2. There is a sterile scale agreeing with *Deltolepis crepidota* to the right.
- FIG. 4. Specimen showing the interior with pollen sacs, V.25901. × 4.
- FIG. 12. Apex of cone, V.25898. × 2.

### *Androstrobos* sp. A

- FIG. 2. Specimen showing fibrous distal end of scale above and pollen sacs below. × 4. Roseberry Topping.

### *Beania gracilis* Carruthers

#### Gristhorpe Bed

- FIG. 3. Typical immature cone showing loose construction and relatively thick axis, V.41824. × 1.
- FIG. 6. Smallest immature cone, V.23934. × 1.
- FIG. 10. Part of a mature cone showing a seed and half of the oval head of a scale (here pressed into the bedding plane), V.24673. × 1.

### *Androstrobos prisma* Thomas & Harris

#### Hasty Bank

- FIG. 5. Head of isolated scale with pollen sacs, V.42381. × 1.
- FIG. 8. Part of the holotype, V.42380. × 1.

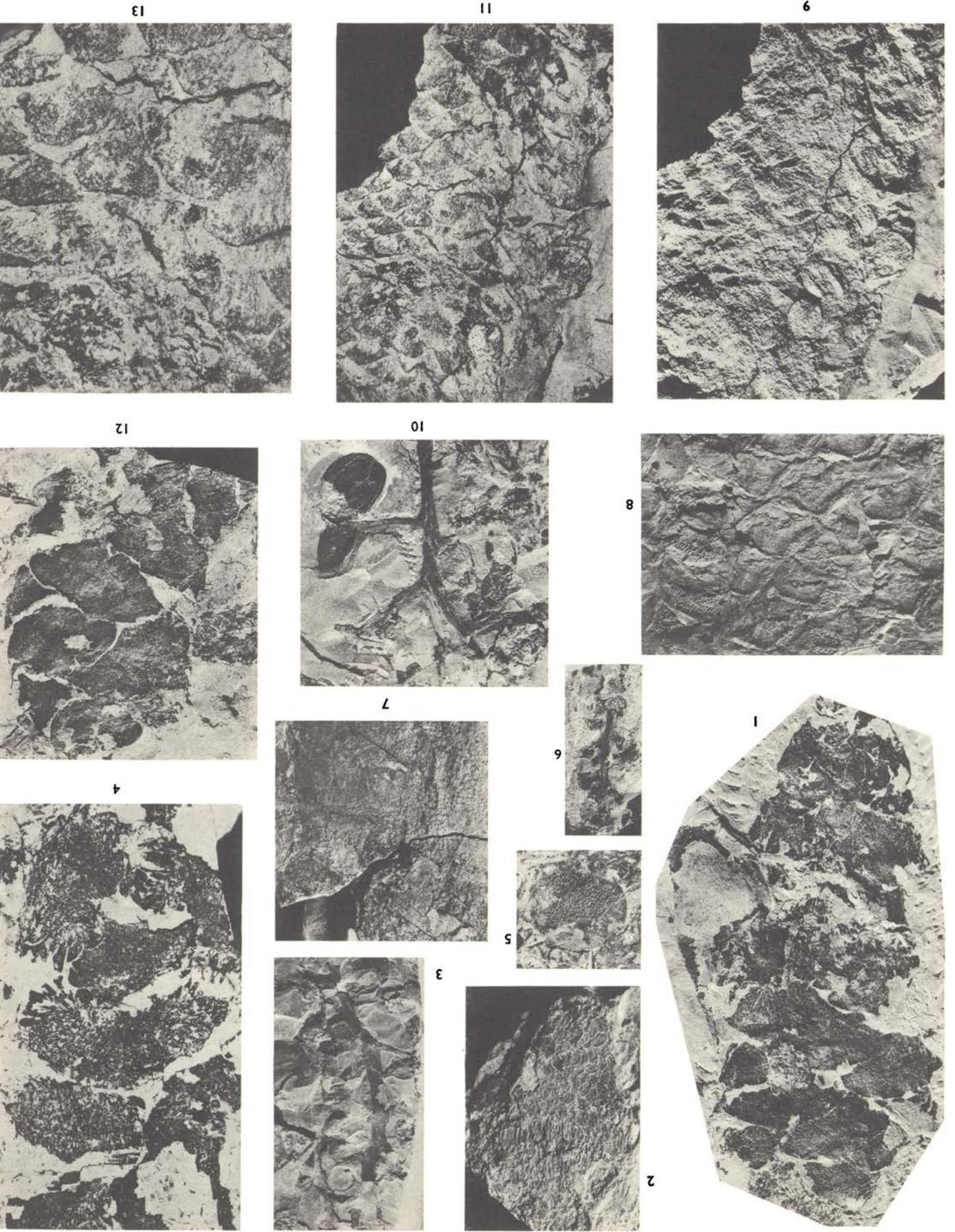
### *Pachypteris papillosa* (Thomas & Bose)

- FIG. 7. Detached bark of a large axis showing a few round berets, V.45470. × 1. Roseberry Topping.

### *Androstrobos szei* sp. nov.

- FIG. 9. Holotype, photographed dry with NH<sub>4</sub>Cl coat, V.45487. × 1. Gristhorpe Bed.
- FIG. 11. Holotype, photographed under paraffin. × 1.
- FIG. 13. Details from Fig. 11. Some of the upper sporophylls have broken away and show pollen sacs. Fibres also are visible. × 2.

FIGS. 1, 4, 6, 10, 12 are from Harris (1941) by permission of the Royal Society. FIGS. 3, 5, 8 are from Thomas & Harris (1960) by permission of the publishers of *Senckenbergiana*.



## PLATE 7

### *Pteroma thomasi* sp. nov.

Hasty Bank

- FIG. 1. Isolated heads, V.45489. × 2.  
FIG. 3. Small block with heads and rachises, V.45490. × 2.  
FIG. 5. Forked rachis, V.45491. × 2.  
FIG. 7. Block with several sporophyll fragments, V.45492. × 2.  
FIGS. 10, 11. Holotype, part and counterpart. There are fragments of *P. papillosa* also, V.45493. × 2.  
The above were all photographed under oil.

### *Pachypteris papillosa* (Thomas & Bose)

Roseberry Topping

- FIG. 2. Axis with berets, V.45471. × 1.  
FIG. 4. Small axis with berets, V.45472. × 1.  
FIG. 8. Detached bark of axis (imprint) showing scattered berets, V.45473. × 1.  
FIG. 9. One of the longest beret-bearing axes, V.45474. × 1.

### *Pachypteris lanceolata* Brongniart

- FIG. 6. Leaf apex, V.45481. × 1. Goathland.

