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THE YORKSHIRE JURASSIC FLORA

III. BENNETTITALES

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BRITISH MUSEUM (NATURAL HISTORY)

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III

BENNETTITALES

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and sixty-nine figures in the text

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Introduction

The Class. In this work I have included in the Bennettitales all the leaves and other organs commonly included. The most important character distinguishing them is their stoma which shows a pair of subsidiary cells opposite the two guard cells, the whole group looking as though formed by the division of a single cell. Florin (1933) in particular has discussed this and has concluded that it does result from the division of a single cell (syndetocheilic arrangement) while in almost all other Gymnosperms the subsidiary cells have a different arrangement, not being sister cells of the guard cells but have independent origin (haplocheilic). It is true that in some plants, for instance the grasses, the guard cells and subsidiary cells may look to have a common origin though they do not, and the validity of Florin's conclusion will only be fully proved by a study of young Bennettitalean stomata, perhaps in a bud of *Cycadeoidea*. Yet even if he were proved wrong and I think that most unlikely, the division would remain just as practical, for almost all Mesozoic Gymnosperms with preserved cuticles at once separate as Bennettitalean or else not on this character.

The cuticles show additional features which are often characteristic though less reliable for distinguishing a Bennettitalean leaf or other organ from one of the Cycads for example. In a Bennettitalean leaf the cell outlines are very commonly sinuous, often strongly so, but this is much less usual in Cycads. In Bennettitales the stomata, if orientated, mostly have their apertures transverse to the veins, but in Cycads they are more often longitudinal. In the Bennettitales the common wall between the guard cell and subsidiary cell has a well marked plate of cuticle, forming a wing-like extension which is well developed even in species with delicate cuticles. This mimics the dorsal lignine thickening of normal Gymnosperm stomata. In most Gymnosperms no such thickening is obvious, though something very like it may be seen in species with rather thick cuticles. Further the exposed surface of the guard cells at the sides of the aperture is thickened in Bennettitales but not as a rule in other Gymnosperms. The shape of the guard cells is however similar.

A strange feature one often meets in Bennettitaleans is that the upper cuticle though thicker than the lower is crumbly and often impossible to mount, while the thin lower cuticle is coherent. This is unexplained but is evidently a special effect of preservation.

Although the Bennettitales were originally classed as Cycads, and later linked with Cycads, it seems that any phylogenetic connection between them must be remote. One can indeed imagine many alternative possible links between these two classes, but until there is good reason for preferring a particular link it is best to consider them unconnected. This is true also of other classes; the Bennettitales are or seem remarkably isolated. Thus the term 'Cycadophyte' which was intended as a major phyletic group means no more than 'Gymnosperm with a pinnate leaf'.

Subdivision. Several authors have divided the Bennettitales, or the dozen better known members, into families. Progress in knowledge has however shown that the basis for this is insecure, for instance the recent studies of *Cycadeoidea* by Delevoryas (1963) has shaken any complacency about that, the most studied of all genera. For this reason no families are distinguished here. The best treatment at present is to continue to be cautious, to keep the different organs apart under different names, and where one feels sure that certain groups of organs belong to a single plant to say so but without affecting the name.

The leaves, by far the most abundant organs as fossils, fall into species which though satisfactorily definable are so numerous that the differences between them are rather small and they thus form a nearly continuous series. How such a series is to be divided into genera is arbitrary, and I have kept to the old-fashioned genera, merely trying to make their boundaries better defined where authors have differed in their rulings. Where possible I have followed Halle (1913). We can be nearly certain that some of these old genera, e.g. *Pterophyllum*, are rather heterogeneous, for very different flowers have been attributed to different leaf species and very likely all our leaf genera are heterogeneous in this sense. Though leaf species are strongly characterised by their cuticles, I can recognise no styles of cuticle characterising genera. At best certain groups of species, e.g. part of *Otozamites*, share a peculiarity.

Some of the terms used to describe leaf form lack precise definition and different authors vary, this is particularly true of the word auricle. All agree that the greatly enlarged basal angle of an *Otozamites graphicus* pinna is an auricle, the differences arise with smaller expansions. Thus in *Dictyozamites hawelli* where the basal margin is at right angles to the long axis of the pinna and then curves outwards to join the acroscopic margin, Seward calls this basal angle an auricle but most do not. In *Zamites gigas* where the pinna is attached by a small region in the middle of the basal margin the two basal angles are commonly of very similar shape. Most authors call neither an auricle but Semaka (1962) calls the distal one an auricle in the similar leaf, *Zamites schmiedeli*, and accordingly transfers it to *Otozamites*.

In this work I restrict it to pinnae with an asymmetric base, ones in which the attachment is nearer the basiscopic margin or ones in which the acroscopic angle is differently shaped from the basiscopic one. Then I restrict it to the pinnae in which the acroscopic angle is expanded, and I deem it expanded if the first acroscopic vein diverges from the long axis of the pinna at an angle greater than 90°. Even thus defined trouble is not wholly avoided for in certain unusual specimens of *Zamites gigas* for example, occasional pinnae would have to be defined as slightly auriculate.

On this definition of auricle, normal leaves of *Otozamites* have one while normal leaves of *Zamites* and *Ptilophyllum* do not.

It is tempting to avoid taxonomic difficulty in a particular flora by creating new genera and several have been made though they are not used widely. Every one of these genera creates fresh boundary problems. It is fortunate that the Bennettitales have escaped the multiplication of leaf genera that hampers work in some other families.

Bennettitalean flowers cause taxonomic difficulty because hardly any two are known equally and in precisely comparable ways, and rather few show convincingly the characters of the established flower genera. Again it seems wise to be cautious. I have kept *Williamsonia* for female flowers which convincingly show the generic characters; but ones in which these are merely guessed are placed in *Bennetticarpus*. I restrict *Williamsoniella* to hermaphrodite flowers with a peculiar kind of microsporophyll. The male flowers are all placed in *Weltrichia*, as I think should have been done long ago. *Weltrichia* could indeed be subdivided, but we have as yet so few species that this seems unnecessary and a nuisance.

All simple scale leaves with Bennettitalean stomata are placed in *Cycadolepis* and this removes a few generic names.

Key to the Yorkshire genera of leaves

1	Leaf simple	*Nilssoniopteris*
	Leaf divided into pinnae	2
2	Pinnae not contracted basally	3
	Pinnae contracted basally	4
3	Pinnae about as long as broad	*Anomozamites*
	Pinnae much longer than broad	*Pterophyllum*
4	Lower basal angle of pinna slightly expanded (decurrent)	*Ptilophyllum*
	Lower basal angle of pinna contracted	5
5	Pinna base symmetrical	*Zamites*
	Pinna base asymmetrical	6
6	Veins free	*Otozamites*
	Veins forming a net	*Dictyozamites*

Genus ZAMITES Brongniart 1828

Emended Diagnosis. Leaf simply pinnate, pinnae attached to upper side of rachis; pinnae lanceolate; base of pinna symmetrically contracted and attached by a small area in middle of basal margin; apex of pinna acute; veins diverging from pinna base, dichotomising but not anastomosing; ending in pinna margins and apex. Cuticle developed, stomata syndetocheilic with one subsidiary cell beside each guard cell; confined to under surface; epidermal cell walls sinuous.

Type Species. *Zamia gigas* Lindley & Hutton 1835, p. 45, pl. 165. (Selected by Andrews 1955, p. 261).

Key to the species of *Zamites*

Pinna broadest at a few cm. from the base	*Z. gigas*
Pinna broadest very near base	*Z. quiniae*

Zamites gigas also differs in many details of its cuticle, particularly in the crowded hair bases among the stomata, while *Z. quiniae* has only a few and these are different.

I have accepted specimens with broadly lanceolate pinnae as *Z. gigas* and accordingly I emphasise the symmetrical base of the pinna as the chief character for separation from *Otozamites*. As mentioned later a few specimens which I am sure are forms of *Z. gigas* have in fact a slightly asymmetrical pinna base. Semaka (1962) however, emphasising the expanded acroscopic angle rather than symmetry, places leaves like those described here in *Otozamites*.

Zamites gigas (L. & H.)

Text-figs. 1, 2

(Description written and figures drawn by Miss F. M. Quin)

The following are Yorkshire leaves. Other plant organs described as *Z. gigas* are omitted.

1822 (No name), Young & Bird, p. 182, pl. 2, fig. 2.
1828 (No name), Young & Bird, pl. 2, figs. 4, 6; pl. 3, fig. 2.
1835 *Zamia gigas* Lindley & Hutton, p. 45, pl. 165. (Good leaf.)
1841 *Zamites gigas* (L. & H.) Morris, p. 116. (Name.)
1875 *Zamites gigas* (L. & H.); Saporta, p. 87, pl. 81, fig. 1. (Leaves attached to stem, discussed by Seward 1900.)
1897 *Zamites gigas* (L. & H.); Seward, p. 273.
1900 *Williamsonia gigas* (L. & H.); Seward, p. 178, pl. 5 (leaf); pl. 7, fig. 4 (petiole base); pl. 7, fig. 6 (leaf). Other figures represent other organs; pl. 7, fig. 5 is *Z. quiniae*.
1900 *Otozamites acuminatus* (L. & H.); Seward, p. 214, pl. 2, fig. 1; pl. 6, fig. 1. (Leaves, see pp. 7, 19.)
1913 *Zamites gigas* (L. & H.); Halle, p. 375, pl. 10, fig. 7. (Good leaf, comparison.)
1913 *Zamites* (*Williamsonia*) *gigas* (L. & H.); Thomas & Bancroft, p. 184, text-fig. 31 (stoma of leaf); p. 185, pl. 19, fig. 2 (stoma of scale leaf).
1917 *Zamites gigas* (L. & H.); Seward, p. 532, text-fig. 599. (Reduced copy of leaf from Seward 1900.)
1932 '*Zamites gigas* (aggregate species)'; Harris, p. 97, text-fig. 39 A–C. (Stoma.)

Somewhat similar Middle or Upper Jurassic leaves have been described without microscopic details under the names:

Zamites feneonis by Ettingshausen (1852), Saporta (1875), Salfeld (1909), Oishi (1940).
Zamites moreaui, *Z. acerosus*, *Z. claravallensis*, *Z. fallax*, *Z. distractus*, *Z. confusus* by Saporta (1875).
Zamites schmiedelii (Sternberg) Semaka (1962).
Zamites weberi Seward (1907).

Most or all of these may be distinct but we lack the information about cuticles needed to make this certain. *Z. feneonis* as described by Carpentier (1938) has a distinct cuticle and is certainly different.

Emended Diagnosis. Petiole base expanded, striated; rachis striated with irregular short longitudinal grooves. Lamina as a whole, broadly lanceolate; typically 30 cm. × 12 cm., but often larger. Pinnae of uniform length and breadth over most of leaf, sometimes becoming shorter towards apex and base, typically 5–8 cm. by 0·6–1·0 cm., but occasionally up to 15 cm. long and 1·3 cm. wide; shape linear lanceolate to broadly lanceolate, typically straight but sometimes curving towards apex of leaf; lower two-thirds of pinna parallel-sided; tapering in upper third to an acute apex. Shorter pinnae tapering from near base, to a more obtuse apex. Base of pinna narrowed to about half at point of attachment, narrowing symmetrically, but occasionally upper side of pinna swollen and base therefore slightly asymmetrical. Pinnae with well marked rim on lower surface, typically 1 mm. wide. Veins forming well-marked ridges at a concentration of 15 per cm. Pinnae usually attached at about right angles in middle region of leaf becoming progressively more acute towards leaf apex; often pointing backwards at angle of about 110° at leaf base, but in some leaves angle less than 90° throughout.

Cuticle of pinna about 2μ thick above and 1μ below (measured in folds).

Upper cuticle showing uniform cells, forming longitudinal rows; cells rectangular. Lateral walls strongly sinuous, sinuosities mushroom shaped; surface flat, not papillate, nor distinctly sculptured; trichomes absent except at margins.

Lower cuticle composed of two regions, the main part and the marginal part. Main part

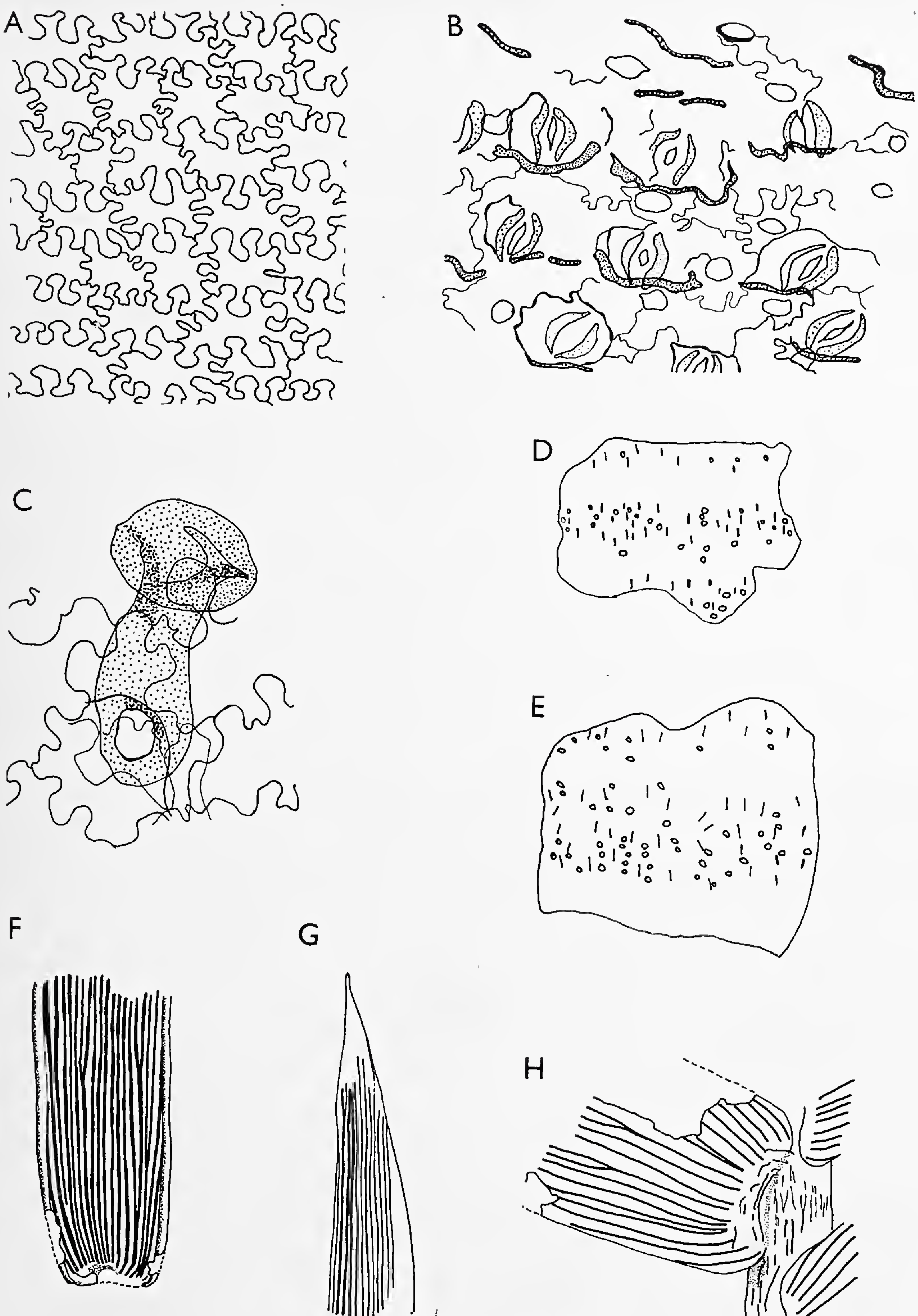

Fig. 1. **Zamites gigas** (L. & H.)
Drawings by F. M. Quin

A, upper cuticle, V.53004*a*, ×200. B, lower cuticle, a vein runs horizontally along the top, V.53004*b*, ×200. C, trichome type 2, V. 53482, ×800. D, lower cuticle with two veins, showing stomatal apertures and trichomes (rings), V.53483, ×40. E, lower cuticle; marginal region at bottom, V.53482, ×40. F, pinna base, lower surface showing margin, ×2. G, pinna apex, upper surface, J5002 Oxford Museum, ×4. H, pinna base and rachis, V.53009, ×4.

A and B are from Haiburn Beck; C and E from Snilesworth, Stoney Moor Sike 2; D from Gristhorpe, Yons Nab Marine Series; H from Saltwick, Waterfall.

showing stomata at a concentration of 100 per square mm.; stomata forming bands about 300μ wide between veins. Veins about 150μ wide often with slight compression folds present at sides. Epidermal cells along and between veins roughly square or irregularly shaped with sinuous walls, walls often obscurely marked, folds irregular, not highly thickened. Surface without papillae.

Stomata orientated transversely to the vein, sometimes slightly oblique in more or less regular rows, typically 5 rows in each intervenal band; spacing in rows not constant. Stomata sunken, guard cells and subsidiary cells found together at a deeper level forming the base of a shallow pit (pit depth estimated in an obliquely compressed stomata at 16μ). Margins of pits formed by adjacent cells, often overhanging subsidiary cells and forming well marked folds. Subsidiary cells smaller than epidermal cells, outlines not sinuous. Surface thin with no papillae. Guard cells well cutinised with crescent-shaped thickenings, typically 50μ long, aperture typically 22μ long.

Trichome bases very frequent, both on and between veins, irregularly spaced. Four types of trichome bases occur.

Type 1 of frequent occurrence, both on and between veins, irregularly spaced, consisting of small cell with sinuous walls bearing at middle a conspicuous hole, oval or circular in shape, varying from about 18μ–25μ. Cuticle around hole forming a short thin-walled tube, widest at base and narrowing to apex which is open.

Type 2 of less frequent occurrence, found at junction of main part of lower epidermis with the marginal region, and on veins; consisting of a small cell with sinuous walls from which protrudes a thick-walled mushroom-shaped closed tube composed of two distinct portions, stalk and head. Stalk about 45μ long and 25μ wide at base narrowing slightly towards top before expanding to form the spherical head, about 36μ wide.

Type 3, found very close to margin, composed of a cell with sinuous walls and covered

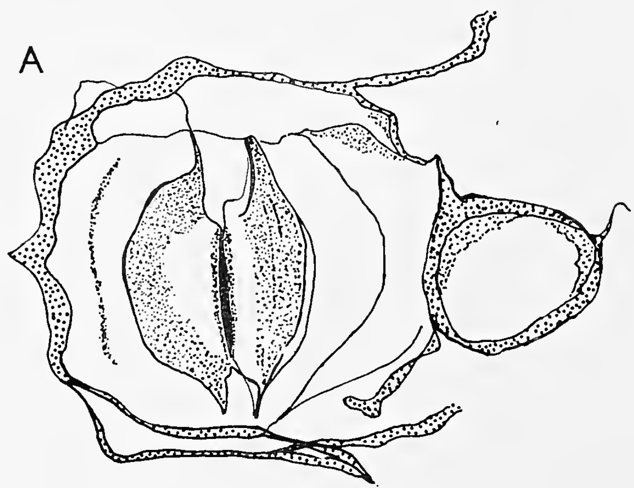

Fig. 2. **Zamites gigas** (L. & H.)
Drawing by F. M. Quin

Stoma and trichome of type 1. An encircling cell may be present. V.53482, ×800. Snilesworth, Stoney Moor Sike 2.

by a thick cuticle rising abruptly at centre of cell to form a short cone open at the apex by a small hole, about 6μ wide.

Type 4 also occurring at margin, composed of circular group of cells with sinuous walls and cuticles thinner than those of surrounding cells, rising slightly above level of epidermis (possibly forming base of a multicellular hair).

Marginal region of lower cuticle about 400μ wide, different from main part and very like upper cuticle. Stomata absent. Cells in longitudinal rows, rectangular with strongly marked sinuous folds, slight compression folds occurring between marginal and stomatal region.

LECTOTYPE. Specimen figured by Lindley & Hutton (1835, p. 45, pl. 165).

DESCRIPTION. Not only are the pinnae borne on the upper surface of the rachis, but the bases of the pinnae rise abruptly from the point of attachment before spreading out horizontally. Seward (1900) emphasised the basal callosity which he believed indicated the existence of a callus or thickening at the pinna base. I am sure that what is seen can be explained in terms of the compression and collapse of the upstanding part of the pinna base, resulting in the formation of a median concavity.

All pinnae have a contracted base of attachment and most are almost perfectly symmetrical. In a few specimens, however, some of the pinnae show slightly more enlargement above the point of attachment than below. (These specimens have normal *Z. gigas* cuticles). Such specimens do overlap the generic distinction from *Otozamites* to a slight extent. At the apex and base of some leaves, the pinnae do not show the typical *Z. gigas* linear-lanceolate form. They are short, typically 2·5 cm. long and 1·5 cm. wide at the base and narrow from the base to a less acute apex than is usual. In the middle region of the leaf, the typical *Z. gigas* form of pinna occurs. The smallest leaf seen has pinnae 25 mm. × 4·5 mm. but of normal shape and its cuticle is normal.

There is usually one subsidiary cell beside each guard cell. In certain cuticle preparations, obtained from bulk macerations, a pair of additional small cells lacking sinuosities and looking like the subsidiary cell occurred outside the usual subsidiary cells.

The short open tube trichome is the most abundant type. Occasionally the tube is closed by a delicate cap of cuticle, and it is probable that these are better preserved forms of the short open tube type described earlier.

DISCUSSION AND COMPARISON. *Zamites gigas* proves not to have been a satisfactorily understood leaf. Seward (1900) distinguished leaves or leaf fragments with broadly lanceolate and more gradually tapering pinnae as *Otozamites acuminatus* (L. & H.). I have examined all Seward's specimens given this name in the British Museum (Natural History) and am convinced that they are all *Z. gigas*. The form intergrades with typical *Z. gigas* and all specimens have typical *Z. gigas* cuticles. I have not examined the original of Lindley & Hutton's *Otozamites acuminatus* but the figure is different in showing distinctly asymmetrical pinna bases and I think it is *Otozamites graphicus*. I have examined the specimen figured by Phillips (1829) under the name *Cycadites latifolius* and included by Seward (1900) in '*Otozamites acuminatus*'. The leaf base is asymmetrical and the cuticle agrees with that of *O. graphicus*. *Z. gigas* is distinguished from *Z. quiniae* on p. 10.

Zamites ivanovii Kryshtofovich & Prinida as described by Samylina (1961) is like a form of *Z. gigas* with crowded pinnae. Its cuticle differs in lacking the ring shaped hair bases of *Z. gigas*.

As suggested in the synonymy, there are many specimens from the Upper Jurassic of France and some other countries which look much like *Z. gigas*, but none has been examined to provide the fine details needed for secure identification.

OCCURRENCE. *Z. gigas* is known from all stages in the Deltaic Series of Yorkshire; but nearly all good specimens are probably from near Whitby where it is abundant in the Abbey Cliff. Its distribution is as follows:

Upper Deltaic	6 localities
Middle Deltaic Gristhorpe Series . .	4 localities
Millepore Limestone Series . . .	1 locality
Middle Deltaic Sycarham Series . .	6 localities
Ellerbeck and Hydraulic Limestone Marine Series	2 localities
Lower Deltaic	23 localities

In view of the number (135) of Gristhorpe Series localities with determinable plants its rarity there is noteworthy. I reject a specimen (Oxford Museum J 500S) labelled 'Forchhammer 1837' and by another hand 'Gristhorpe' which I think most probably comes from Whitby.

Zamites quiniae sp. nov.
Text-fig. 3

1900 *Williamsonia gigas* (L. & H.); Seward, p. 185 (pars) – description of V.3514 and pl. 7, fig. 5 only.

DIAGNOSIS. Leaf as a whole probably lanceolate (middle and lower parts alone known). Rachis stout, longitudinally grooved, pinnae narrowly lanceolate, base rounded, width greatest just above base and then tapering evenly to acute apex. Bases of pinnae overlapping most or all of upper surface of rachis. In middle region of leaf, pinnae typically 65 mm. × 13 mm. up to possibly 100 mm. × 18 mm., straight, but in lower part of leaf pinnae becoming shorter and narrower; and curving forward. Pinnae arising at an angle of 70°–80° to rachis in middle of leaf but angle decreasing to about 40° below. Pinna margin making a thick rim about 0·6 mm. broad. Veins fine, diverging from region of attachment but nearly parallel in distal region of pinna, forking to maintain a concentration of 25–40 per cm.

Upper surface of pinnae glabrous, lower surface finely hairy, cuticles about 2μ thick. Upper showing uniform rectangular cells with strongly sinuous walls, sinuosities mushroom shaped. Cell surface flat, not strongly sculptured. Lower cuticle divided into two regions, main part and marginal part. Main part showing stomata at a concentration of about 100 per sq. mm.; stomata forming bands about 200μ wide between veins, separated by strips 50μ wide along veins, vein strips only showing very slight compression folds along their edges. Cells along veins elongated, lateral walls conspicuous, showing semicircular sinuosities, end walls less clearly marked and straighter, cell surface flat, not papillate or strongly sculptured. Stomata of stomatal strips variably orientated but mostly transverse, stomata not in longitudinal rows or only in very short rows. Cells of stomatal strips of irregular shape, walls sinuous, surface flat. Stomata scarcely sunken, subsidiary cells on surface and not overhung by surrounding cells. Subsidiary cells rather smaller than epidermal cells, outlines not usually sinuous. Surface distinctly thickened, not papillate. Guard cells with well developed crescent

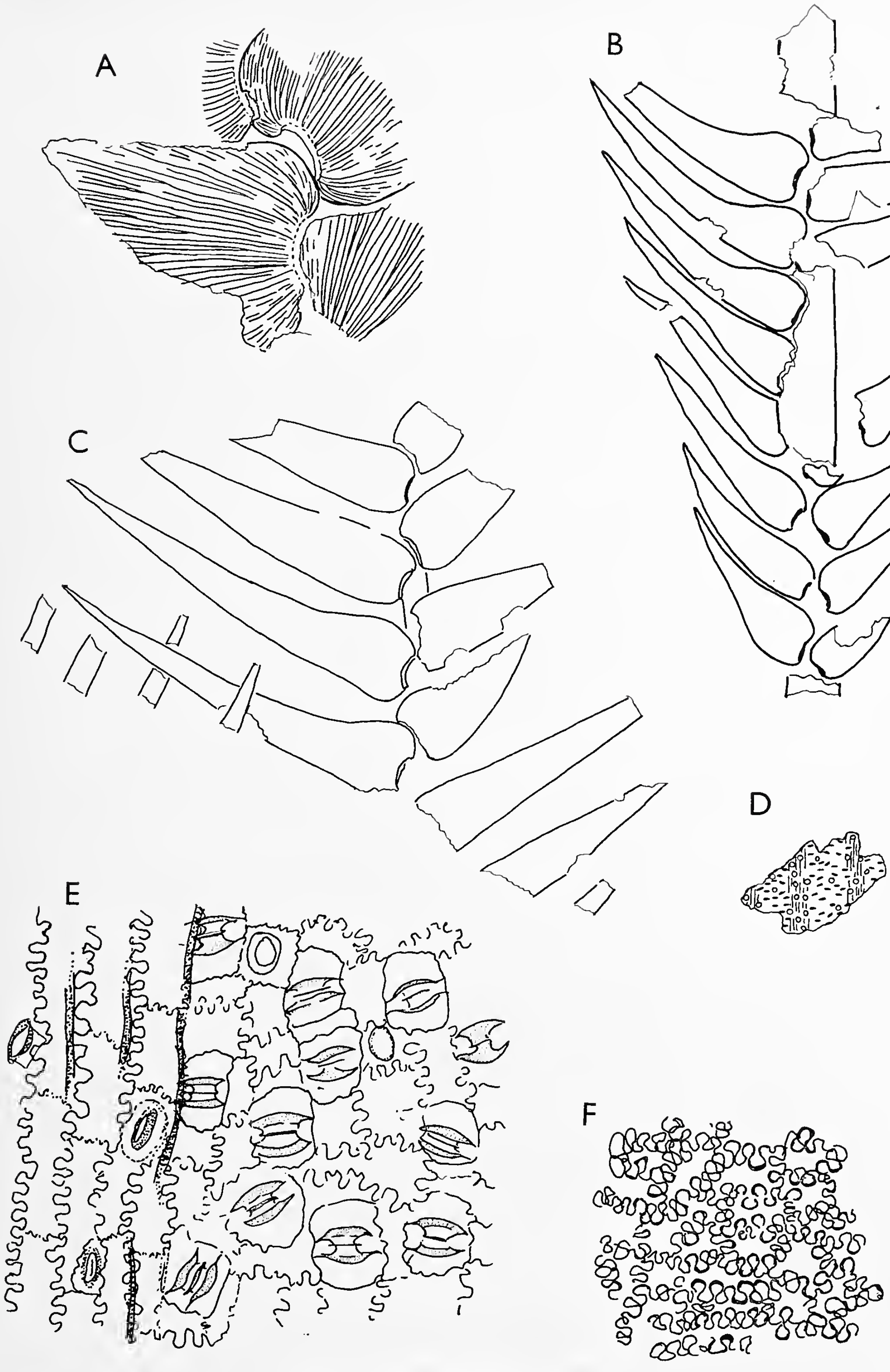

Fig. 3. **Zamites quiniae** sp. nov.

A, part of holotype showing veins, V.3514, ×2. B, base of leaf from fallen block at High Whitby, V.53020, ×1. C, middle region of leaf from Roseberry Topping, V.53019, ×1. D, fragment of lower cuticle showing veins, stomatal apertures (short black lines and trichomes (ring)). A few trichomes may have been missed, V. 3514*a*, ×20. E, lower cuticle showing folds by a vein, V.3514*a*, ×200. F, lower cuticle near margin, V.3514*a*, ×200. The upper cuticle is similar but has elongated cells.

shaped thickenings. Trichome bases of one type only, frequent on and between veins; consisting of small cell bearing thick oval area usually marked with thin longitudinal slit or occasionally broader thin area.

Cells of marginal region showing elongated epidermal cells with almost straight walls but with very slight ridges passing on to cell surface.

HOLOTYPE. V.3514, figured Seward 1900, pl. 7, fig. 5.

DISCUSSION. In addition to the holotype *Zamites quiniae* is represented by two specimens which Miss M. Quin picked out when working through the available material of *Z. gigas*. The holotype was partly figured by Seward (1900) and I now figure the whole after cleaning it. It is unlocalised and the matrix, while of a kind widespread particularly in the Lower Deltaic, is not characteristic. One other specimen was collected many years ago by Hamshaw Thomas from the Lower Deltaic of Roseberry Topping. The only other specimen was isolated on a fallen block near Whitby. No dispersed cuticle fragment has been found which could be identified as *Z. quiniae*.

COMPARISON. Seward determined the holotype as *Z. gigas* or possibly *O. acuminatus*. From *Z. gigas* it differs in the exceptional width of its pinnae which are widest very near their bases instead of at about 2 cm. I have abandoned the name *acuminatus* as a source of confusion; Lindley & Hutton's original which I call *O. graphicus* has an asymmetric pinna base, while the two specimens figured by Seward are fairly typical *Z. gigas*.

Thomas' specimen which had not been determined differs from the holotype only in its smaller size and less crowded pinnae.

The estimate of 'possibly 10 cm. long' given for the pinna is made on the assumption that the pinna of the holotype tapered evenly. The hairs on the under side of the lamina are clearly visible when it is moistened with oil, and a celloidin pull yielded fragments of what look like simple straight hairs, $150\mu \times 25\mu$.

Zamites quiniae is distinguished from *Z. gigas* both by its form and its cuticle. In both the pinnae have small basal areas of attachment and then expand almost symmetrically. In *Z. gigas* they retain their width for 2–4 cm., but in *Z. quiniae* they start to taper at once, that is within 1 cm. of the base. Thus the proximal parts of the pinnae in *Z. gigas* have parallel sides but those of *Z. quiniae* do not. *Z. quiniae* also has distinctly broader pinnae. Both have thickened margins and similarly distributed stomata, but in *Z. gigas* the stomata form well marked longitudinal files while those of *Z. quiniae* are scattered in the areas between veins. In *Z. gigas* they may be more strictly transverse and the whole apparatus is slightly sunken, but superficial in *Z. quiniae*. There are more trichome bases among the stomata in *Z. gigas* and the hair bases are round but often elongated in *Z. quiniae*.

OCCURRENCE. *Zamites quiniae* is a rare species of the Lower Deltaic. The three specimens are from different localities.

Genus OTOZAMITES Braun 1842

TYPE SPECIES. Perhaps *Filicites bechei* Brongniart or *Filicites bucklandi* Brongniart 1825.

Kilpper (1965) recommends that *Otozamites* Braun be conserved against *Otopteris* L. & H. I agree.

The first described species of *Otopteris* is *O. obtusa* L. & H. 1832, but a still earlier name of this species is *Filicites bechei* Brongniart 1825 (for the 'Fossil Fern' of de la Beche – see Harris 1961). In the same paper Brongniart described *F. bucklandi* which is probably the same, and *F. bucklandi* var. *oolitica* which may be the same as *O. graphicus*.

Otozamites is distinguished from *Zamites* by the asymmetry of the pinna base. In *Otozamites* the pinna is usually attached below the middle and the acroscopic basal angle is enlarged as an auricle, while in *Zamites* the pinna is attached at the middle of the base and the two basal angles are equal. *Ptilophyllum* differs in the base of its pinnae, the lower basal angle is decurrent. These characters are shown best by pinnae of the middle two-thirds of the leaf. Certain species come very close to the borders between genera as indicated here and occasionally in a species which otherwise falls satisfactorily into one of these genera an unusual leaf shows the pinna base of a different genus.

Most species of *Otozamites* are readily distinguished from *Zamites* by the distinct asymmetry of the leaf base which forms an auricle overlapping the rachis and from *Ptilophyllum* by the contraction of the basiscopic basal angle of the pinna. Sometimes these features are hard to recognise and certain specimens of certain species might be placed in a different genus from the bulk of the specimens of the same species. The small pinnae of the leaf apex and base may fail to show their character, even in a leaf where the pinnae of the whole middle region are strongly characterised.

In the following field key I have used pinna shape and dimensions over the middle two-thirds of the leaf. A fraction, possibly as great as one-tenth of the leaves of a species, may be abnormal enough to be placed wrongly on this character, but most commonly the leaves are gregarious in the field and this difficulty may not matter. 'Auricle height' is taken by first imagining the leaf base like the lower side above as well as below and then the excess extension of the upper angle (auricle) is measured.

Field Key to the Yorkshire species of *Otozamites* based on the middle region of a typical leaf

1	Leaf over 4 cm. wide	2
	Leaf under 4 cm. wide	9
2	Auricle large (crossing rachis)	3
	Auricle small (not crossing rachis)	5
3	Pinna length over 3 × width	4
	Pinna length under 3 × width	*O. beani*
4	Pinna over 4 mm. wide at middle	*O. graphicus*
	Pinna under 4 mm. wide at middle	*O. gramineus*
5	Pinna apex obtuse	6
	Pinna apex acute	8
6	Pinna length over 4 × width	*O. venosus*
	Pinna length under 4 × width	7
7	Pinna attached at basal angle only	*O. thomasi*
	Pinna attached by half of basal margin	*O. parallelus*
8	Attachment by half of pinna base, veins 40 per cm.	*O. leckenbyi*
	Attachment by one-third of pinna base, veins 50 per cm.	*O. venosus*
9	Veins fewer than 20 per cm.	*O. anglica*
	Veins more than 20 per cm.	10
10	Leaf over 2 cm. wide	11
	Leaf less than 2 cm. wide	15

11	Pinna rounded, with a sharply defined margin	*O. marginatus*
	Pinna elongated, margin not sharply defined	12
12	Margins of pinnae parallel	*O. parallelus*
	Pinnae tapering from base	13
13	Leaf linear (30 cm.), underside densely hairy	*O. simpsoni*
	Leaf linear to lanceolate 15–20 cm., underside with few hairs	14
14	Pinnae separate, leaf usually over 2·5 cm. broad	*O. leckenbyi*
	Pinnae often crowded, leaf often under 2·5 cm. broad	*O. penna*
15	Pinna length up to 2 × width	16
	Pinna length over 2 × width	18
16	Pinnae round, attachment narrow	*O. tenuatus*
	Pinnae not round, attachment broad	17
17	Pinna apex rounded	*O. mimetes*
	Pinna apex truncate	*O. falsus*
18	Underside densely hairy	*O. simpsoni*
	Underside sparingly hairy	*O. penna*

Exceptional specimens would be wrongly placed in this key and all determinations need confirmation by the cuticle.

Cuticle fragments resembling those of one or another of the *Otozamites* species are frequent in bulk macerations and many hundreds of microscopic preparations were made from shales of some 200 localities. In the end I decided that it was wiser not to determine them as there are so many Yorkshire *Otozamites* species already and few of them are uniquely distinguished by their cuticles alone. In addition to those that I had tentatively determined there were a few dozens which apparently represent species not hitherto recognised in Yorkshire. Again it seemed a mistake to describe them as new, particularly as many of them cannot even be placed securely in their genus. What is clear is that the numerous Bennettitalean leaf species described here do not exhaust the flora.

Otozamites beani (L. & H.)

Text-figs. 4, 5

The following are all Yorkshire specimens:

1832 *Cyclopteris Beani* Lindley & Hutton, p. 127, pl. 44. (Good leaves.)
1849 *Otozamites Beani* (L. & H.) Brongniart, p. 106. (Name.)
1864 *Otopteris mediana* Leckenby, p. 78, pl. 10, fig. 2. (Good leaf.)
1875 *Otozamites Beanii* (L. & H.); Phillips, p. 220, lign. 45. (Poor figure, probably redrawn from Lindley & Hutton.)
1875 *Otozamites Beani* (L. & H.); Saporta, p. 128, pl. 95, fig. 2. (Good leaf.)
1900 *Otozamites Beani* (L. & H.); Seward, p. 207, pl. 1, figs. 3, 4; pl. 2, fig. 3. (Good leaves.)
1900 *Otozamites* sp. cf. *O. Beani* (L. & H.); Seward, p. 210, text-figs. 37, 38. (Leaf fragments.)
1944 *Otozamites beani* (L. & H.); Harris, p. 419, text-figs. 1, 2. (Veins, cuticle, figures repeated here.)
1950 *Otozamites beani* (L. & H.); Harris, p. 570, text-fig. 4 D. (Epidermal cell, comparison with *O. graphicus*.)

See p. 16 for a list of specimens from other floras which more or less resemble *O. beani*. None of these is here regarded as securely identified with *O. beani*.

Emended Diagnosis. Leaf as a whole of medium size, shape as a whole narrow lanceolate with tapering base and more gradually tapering apex. Length typically 30 cm., width in middle typically 5 cm. but larger and also smaller leaves occurring. Petiole short, widening below, longitudinally striated. Pinnae in middle region typically with their long axis at an angle of about 70° to rachis, but angle reduced near apex and increased near base. Pinnae of middle region typically ovate or ovate-rhomboid about 30 × 15 mm. or proportionately larger, but often relatively broader; towards leaf apex pinnae becoming narrow and lanceolate, towards base of leaf becoming at least as broad as long and rounded or broadly triangular. Shape of pinnae of middle region most frequently broadly oval or obtusely pointed, but sometimes between oval and broadly rhomboid or rectangular. Region of attachment always contracted, usually near basiscopic angle, but sometimes near middle of basal margin. Acroscopic angle overlapping rachis strongly and usually concealing it entirely, rounded, not usually much expanded (except in so far as the asymmetric pinna base makes it appear ex-

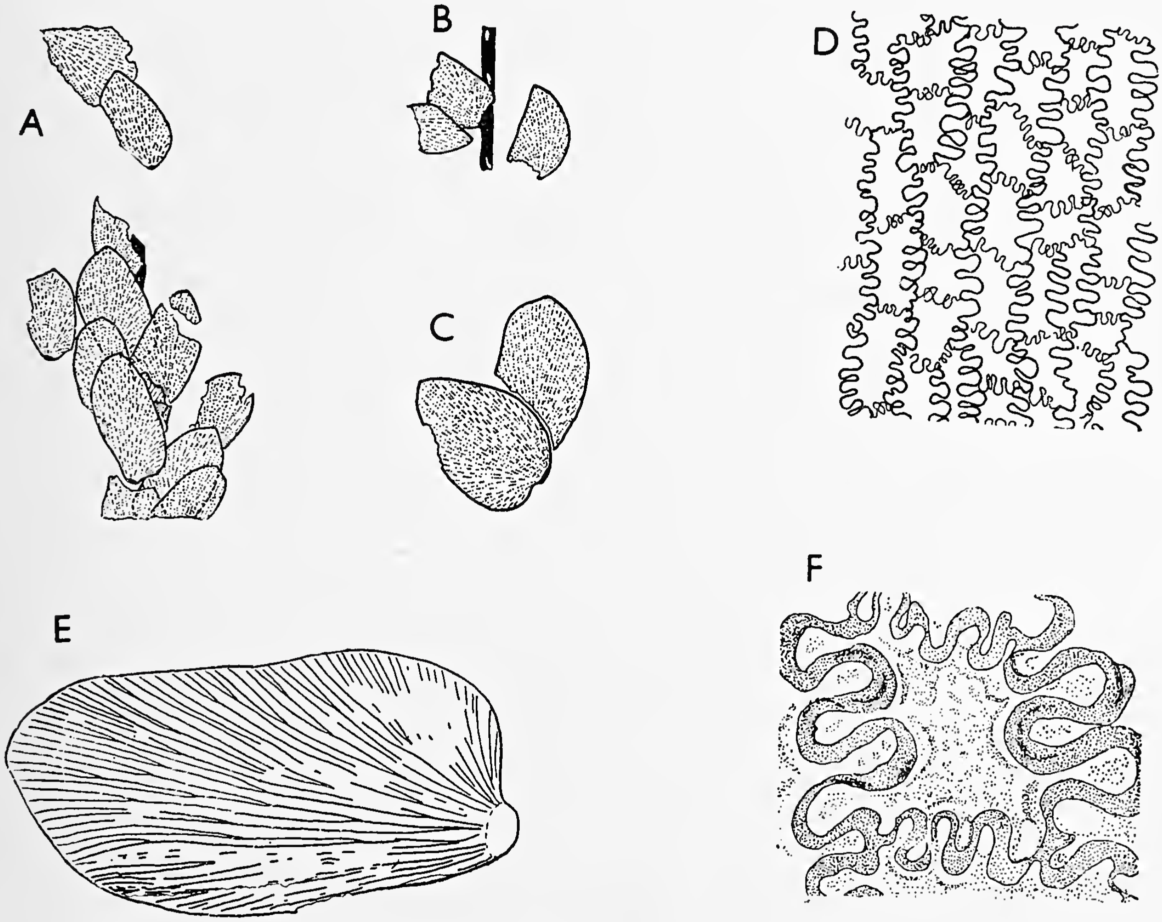

Fig. 4. **Otozamites beani** (L. & H.)

A, B, C, fragments of leaves (V.26878, V.26880, V.26879). The stippling represents the direction of veins, but not individual veins; in A, which is drawn from above, overlapped parts are indicated by broken lines. All ×1. D, upper cuticle, V.26879, ×200. E, one pinna from A, ×4. F, one cell of upper cuticle, V.26879, ×800.

panded). Margins of pinna distinctly thickened, forming a rim on under side; adaxial surface distinctly convex.

Veins rather obscurely marked above, more conspicuous below (where they are distinguished by the longer cells), but under surface often obscured by hairs. Veins fine, radiating from point of attachment, forking to maintain a concentration of about 40 or 50 per cm.

ending in the marginal rim. Substance of lamina moderately thick, obscurely marked by transverse ridges. Epidermal cells smooth and inconspicuous above, but more conspicuous and papillate below unless concealed by hairs.

Upper cuticle about 3μ thick (in folds), lower rather less. Upper showing almost uniform rectangular cells with very coarsely sinuous lateral walls and more finely sinuous end walls. Veins scarcely indicated. Lateral wall folds typically about 9μ apart (crest to crest); crests of folds often thickened; remaining surface of cell flat and obscurely mottled; no papillae present.

Lower cuticle divided into a marginal rim resembling the upper cuticle and main region showing equally wide bands along veins (without stomata) and intervenal bands with stomata. Epidermal cells along veins elongated and tending to be rectangular, those between veins irregular. Anticlinal walls often inconspicuous, strongly sinuous. Surface wall finely mottled and each cell bearing conspicuous, hollow papilla. Trichome bases frequent, consisting of isolated cells with a thickened surface and a ring shaped scar. Free part of trichome not always retained, $30 \times 250\mu$, uncutinised, simple, tapering to a point.

Stomata often forming one, two or three rows between veins, but irregularly spaced and rows sometimes indefinite. Aperture transverse to veins. Guard cells and subsidiary cells both deeply sunken at bottom of large oval pit formed by about six surrounding epidermal cells, mouth of pit on general surface, constricted by irregular ingrowths of epidermal cells; mouth of pit not above guard cells but nearer rachis. Subsidiary cells small, outer wall strongly marked, forming an arc parallel with guard cell thickening, not sinuous; surface not papillate.

DISCUSSION. There is little reason to attribute any other organs to the same plant as *O. beani*. The hairy scale leaf *Cycadolepis eriphous* has been noted (Harris 1953) in association at its one locality with *O. beani* as well as *O. graphicus*; while the female flower *Williamsonia himas* was noted in association with *O. beani* (the bracts of *W. himas* are however quite different from *C. eriphous*). Such associations provide a suggestion and if supported by further association would give useful evidence.

O. beani is widespread but mostly as fragments, although there are a few fine specimens in the old collections. When preserved as a cast in sandstone, or in a hard ironstone, the pinnae have a convex surface. The veins are always fine and crowded, even in large leaves. Seward (1900) refers to a petiole 9 cm. long (B.M.N.H. no. 13500), but I feel sure that a number of the lower pinnae of this specimen had been lost and so the petiole length seems exaggerated.

The specimens figured by the older authors show the shape of the leaf and pinnae very well but the veins, if sketched at all, are shown too far apart.

The thin covering of trichomes on the underside is best seen when the imprint of the underside is mounted in oil, or else transferred. Some specimens show very few hairs, but they may have been lost before preservation. Some variation was noted in the cuticle; the papillae may be larger and more conspicuous than in the specimen figured (when cell outlines are scarcely to be seen). Certain specimens have round stomatal pits, and the aperture of the pit is occasionally wider than in the specimen figured.

COMPARISON. *O. beani* seems not to have been confused with other Yorkshire species, unless perhaps the leaf apex (with its narrow pinnae) has been taken for a small *O. graphicus*. A few *Otozamites* leaves of other countries have been closely compared or even identified with it, but these comparisons assumed that the veins were much as figured earlier – that is

10–20 veins per cm.; they are in fact at 40–50 per cm. None of these specimens can now be accepted as similar at least until it is re-examined.

The cuticle of *O. beani* is very like that of *O. graphicus* but the two are usually distinguishable. One difference is that *O. beani* has many trichome bases on the underside, and another

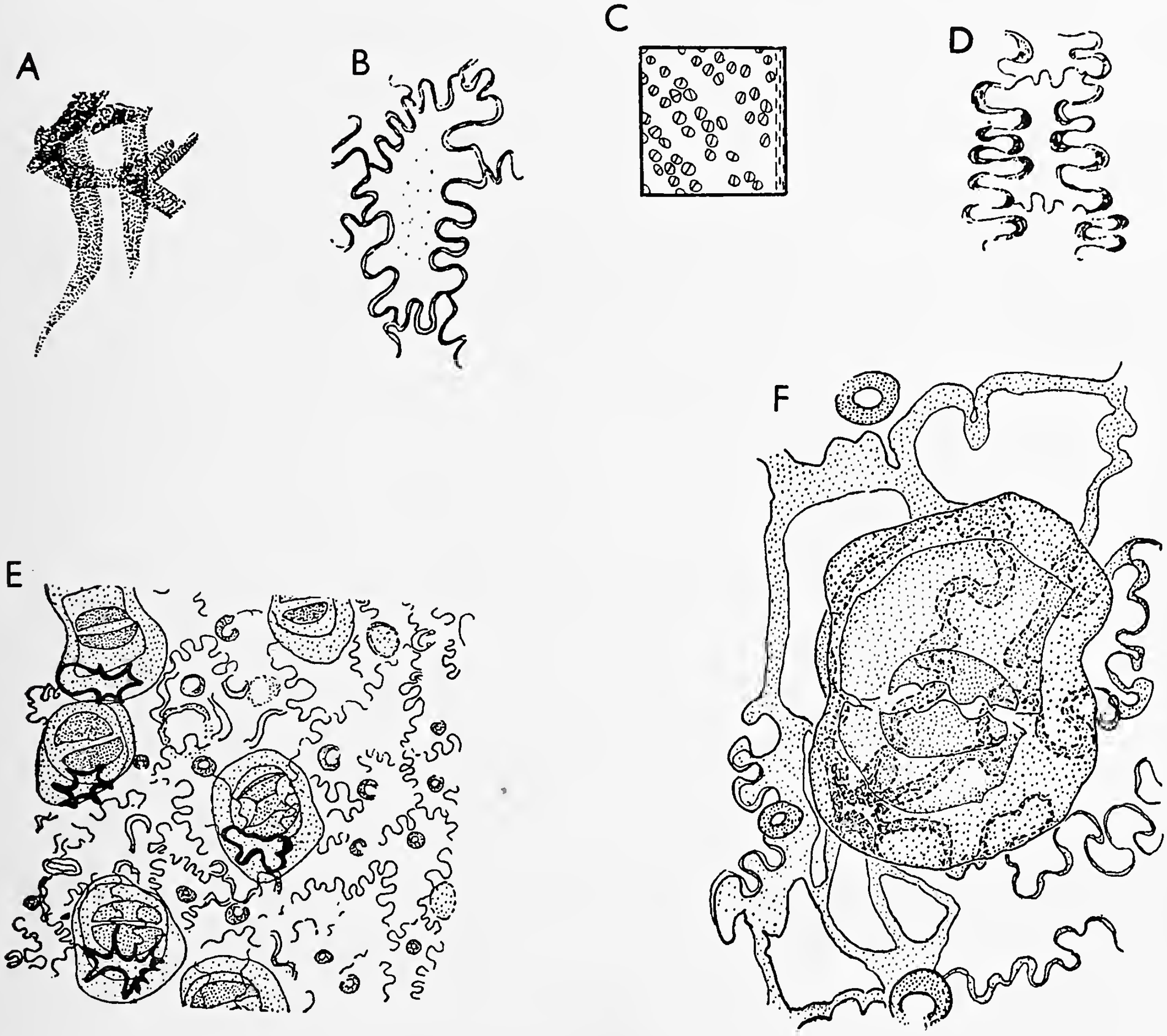

Fig. 5. **Otozamites beani** (L. & H.)

A, hairs on under surface; seen on transfer from imprint of under side, V.53493, ×100. B, typical cell of marginal region of under side, V.27717, ×500. C, distribution and orientation of stomata in 1 sq. mm. of under surface. The margin is to the right. D, typical cell of upper cuticle. The ends of the folds project from the flat plane, V.27717, ×500. E, lower cuticle, the cells on the left are over a vein, V.26878, ×200. F, stoma, from within, V.26878, ×800. B, D are from Harris (1950); C, E, F from Harris (1944).

is that on the upper side the cell wall folds average less than 10μ apart, but in *O. graphicus* they commonly average more.

The following leaves all looking like *O. beani* have less crowded veins and are no doubt distinct. These specimens (which have all been identified as *O. beani* by authors) are:

1875 *Otozamites marginatus* Saporta, p. 168, pl. 39, fig. 1, 1*a*, 1*b*. (Identified by Oishi 1940.)
1881 *Otozamites Trevisani* Zigno, p. 99, pl. 37, figs. 7, 8. (Identified by Oishi 1940.)
1894 *Otozamites obtusus* L. & H.; Bartholin, p. 93, pl. 10, figs. 6, 9. (Identified as *O. beani* by Seward 1903; Liassic of Bornholm.)
1940 *Otozamites beani* (L. & H.); Oishi, p. 328, pl. 29, figs. 7, 8*a*. (Detached pinnae. Jurassic; Japan.)
1940 *Otozamites klipsteinii* (Dunker); Oishi, p. 331, pl. 29, fig. 8*b*; pl. 30, fig. 6; pl. 31, fig. 2. (These and the previous Japanese Jurassic specimens have less crowded veins.)
1961 *Otozamites cf. beani* L. & H.; Kimura, p. 27, text-fig. 5. (Lower Cretaceous; Japan.)

The Wealden *O. klipsteinii* which as Seward (1895, p. 61) remarks is rather like *O. beani* has not been confused with it as its leaves are two or three times as broad.

OCCURRENCE. *O. beani* though seldom abundant occurs throughout the Deltaic Series both as hand specimens and as determinable cuticle fragments. It is distributed as follows:

Upper Deltaic	8 localities
Middle Deltaic Gristhorpe Series . .	17 localities
Millepore Bed	2 localities
Middle Deltaic Sycarham Series . .	2 localities
Lower Deltaic	10 localities

It is relatively rare in the Lower Deltaic (which has 238 localities with determinable plants), in fact its relative frequency probably increases slightly with time. The Type locality is the Gristhorpe Bed (where it is uncommon), but most of the best specimens both in the British Museum (Natural History) and in the Leckenby Collection at Cambridge, are probably from the Cloughton *Solenites* Bed.

Otozamites graphicus (Leckenby)
Text-figs. 6, 7

The following are Yorkshire specimens:

1828*a* *Zamia Youngii* Brongniart, p. 94. (*Nomen nudum*. See Saporta 1875 below.)
?1828*a* *Zamites laevis* Brongniart, p. 94. (*Nomen nudum*. See Saporta 1875 below.)
1829 *Cycadites latifolius* Phillips, pl. 10, fig. 1. (Inaccurate figure of specimen in York Museum.) See Saporta (1875) under *O. Youngii*, specimen redrawn here.
1829 *Cycadites lanceolatus* Phillips, pl. 10, fig. 3. (Specimen at Oxford Museum. Inaccurate figure.)
1834 *Otopteris acuminata* Lindley & Hutton, p. 141, pl. 132. (Specimen at Scarborough Museum.)
1864 *Otopteris graphica* Leckenby, p. 78, pl. 8, fig. 5. (Specimen K.215 in Leckenby Collection, Cambridge.)
1875 *Otozamites graphicus* (Leck.) Phillips, p. 222, lign. 49.
1875 *Otozamites acuminatus* (L. & H.) Phillips, p. 222, lign. 50. (? Redrawn from Leckenby.)
1875 *Otozamites obtusu* (sic) Phillips, p. 222, lign. 48.
1875 *Otozamites lanceolatus* (Phillips) Phillips, p. 223, pl. 10, fig. 3. (As 1829.)
1875 *Otozamites latifolius* (Phillips) Phillips, p. 224, pl. 10, fig. 1. (As 1829 and see Saporta (1875) under *O. Youngii.*)
1875 *Otozamites graphicus* (Leck.); Saporta, p. 153, pl. 103, fig. 2. (Copied from Leckenby.)
1875 *Otozamites Youngii* (Brongniart) Saporta, p. 128, pl. 96, fig. 1. (Same specimen as Phillips' *O. latifolius* and origin of Brongniart's 1828 *Zamia Youngii*. Phillips' whole specimen refigured more accurately but outlines of pinnae and rachis restored.)
1875 *Otozamites pterophylloides* Brongn.; Saporta, p. 163, pl. 107, fig. 3 only. (Also named *O. acuminatus* Bgt.)
?1875 *Otozamites laevis* Brongniart; Saporta, p. 127, pl. 94, fig. 3. (But only if veins are badly drawn.)
1900 *Otozamites graphicus* (Leck.); Seward, p. 213, pl. 1, fig. 2; pl. 2, fig. 6. (Good drawings of pinnae.)
1950 *Otozamites graphicus* (Leck.); Harris, p. 561, text-figs. 1–3, 4 A–C. (Leaf form, venation, cuticle.)

The specimens from Marske described as *O. graphicus* by Thomas (1913, p. 238) and by Thomas & Bancroft (1913, pl. 19, fig. 4) differ in cuticle.

Somewhat similar specimens from other regions:

1825 *Filicites Bucklandii* var. *gallica* Brongniart, p. 422, pl. 19, fig. 3. (Refigured by Saporta (1875, pl. 103) as *O. graphicus.*) Bathonian; France. See p. 19.

1875 *Otozamites graphicus* (Leck.); Saporta, p. 153, pl. 103, fig. 3. (Brongniart's *F. Bucklandi* var. *gallica* refigured.)

1904 *Otozamites* sp. indet., Seward, p. 116, no figure. Lower Oolite; English Midlands (specimen in Oxford Museum).

In addition there are many specimens of somewhat similar form which are imperfectly known, and in the absence of microscopic details are not fully distinguishable. Such specimens have been described under the names of *O. bechei* and *O. pterophylloides.*

Also a series of leaves from the Bathonian of France figured under the names *O. recurrens*, *O. brongniarti*, *O. pterophylloides* and *O. decorus*. The Liassic leaves figured by Saporta (1875) under the names *O. obtusa*, *O. brevifolius*, *O. hennoquei* and *O. disjuncta* are also of similar appearance.

Emended Diagnosis. Leaf large, estimated length 50–70 cm., shape of leaf as a whole lanceolate with a tapering base and apex. Middle region of full-sized leaf up to about 10 cm. broad, but smaller leaves only half as broad. Pinnae over most of the leaf arising at an angle of 70°–80°, but arising at a smaller angle near the apex. Pinnae of middle region typically 5 cm. long, 8 mm. broad above the auricle, varying from nearly straight to slightly falcate. Pinnae becoming shorter but also relatively narrower in upper part of leaf and the auricle being scarcely developed. Near the leaf base, pinnae becoming shorter but still broad with a well-developed auricle. Pinnae in some leaves in contact, on others separated by 1–2 mm. Auricle well developed in middle region of leaf, rounded, enlarging width of pinna by 2–4 mm., often overlapping the auricle of the opposite side. Apex of pinna very varied; rounded, obtuse, acute, acuminate or irregular; different forms occurring in adjacent pinnae.

Veins arising from proximal half of pinna base and radiating into the auricle and rest of pinna, those of the auricle being less conspicuous. Veins not very prominent, traversing lamina at a concentration of 27–37 per cm., branching at all levels. Margin of pinna flat and unspecialised, both surfaces glabrous, substance of lamina not very thick.

Rachis showing slight longitudinal striae but no wrinkles, without hairs. Rachis up to 6 mm. thick.

Cuticle moderately thick (1–2μ) on both sides, the upper being the more fragile.

Lower cuticle divided into two regions, the main part and the margin. Main part showing stomata at a concentration of about 70 per sq. mm., stomata forming broad bands between veins. Epidermal cells usually rather obscurely marked, shape roughly square or irregular, margins with strong rounded, sinuous folds. Surface bearing a single conspicuous hollow papilla of thickened cuticle. Surface not markedly sculptured. Cells forming longitudinal rows but rows not obvious among stomata.

Stomata always transversely orientated, often forming two somewhat regular files, but sometimes irregularly placed in a broader band and then not forming definite files. Stoma and subsidiary cells sunken, at bottom of large oval pit. Subsidiary cells small, surface not much thickened, forming an oval group. Stomatal pit covered by about eight epidermal cells which form a dome-shaped roof with a round or stellate hole. Roofing cells somewhat thickened towards the hole, their free margins bulging more or less over the hole as thick-walled but hollow papillae. Margins of roofing cells at first sinuous, but becoming straighter and thicker

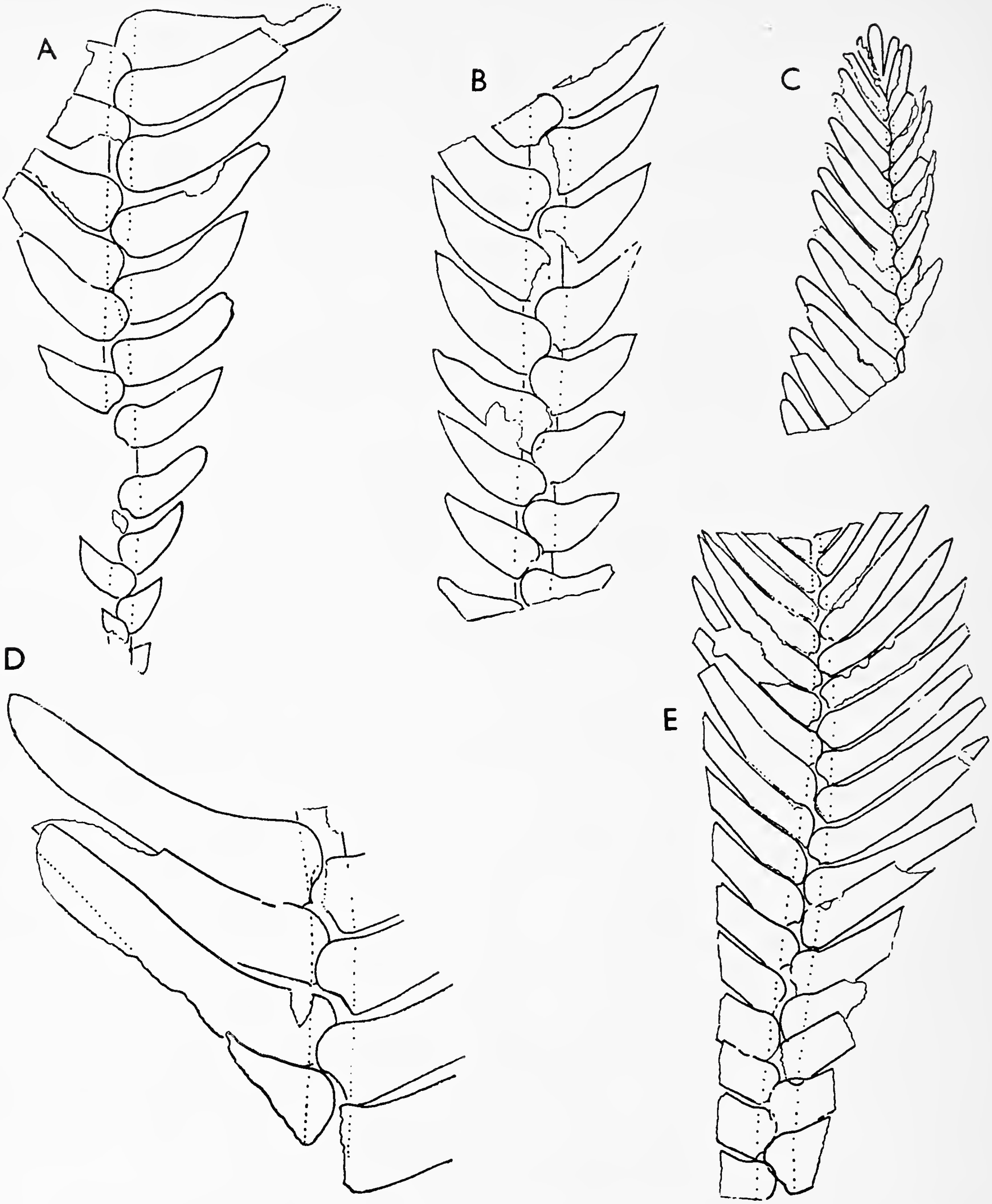

Fig. 6. **Otozamites graphicus** (Leckenby)

A, rapidly tapering leaf base, Oxford Museum, J.5011, labelled '*O. obtusa*', ×1. B, more gradually tapering leaf base, Yorkshire Museum specimen 'York 2' labelled '*Otopteris acuminata*', ×1. C, apex of leaf, Oxford Museum J.5018, labelled '*O. gramineus*', ×1. D, pinnae from the base of a fragment 24 cm. long. At the top of the fragment (where the rachis is still 1–2 mm. wide) the pinnae are 3 cm. × 0·4 cm. and have scarcely developed auricles. Oxford Museum specimen labelled '*O. obtusus*' (crossed out) and '*O. pterophylloides* Sap. J.T.R.', ×1. E, middle and upper parts of leaf, Oxford Museum J.5015, labelled '*Otoz. pterophylloides* Sap. J.T.R.', ×1.

The figures are taken from Harris (1950).

near the hole. Hole not situated over stoma but at end near rachis, while stoma is at distal end.

Marginal region of lower side (up to 200μ) widely different from the rest and approaching the upper side in structure. Stomata absent. Cells almost uniform, feebly or not at all papillate, lateral walls exceptionally strongly marked, showing rounded sinuosities.

Upper cuticle showing almost uniform cells; veins scarcely indicated. Cells rectangular, forming longitudinal rows. Lateral walls showing strong rounded sinuosities averaging about 13μ from crest to crest. Surface flat, non-papillate, obscurely sculptured.

Discussion. The finest specimen known to me is specimen K.225 in the Sedgwick Museum, Cambridge. It is a fragment of barely average width (7 cm.), its length is 39 cm. and shows the petiole base, lower, middle and some of the upper parts of the leaf but not the apex. The petiole expands to 18 mm. wide at its very base.

Name. Although *O. graphicus* is a familiar and definite species, its name is certainly not valid. I continue to use the name because I cannot be certain which of the possible older names really does refer to the present species. There is no question of conservation.

Very possibly the French Bathonian fragments described by Brongniart (1825) under the name *Filicites Bucklandi* var. *gallica* refers to this species, in which case it is its earliest name. The name *Filicites Bechei* refers primarily to another species (de la Beche's 'fern' from the English Lower Lias); the status of the other name is not clear to me. In any case the specimens are poor and if as I suspect they have no cuticles they are not precisely determinable and in my view unworthy to be Types. Brongniart's specimen of *F. Bechei* was determined by Lignier (1910) as *Zamites approximatus* Eichwald, but Zeiller (1912) upheld the name *Bechei* and gave it priority over *obtusus*, *Brongniarti*, *approximatus* and *Bucklandi*.

Cycadites latifolius Phillips 1829 proves to be very like typical *O. graphicus* though this would never have been guessed from Phillips' figure. Its pinnae are, however, broader than in any other specimen of *O. graphicus* and this does raise some doubt about its identity. Phillips' figure shows a narrow rachis (it was still largely covered by rock) and about 7 veins per cm. instead of about 40, and the restoration of the pinna bases is wrong. (The figure, like all Phillips' early lithographs, is a mirror image.) Saporta's (1875) figure of the same specimen is better but again is partly a restoration, the pinna bases are still shown as perfect where they are in fact broken. The top pinna which has been drawn again is, however, nearly complete and shows most of its auricle. The veins are drawn as well as I could (they are only partly visible). The cuticle agrees with that of typical *O. graphicus*.

Cycadites lanceolatus Phillips 1829 may also refer to the present species, but I have not examined the specimen.

The first good figure is *Otopteris acuminata* Lindley & Hutton 1834 (pl. 132), a careful drawing of typical specimens from two parts of the leaf. Unfortunately the name *acuminata* became applied to forms of *Zamites gigas* and (in old Museum collections) to a number of other species of *Otozamites* and no doubt as a result of this confusion its use has been dropped.

Otozamites graphicus is well represented in the older collections, and there is seldom difficulty in determining it (see *O. beani* on p. 15).

There are, however, a number of other Yorkshire leaves which resemble *O. graphicus* in form, though not exactly, and which differ considerably in cuticle. Two of these are described here, namely *O. venosus* and *O. thomasi*. This group all have exposed stomata, while *O. graphicus* has stomata sunk at the bottom of oval pits. I have examined many preparations of

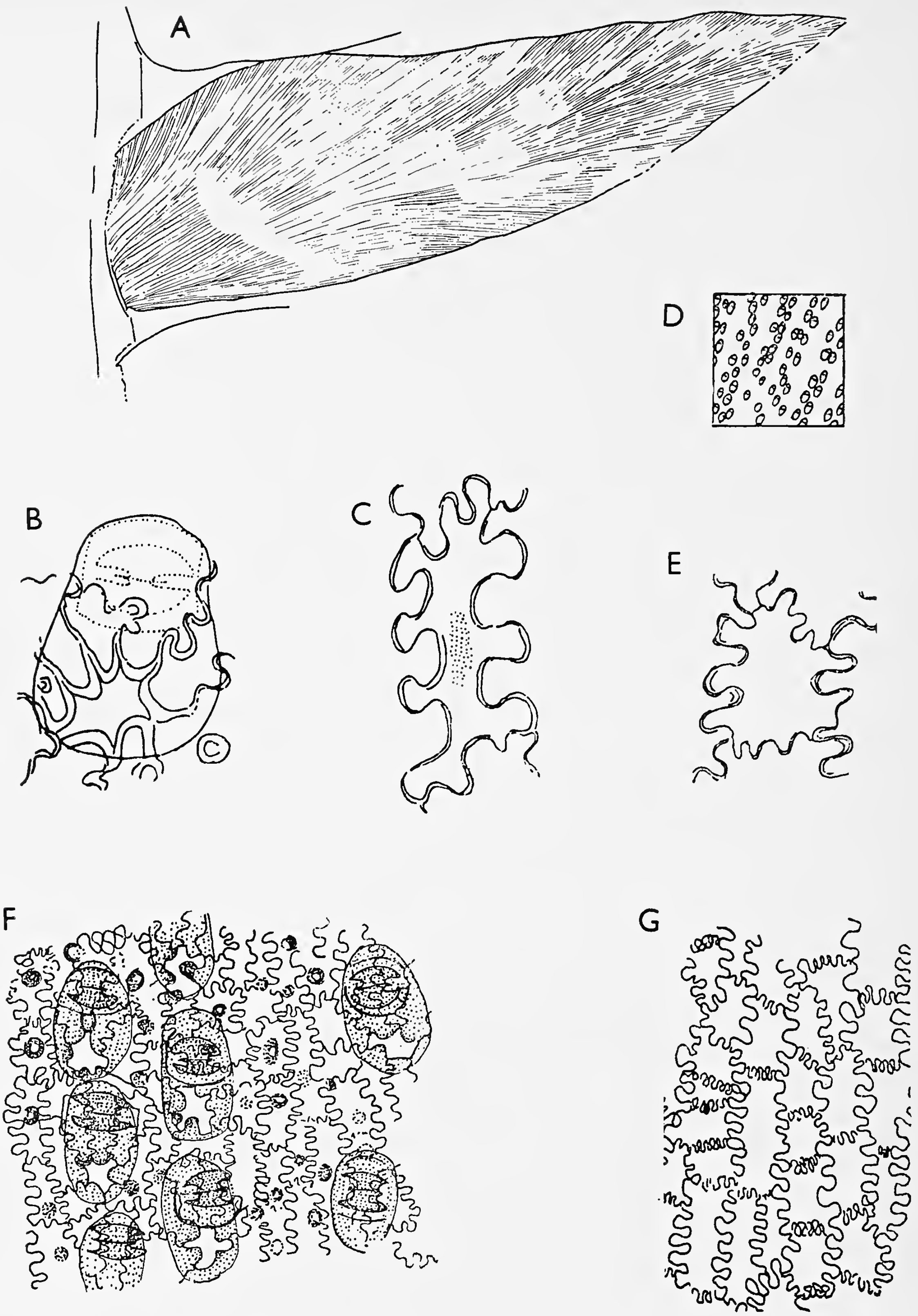

Fig. 7. **Otozamites graphicus** (Leckenby)

A, pinna of specimen from Saltwick figured by Phillips (1829, pl. 10, fig. 1) as *Cycadites latifolius* (also labelled *Otozamites latifolius* and *Otopteris acuminata*, 5497 Yorkshire Museum). A little of the auricle has been broken away (it probably just crossed the rachis) and many of the veins are too obscure to represent, ×2. B, stoma (from the outside), V.27687*b*, ×400. C, cell from marginal region, J.5011, Oxford Museum, ×500. D, orientation and distribution of stomata in 1 sq. mm., V.27687*a*. E, cell of upper cuticle, V.27687*a*, ×500. F, lower cuticle showing one stomatal band and part of another, V.27687*a*, ×200. G, upper cuticle, V.27687*a*, ×200.

A is a new figure; all the others are from Harris (1950).

O. graphicus and in none do the stomata approach those of these other species. Thomas & Bancroft (1913) seem to have had one of these other species when they figured the stoma of what they called *O. graphicus*, but I have not traced their specimen.

As indicated on p. 17 there are numerous species in other countries which resemble *O. graphicus* though I do not suggest that any is identical; strict identification is indeed impossible without studying the cuticle. One of the most similar of these is *O. pterophylloides* which *is* known, at least in the Bornholm material, to have stomata like *O. graphicus*, though we do not know whether the rest of the cuticle is similar.

O. bechei from the English Lower Lias is a smaller leaf well distinguished by its much more exposed stomata (Harris 1961).

Possible reproductive organs – see *Cycadolepis eriphous* and *Williamsonia himas*; also p. 14. Cuticles like the bracts of these two have been found repeatedly but their determination is not secure. Deliberate search for bract cuticles associated with *O. graphicus* and *O. beani* might well yield significant evidence.

OCCURRENCE. *O. graphicus* is frequent at all levels. Although most of the best specimens are probably from the Lower Deltaic Whitby plant bed, or from blocks fallen from the cliffs, the great majority of its localities are in the Middle Deltaic Gristhorpe Series where cuticle fragments have been found in macerations of many coals, and more or less good leaves are sometimes found in the associated shales. It is distributed as follows:

Upper Deltaic	5 localities
Middle Deltaic Gristhorpe Series . .	24 localities
Middle Deltaic Sycarham Series . .	5 localities
Lower Deltaic	9 localities

There is a specimen from Stamford preserved in ironstone in the Collection of the Geological Survey & Museum. Its age must be overlapped by the range in Yorkshire.

Otozamites thomasi sp. nov.
Text-fig. 8

DIAGNOSIS. (Based on holotype, a fragment from the middle region of the leaf.) Leaf 7 cm. wide; pinnae oblong, obtusely pointed, attached near basal angle, auricle scarcely expanded and only partly concealing rachis, pinnae diverging from rachis at an angle of 80°, separated from one another by about 2 mm. Pinnae about $3 \cdot 5 \times 1 \cdot 0$ cm., margins not thickened. Rachis about 5 mm. broad, nearly smooth, glabrous.

Veins fine, forking to maintain a concentration of 30–40 per cm., becoming very slender near auricle and margins. Both surfaces of lamina without trichomes. Cuticles 2–3μ thick; upper showing uniform cells; cells mostly rectangular, short, not forming obvious rows; lateral walls strongly folded, often forming closed loops; interior of cell somewhat thickened, showing ridges concentric with loops of wall, but not forming a papilla.

Lower cuticle showing bands along veins without stomata and broader interstitial bands with stomata; margin resembling a vein. Epidermal cells along veins rectangular, slightly elongated and forming longitudinal rows, surface very finely marked with longitudinal striae. Cells between veins short, rather irregular, not forming obvious rows. Cell outlines strongly folded, often very obscurely marked. Each cell bearing a very prominent hollow, thickly cutinised papilla. Trichome bases probably absent.

Stomata forming two or three rows between veins, irregularly spaced but nearly transverse. Guard cells and subsidiary cells not sunken, subsidiary cells small, outer wall somewhat thickened and not sinuous. Guard cells not strongly cutinised. Papillae of surrounding cells not converging over stoma.

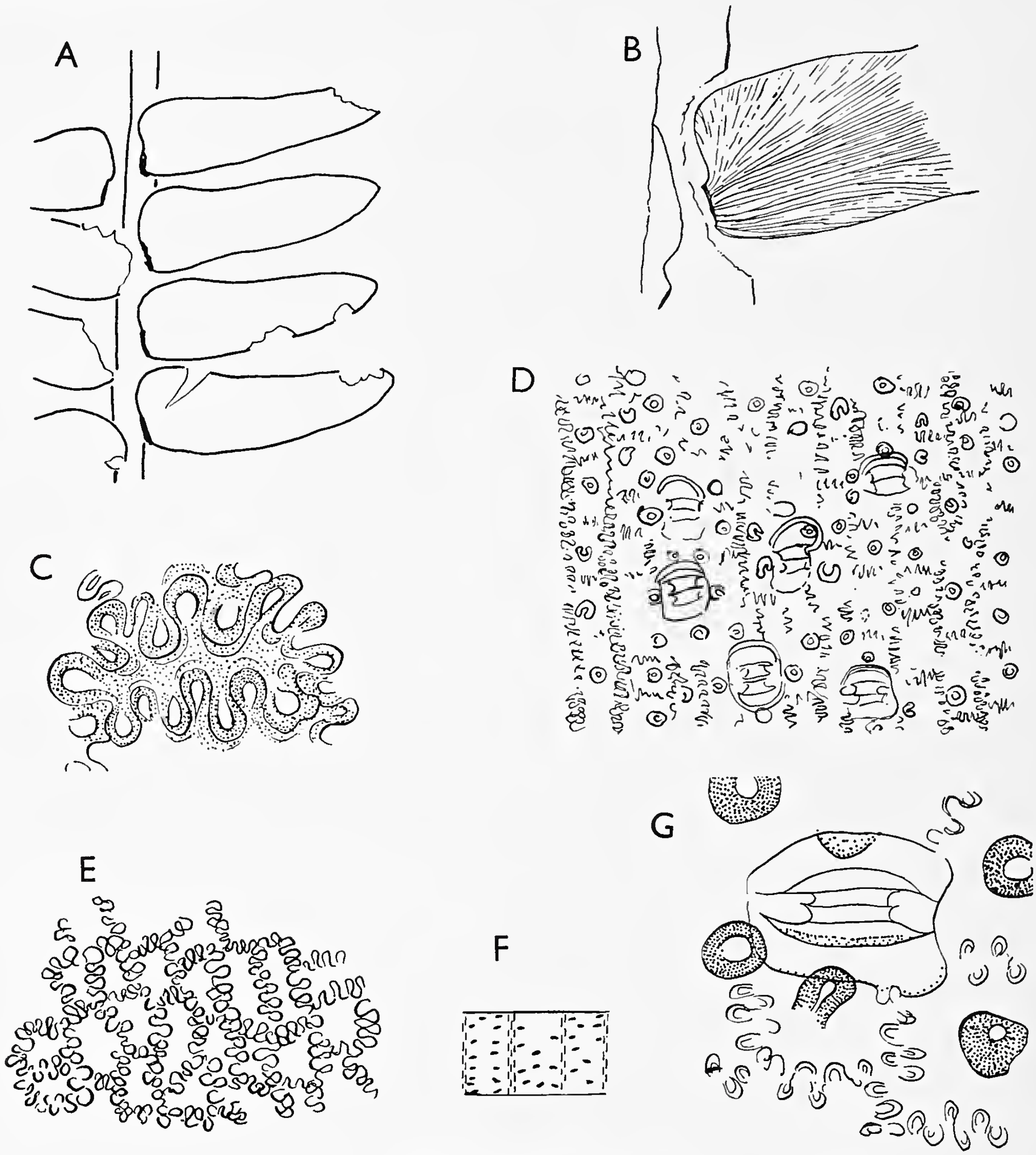

Fig. 8. **Otozamites thomasi** sp. nov.

A, upper part of the specimen. The basal 3 cm. which has similar but damaged pinnae has been omitted, V.52946, ×1. B, base of upper pinna, ×2. C, cell of upper cuticle, ×800. D, lower cuticle, ×200. E, upper epidermis, ×200. F, orientation and distribution of stomata in a strip 1 mm. wide. The stomata are hard to see and some may have been missed. G, stoma and adjacent cells, ×800.

All the figures represent the holotype.

HOLOTYPE. V.52946 (Text-fig. 8). Upper Deltaic; Cayton Bay (Upper Beds).

DISCUSSION. *O. thomasi* is represented by a single specimen collected by Hamshaw Thomas. It is localised as 'Cayton Bay Upper Beds' and since the matrix looks like an Upper Deltaic sandstone I feel sure it is from the Upper Deltaic. The three lower pinnae on the right are much damaged and have been omitted, but they were probably like those shown. A little has been omitted on the left also.

The cuticle is only moderately well preserved and shows a number of pits caused by mineral grains: but I do not think any of these features represent true trichome bases.

COMPARISON. I took *O. thomasi* to be an unusual form of *O. graphicus* until I prepared its cuticle. It differs in form from *O. graphicus* in its broad, obtuse pinnae which are attached at the basal angle (instead of rather nearer the middle) and by the fact that the auricle does not cross the rachis. The upper cuticle differs in its shorter cells with folds that often appear as closed loops. Its lower cuticle also shows more or less closed loops, but the main difference is in the stomata which are on the surface instead of being in a deep pit with a constricted mouth. The guard cells are less thickly cutinised. From forms of *O. beani* with elongated pinnae it is distinguished by lacking a thickened margin and by its stomata and by the cell wall folds and probably also by lacking trichomes.

O. thomasi resembles many species of *Otozamites*, in fact what may be called the *O. graphicus–O. bechei* group, and most of the species of this group are of unknown structure and imperfectly distinguished from one another.

Rather similar figures are given by Saporta (1875) for the French Lower Liassic *O. hennoquei* Pomel and the Oolitic *O. pterophylloides* Brongn., but in both the pinnae are more crowded, have larger auricles and (if the figures are to be trusted) fewer veins.

It is also like *O. hsiangchiensis* Sze 1949, from the Lower Jurassic of West Hupeh, China which it resembles in its broad, obtuse and distant pinnae and its scarcely expanded auricle. It differs, however, in having more crowded veins (about 40 per cm. instead of about 20) which are visible in Sze's photos, and also in having less falcate pinnae: they are almost straight.

Otozamites leckenbyi sp. nov.

Pl. 1, fig. 8; Text-figs. 9, 10

1946 *Otozamites gracilis* Phillips; Harris, p. 480, text-figs. 4A, 5. (Figures repeated here. This is not *O. gracili* Phillips; and the name *gracilis* was earlier used for a different plant by Kurr 1846.)

DIAGNOSIS (somewhat emended). Leaf of moderate size, estimated length 15–25 cm., width in middle region 2·5–5 cm., pinnae becoming shorter at ends of leaf. Pinnae up to 25 × 5 mm., arising at an angle of 70°–90°, about 1 mm. apart. Pinnae almost straight, attached by a large area extending from basal corner to above middle of base, upper basal angle rounded, not or only slightly expanded but overlapping rachis to some extent. Auricle scarcely developed. Shape of pinna long-lanceolate with acute apex. Veins slender, occurring at a concentration of about 4 per mm., radiating from region of attachment, the uppermost parallel with rachis or diverging slightly from it. Veins dichotomising at all levels, mostly nearly parallel and ending in lateral margins. Substance of lamina not very thick, margins unspecialised, flat.

Cuticle rather thin (about 1μ above and below). Upper cuticle showing uniform elongated cells with coarsely undulating lateral walls, distance from crest to crest about 15μ. Surface flat, not sculptured. Lower cuticle showing stomata confined to bands about as wide as bands with none along veins. Stomata forming one, two or three rather ill-marked files in a band,

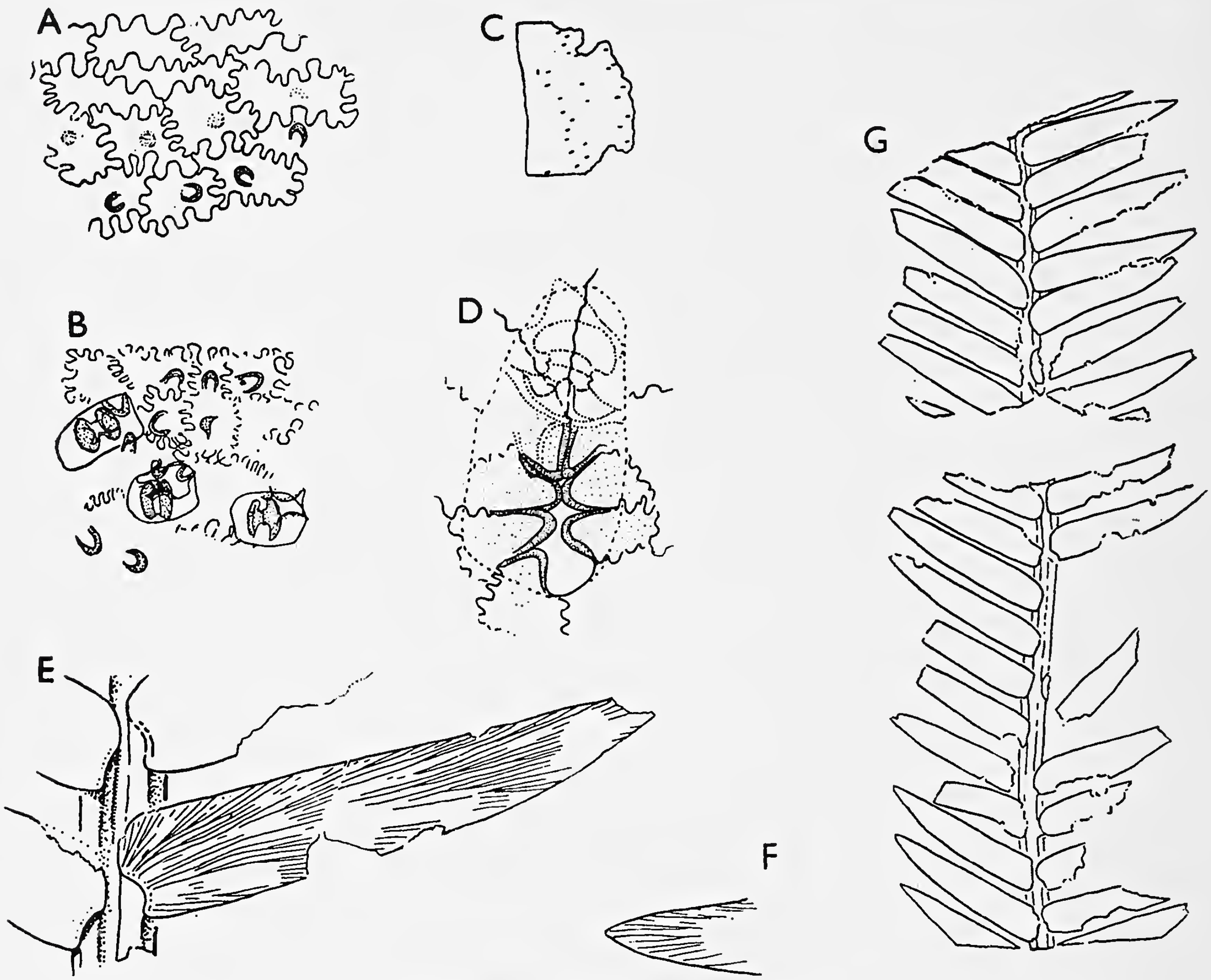

Fig. 9. **Otozamites leckenbyi** sp. nov.

A, lower cuticle of leaf-margin showing marginal cells (drawn at the top) without papillae, $\times 200$. B, lower cuticle showing part of a stomatal band, $\times 200$. C, fragment of lower cuticle (margin on the left) showing stomatal bands, $\times 20$. D, stoma showing mouth of stomatal pit; subsidiary cells and guard cells shown by broken or dotted lines, $\times 500$. E, petiole and greater part of a pinna, $\times 3$. F, apex of a pinna, $\times 3$. G, outline of holotype specimen, Yorkshire Museum, $\times 1$.

All the figures represent the holotype and are from Harris (1946).

apertures mostly transverse to veins. Epidermal cells showing coarsely sinuous walls and a prominent hollow papilla, papillae near stomata projecting over stomatal pit. Stomata in moderately deep oval pit, mouth of pit variable, sometimes wide but usually restricted by a number of wedge-shaped papillae. Subsidiary cells small and rather thickly cutinised, not possessing a papilla. Trichomes occasional both on and between veins; basal cell consisting of a small rounded cell with thickened surface and ring-shaped scar, exceptionally scar double. Free part of trichome lost before preservation.

HOLOTYPE. Specimen figured Harris (1946, text-figs. 4A, 5). Yorkshire Museum. Text-fig. 9.

DISCUSSION. I described this species from a single specimen in the Yorkshire Museum under the name *Otozamites gracilis* Phillips. (It has a label '*Otozamites* probably *O. gracilis*' and another '*Pterophyllum angustifolium* Ph.') It was not properly localised, but the matrix

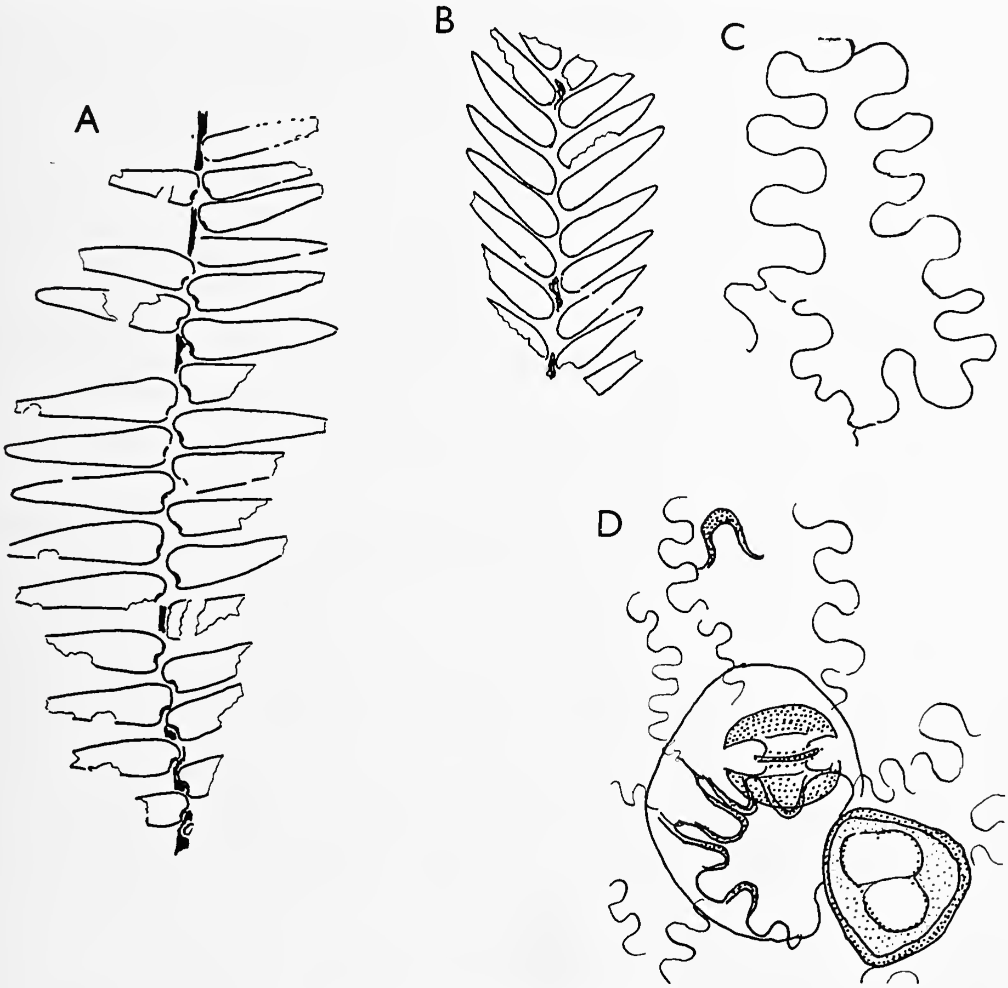

Fig. 10. **Otozamites leckenbyi** sp. nov.

A, specimen K.220 in the Leckenby Collection, Sedgwick Museum, Cambridge, ×1. B, small leaf from Hasty Bank, V.52917, ×1. C, one cell of the upper cuticle of K.220, ×500. D, lower cuticle of K.220 showing a stoma and trichome base, ×500.

suggests a Lower Deltaic sandy shale. Since then I have realised that the name is inadmissible on two grounds.

Firstly the name *O. gracilis* was used earlier than by Phillips. Kurr's (1845) Liassic leaf, *Zamites gracilis* was placed in *Otozamites* by Schimper (1870). Kurr's specimens have been refigured by Salfeld (1907). Probably still another species is the Indian *O. gracilis* of Feistmantel (1877).

Secondly the specimen which I took to be the holotype of *O. gracilis* of Phillips, that is Leckenby's 1864, pl. 8, fig. 4, called by him *O. lanceolatus* and refigured by Phillips (1875) as the holotype of his *O. gracilis* is No. K.171 in the Leckenby Collection at Cambridge. On examination I decided that it is a good and typical specimen of the apex of *O. gramineus* Phillips (1829).

I found that specimen K.220 in the Leckenby Collection (figured here for the first time) agrees closely with the Yorkshire Museum specimen and I have identified it. It is a slightly smaller leaf, and its cuticle is somewhat better preserved. It was possible to see the upper cuticle (though this broke up into tiny fragments when separated from the lower). It was also possible to see that there are a moderate number of trichome bases on the lower cuticle. Another slight difference is that in some of the pinnae there is a slight basal swelling forming a sort of auricle, and in these pinnae the first veins run parallel with the rachis. This second specimen also is unlocalised, but it also is in a hard sandy shale of a kind frequent in the Lower Deltaic. The specimen bears the labels *Otopteris acuminatus* Lindley, *Otozamites gramineus* Phill., and *Otozamites obtusus* var. *ooliticus* Seward?

A still smaller specimen (Text-fig. 10B) was found at Hasty Bank. Its cuticle is well preserved.

COMPARISON. *O. leckenbyi* is like a rather large *Ptilophyllum* leaf but the lower basal angle of the pinna is distinctly contracted instead of being slightly decurrent. It also approaches species of *Zamites* but there is too much asymmetry at the region of pinna attachment. It is interesting that the stomata are like those of several other species of *Otozamites* but not like *Ptilophyllum pecten* nor *Zamites gigas*.

O. leckenbyi is distinguished from *O. graphicus* by the absence or feeble development of an auricle. In *O. gramineus* also there is usually a better developed auricle and the pinna is narrower. The three species have rather similar cuticles, but the stomata of *O. gramineus* are less protected, those of *O. graphicus* usually a little more protected. *O. leckenbyi* alone has trichome bases on the lower side.

Another rather similar Yorkshire species is *O. penna*, but that differs in being a narrower leaf. It is distinguished also by its cuticle which shows less conspicuous papillae, but peculiar sac-like trichomes on the lower side.

Otozamites parviauriculata Menéndez 1966 is similar in both form and in cuticle but *O. leckenbyi* is distinguished by its more attenuated pinnae and fewer rosette cells around the mouth of the stomatal pore.

OCCURRENCE. *O. leckenbyi* is evidently a rare Yorkshire species. It is possible that the two old specimens come from a single locality and this may be Lower Deltaic. Its cuticle is not sufficiently robust or striking for it to have been recognised in bulk macerations. The only other specimen comes from the Lower Deltaic of Hasty Bank.

Otozamites venosus Harris

Text-fig. 11

1950 *Otozamites venosus* Harris, p. 571, text-figs. 5, 6. (Figures and account repeated here.)

DIAGNOSIS (from Harris 1950). Leaf probably rather small, seldom exceeding 7 cm. in width; length and shape unknown.

Pinnae up to 3 or 4 cm. long, 7–9 mm. broad, but smaller ones (? basal pinnae) 1·5 cm. long, 5 mm. broad, frequent. Pinna straight or slightly falcate. Pinna attached by basal angle, auricle scarcely or not at all expanded, margins parallel or slightly tapering in the proximal half, tapering to an acute or obtuse point in the distal half. Upper pinnae small and relatively narrow, rather crowded, arising from the rachis at an angle of about 30°. Surface of pinna flat, margins unspecialised. Veins radiating from the basal angle; exceedingly fine and crowded at a concentration of 50–60 per cm., branching at all levels. Substance of lamina fairly dense.

Cuticle not very thick on either side (up to 1·5μ measured in folds), but tough and easy to prepare. Upper cuticle without stomata or trichomes, veins fairly well distinguished by about two rows of narrow cells. Epidermal cells more or less square. Anticlinal walls well marked, sinuous, often with rather angular folds; sometimes with the folds thickened in such a way that they tend to coalesce into a broad straight ridge around the cells. Cell surface not papillate, flat, marked with ridges extending from the folds of the lateral walls.

Lower cuticle divided into strips along the veins lacking stomata and more or less equally broad interstitial strips with stomata. Epidermal cells square or rectangular, forming longitudinal rows. Anticlinal walls conspicuous, sinuous, but folds sometimes thickened till they coalesce into a nearly straight ridge around the cell. Cell surface flat, not papillose, finely mottled. Stomata rather numerous, forming one or two, occasionally more ill-defined files, transversely orientated, irregularly spaced in their files. Stomatal apparatus forming an oval group only slightly larger than an epidermal cell, not at all sunken. Anticlinal walls of subsidiary cells marked by a conspicuous broad ridge, with feeble sinuous folds or none. Surface of subsidiary cells unthickened. Guard cells rather small, aperture 13μ long, crescent-shaped thickenings about 28μ long.

Trichomes numerous in and alongside the interstitial strips but absent along the veins; irregularly spaced, occasionally occurring in twos or threes. Trichome consisting of a rounded cell with a thickened surface and a circular scar 25μ wide; free part missing.

Marginal region of lamina showing epidermal cells with specially prominent lateral walls, otherwise unspecialised.

HOLOTYPE. V.27695. Figured Harris (1950, text-figs. 5 A, C, G, H, 6 B, C). Text-fig. 11 A, C, G, H, L, N.

DISCUSSION. Although *O. venosus* is a rare species, only known from fragments, it is well distinguished from all others. The pinnae resemble *O. graphicus* in form but are smaller than most specimens of *O. graphicus* and have more crowded veins (typically 55 per cm. instead of typically 35 per cm.). The veins are in fact more crowded than in any other species known to me.

The cuticle is very different from that of *O. graphicus*, for the stomatal apparatus is superficial in *O. venosus* but sunken and roofed over in *O. graphicus* and the lower epidermal cells lack papillae in *O. venosus*, but always show them in *O. graphicus*. *O. venosus* is in fact rather extreme in its cuticle.

A curious feature noticed in the cuticle is that the stomata often appear asymmetric, probably as a result of tilting. The crescent-shaped thickening on the proximal side is flat and inconspicuous, that on the distal side is on edge and very marked.

The upper part of the leaf (which in *Otozamites* seems often to be poorly characterised)

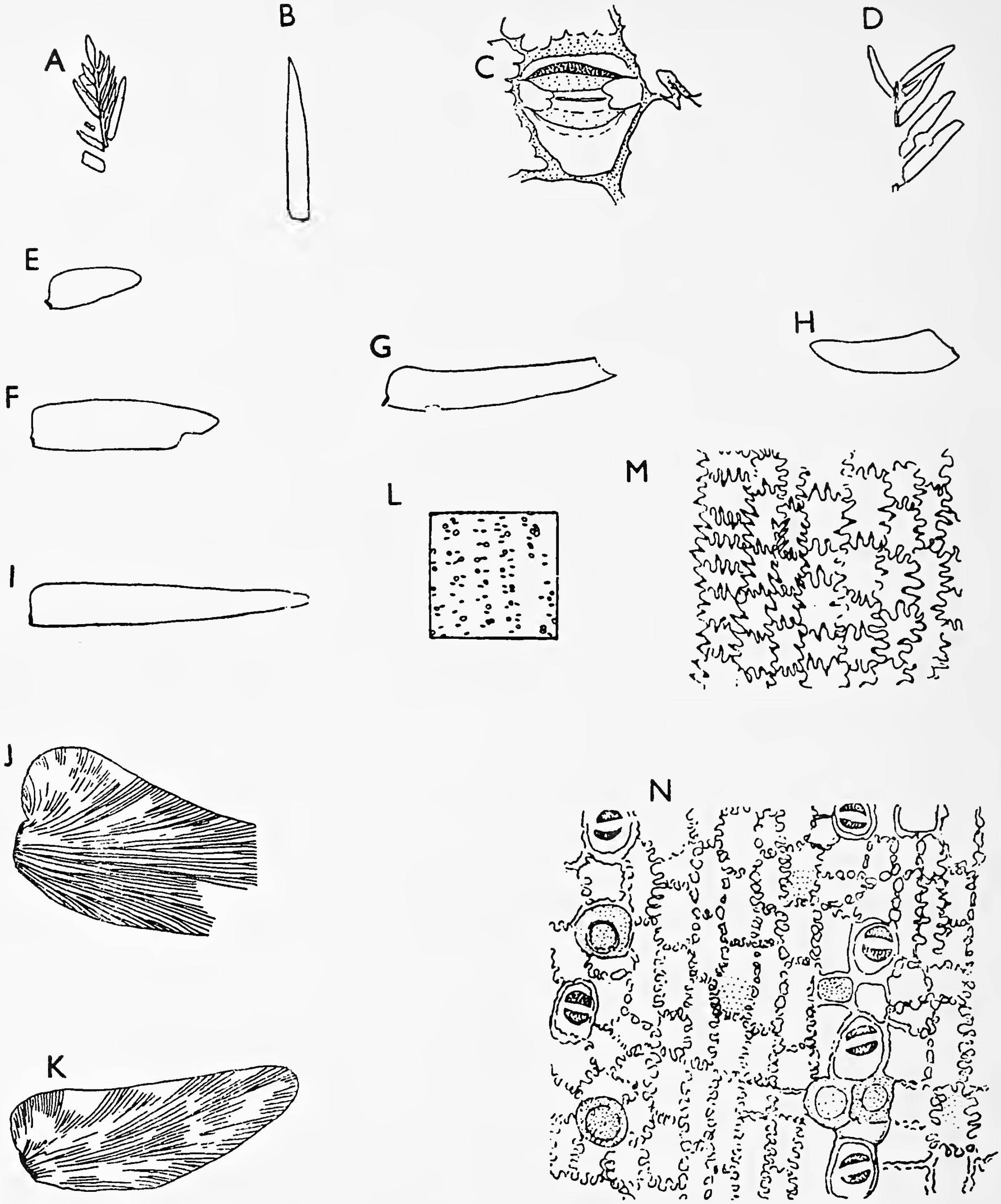

Fig. 11. **Otozamites venosus** Harris

A, leaf apex, V.27695, ×1. B, isolated pinna, attributed to upper part of leaf, V.27696, ×1. C, stoma from holotype, V.27695, ×500. D, near leaf apex, V.27696, ×1. E, isolated pinna, attributed to leaf base, V.27697, ×1. F, isolated pinna, V.27698, ×1. G, H, isolated pinnae, holotype, V.27695, ×1. J, venation of a large pinna, V.27699, ×3. K, venation of a small pinna, V.27700, ×3. L, distribution of stomata (short black lines) and trichomes (open circles) in 1 sq. mm. of cuticle of holotype. M, upper cuticle, a vein is situated near the left, V.27090, ×200. N, lower cuticle of holotype (the strip along the veins is wider here than in many specimens), V.27695, ×200.

All the figures are from Harris (1950).

has narrow pinnae, looking much like those of a *Ptilophyllum*, but even in the leaf apices figured, the basal attachment of the veins is evident.

The specific name refers to the crowded veins.

OCCURRENCE. Upper Deltaic. Burniston Wyke '*Zamites*' Bed at 54° 19′ 19″ N, 0° 25′ 10″ W (the bed is just below the top of the cliffs).

Otozamites gramineus (Phillips)

Text-figs. 12, 13

All the following are Yorkshire specimens:

1828 *Zamia Goldiaei* Brongniart, p. 94. (*Nomen nudum.*)
1829 *Cycadites gramineus* Phillips, p. 154, pl. 10, fig. 2. (Fragment.)
1849 *Otozamites Goldiaei* Brongniart, p. 106. (Name only.)
1864 *Otopteris lanceolata* Leckenby, p. 78, pl. 8, fig. 4. (Leaf apex. Specimen K.171, Sedgwick Museum, Cambridge.)
1875 *Otozamites Goldiaei* (Brongniart); Saporta, p. 128, pl. 95, fig. 1. (Figure but no description.)
1875 *Otozamites gramineus* (Phillips) Phillips, p. 223 (?), lign. 51 (see p. 31), pl. 10, fig. 2. (Leaf fragments, description.)
1875 *Otozamites gracilis* Phillips, p. 224, lign. 52. (Leckenby's *Otopteris lanceolata* redrawn.)
1900 *Otozamites gramineus* (Phillips); Seward, pp. 7, 16, 197. (Name, but no description.)
1913 *Ptilophyllum* (*Williamsonia*) *pecten* (Phillips); Thomas, in part, p. 234, text-fig. 4 only.
1917 *Ptilophyllum pecten* (Phillips); Seward, in part, p. 519, text-fig. 592 only.
1946 *Otozamites gramineus* (Phillips); Harris, p. 475, text-figs. 1–3. (Form and cuticle of Phillips' specimens, figures and description given here.)

DIAGNOSIS (from Harris 1946). Leaf of moderate length (possibly 30 cm. × 6 cm.), narrower near the apex and base. In middle region of leaf, pinnae arising at an angle of 60°–70° to the midrib, usually separated by gaps of 1–2 mm. Pinna attached by a small area at the lower basal corner; upper basal corner (auricle) rounded and expounded to the extent of 1–2 mm., but seldom overlapping the pinna on the opposite side of the rachis. Margins of pinna beyond auricle at first almost parallel, then gradually tapering to an acute point. Pinnae at apex and base of leaf shorter and with a more obtuse apex; those at apex with scarcely any basal lobe; those at base with a well-developed basal lobe.

Veins slender, occurring at a concentration of about 4 per mm., radiating from the point of attachment, the uppermost running parallel with the rachis or slightly across it. Veins dichotomising at all levels in the leaflets, many ending in the lateral margins.

Cuticle of medium thickness, about 1μ on both sides. Upper cuticle without stomata or trichomes, showing uniform rectangular cells in rows. Walls distinctly marked, strongly sinuous; surface flat, without any papilla. Lower cuticle showing stomata in narrow bands separated by slightly wider bands along the veins. Cells rather wide, often nearly square, with finely marked sinuous lateral walls. Nearly all cells showing a thickened area in the middle of the surface, usually forming a round papilla, but sometimes a ridge along the middle of the cell. Papillae solid, only becoming hollow near stomata. Stomata usually forming two (sometimes one, sometimes three) indefinite files in each stomatal band, irregularly spaced, tending to be transversely orientated. Guard cells and subsidiary cells sunken in a wide shallow pit, mouth of pit usually exposed but occasionally sides overhung by the hollow papillae of neighbouring epidermal cells. Subsidiary cells small with a thickened surface;

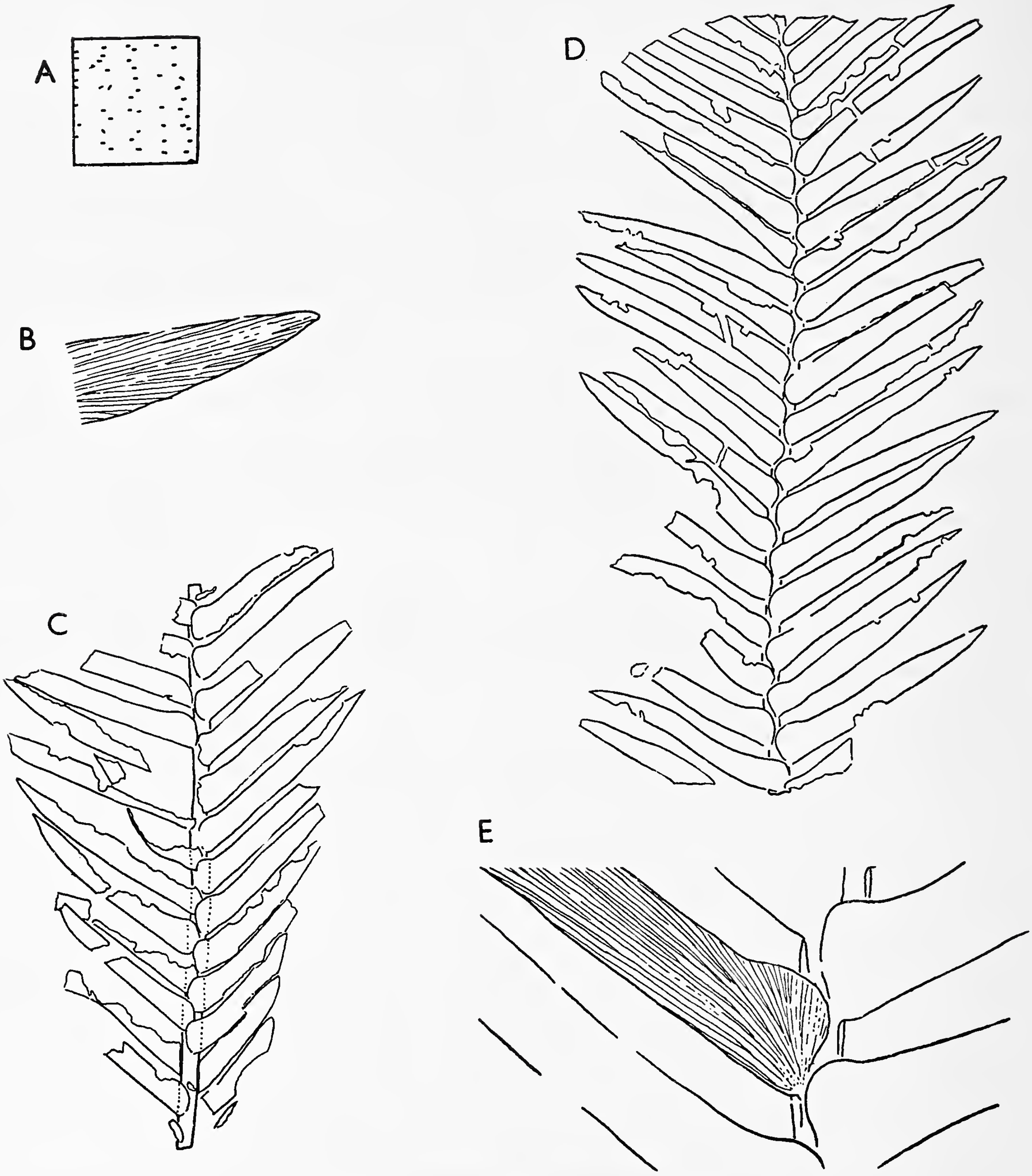

Fig. 12. **Otozamites gramineus** (Phillips)

A, one square mm. of lower epidermis of specimen 'F' showing distribution and orientation of stomata. B, apex of pinna, specimen 'L', ×3. C, specimen 'F', ×1. D, specimen 'A', ×1. E, details of specimen 'A', ×3.

The specimens are in the Phillips Collection, Oxford Museum and are from Whitby and the figures are from Harris (1946).

papillae not or only very slightly developed. Guard cells fairly thickly cutinised. Trichomes absent.

LECTOTYPE. Specimen A, Phillips Collection, Geology Department, Oxford University. Figured Harris (1946, text-figs. 1, 2 D, 3 A, D). Text-figs. 12 D, E, 13 A, D.

DISCUSSION. Most of the new specimens agree fully with the above diagnosis. The extreme range noted in width is from 3 cm. (probably in the middle region of a small leaf) to 12 cm. Usually the pinnae are slightly separated, but in some they are in contact or slightly overlapping, especially in leaves where the pinnae are inclined at an angle of rather less than 60° to the rachis. Towards the leaf apex the leaf becomes narrower and the pinnae themselves are shorter and narrower (for example 15 mm. × 2 mm.) but their shape and their auricle is much as it is below. Towards the leaf base the pinnae become shorter but still retain their width. The petiole, which is up to 5 mm. thick and 5 cm. long, is crossed by many transverse and longitudinal wrinkles.

There is an unusual specimen in the Geology Department of Leeds University which agrees with *O. gramineus* in the form of the pinnae and in cuticle, but the pinnae are separated by gaps 3–4 mm. wide, the gaps being as wide as the pinnae. I assume it is merely an extreme form of *O. gramineus*. It is associated with *Ptilophyllum pectinoides* in a matrix resembling the Whitby Plant Bed.

There is evidence that the scale *Cycadolepis spheniscus* was produced by the same plant as this leaf.

IDENTIFICATION. Phillips' original named figure (pl. 10, fig. 2) is crude and shows too few veins (as usual in his figures), but there is no other species known in Yorkshire with pinnae of this size and shape.

The specimen figured by Phillips (1875, lign 51) is K.216 in the Leckenby Collection, Cambridge. Its appearance is not fully normal and I could not prepare its cuticle. I am doubtful whether it represents the apex of a leaf of this species since all the apices I have seen are different. Still his description (1875) refers to specimens like those figured here and may indeed be based on these very specimens, 'in his cabinet'.

Brongniart (1828*a*) gave the *nomen nudum*, *Zamia Goldiaei*, to a Yorkshire leaf and Saporta (1875) figured it, and I am convinced that the specimen belongs to the present species, though the veins, as in nearly all the early figures, are again too few.

The specimen figured by Leckenby (1864, pl. 8, fig. 4) as *Otopteris lanceolata* is K171 in the Leckenby Collection, Cambridge. It evidently puzzled later authors for Phillips (1875) figured it as his *Otozamites gracilis* (not *O. gracilis* Kurr); Nathorst called it *O. gracilis* and Seward *Ptilophyllum pecten*. It became the original of Phillips' 1875 figure of *O. gracilis*. Another of Leckenby's specimens which I consider is *O. gramineus* is K.179 labelled *Zamia hastula*, *Ctenophyllum pectinoides* and again *P. pecten*. The next figure is that of Thomas (1913) who gave it as an example of the form range of *P. pecten*. (I have examined the specimen and am convinced it was drawn upside down; the auricle is well developed but the pinnae were bent back in preservation.)

Seward (1900) was evidently uncertain how to treat *O. gramineus* since he seems to accept it as distinct (p. 16) but then firmly united it with *Ptilophyllum pecten* (pp. 190, 192); but this was without microscopic evidence.

COMPARISON. Even the narrowest forms of *Otozamites graphicus* have pinnae distinctly

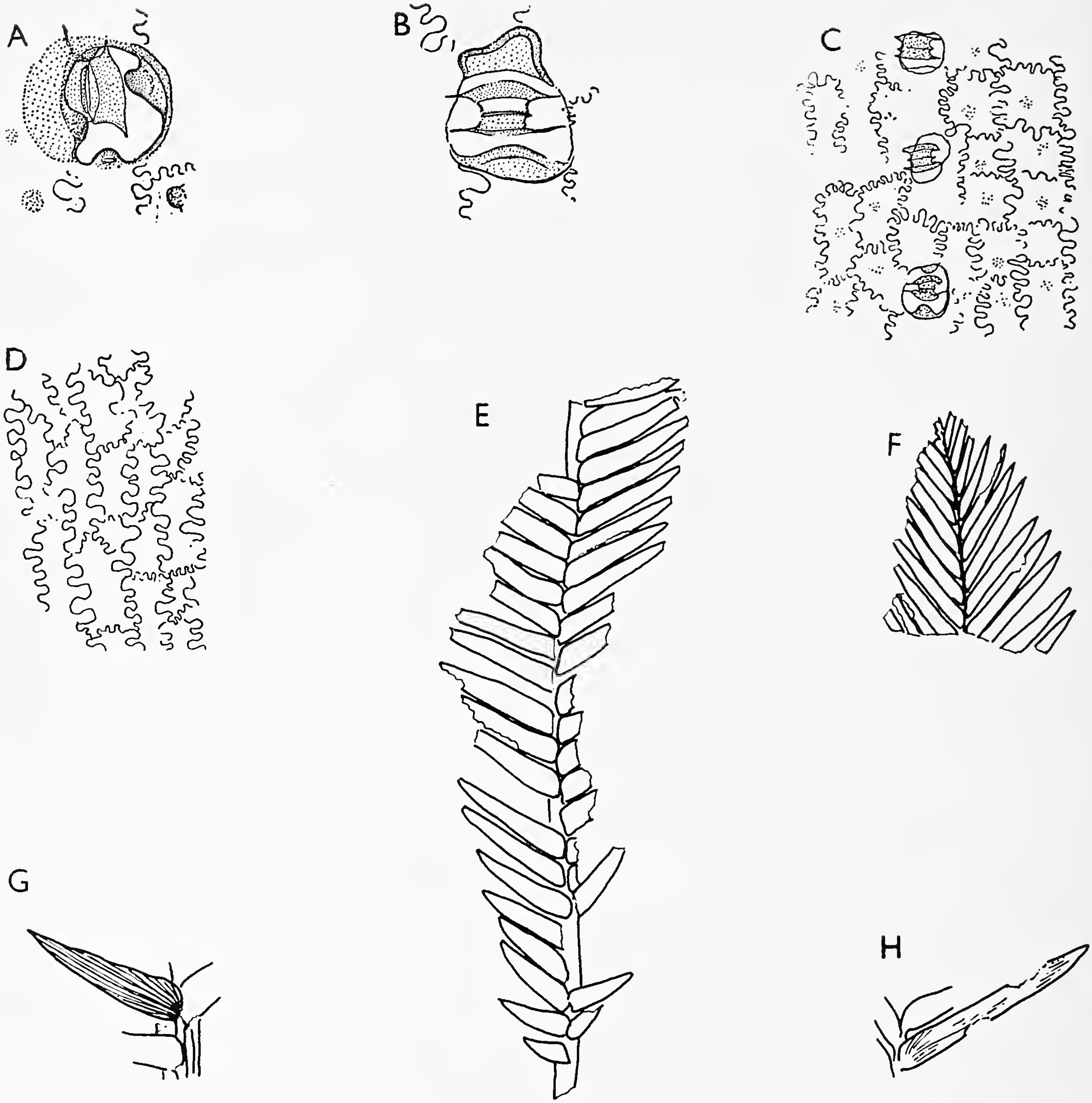

Fig. 13. **Otozamites gramineus** (Phillips)

A, longitudinally orientated stoma with somewhat contracted pit, specimen 'A', ×500. B, exposed stoma, specimen 'F', ×500. C, lower cuticle, specimen 'F', ×200. D, upper cuticle, specimen 'A', ×200. E, lower part of rather small leaf, V.52913, ×1. F, upper part of leaf, V.52912, ×1. G, one of the lower pinnae from E, ×2. H, one of the pinnae from F, ×2.

A–D are in the Phillips Collection, Oxford Museum and are from Whitby, and the figures are from Harris (1946). E–H are from fallen blocks, Maw Wyke, Hawsker.

broader than those of *O. gramineus* and the two are clearly distinguished by their cuticles. In *O. gramineus* the pit around the stoma is shallow and widely open, instead of deep and almost closed. The epidermal cell papillae are much better developed in *O. graphicus*. *O. leckenbyi* differs in its much less developed auricle and in its more protected stomata (like those of *O. graphicus*).

Specimens of *O. gramineus* have been confused with *Ptilophyllum pecten* or perhaps *P. pectinoides*, as for example by Thomas (1913) though not later (as I know from conversation). The auricle is so small that it can be overlooked, especially in the small pinnae at the top of the leaf and *Ptilophyllum* itself may have a rudiment of an auricle. However no specimen which was carefully examined proved truly intermediate and when specimens were separated by the form of the pinna base, the marked differences in stomata confirmed their identification. *O. gramineus* never shows the two large subsidiary cell papillae which are almost constant in *P. pectinoides*.

Another similar looking leaf is '*Ptilophyllum acutifolium* cf. var. *maximum* Feistmantel' of Wieland (1916) from Mexico, especially his pl. 4, fig. 4.

OCCURRENCE. *O. gramineus* has been found in eleven Lower Deltaic localities, all of them probably from the lower half of the Lower Deltaic Series. The species is specially common in the classic Whitby Plant Bed and in the Beast Cliff *Otozamites* Bed. Cuticle fragments more or less closely resembling it are more widespread but I have not determined them as the cuticle alone seems inadequately characterised.

Other organs perhaps belonging to *O. gramineus* are *Cycadolepis spheniscus* p. 106 and *Weltrichia spectabilis* p. 167.

Otozamites parallelus Phillips

Text-fig. 14

1875 *Otozamites parallelus* Phillips, p. 221, lign. 47.
1900 *Otozamites parallelus* Phillips; Seward, p. 217. (Discussion and comparison.)

EMENDED DIAGNOSIS. Leaf as a whole long and relatively narrow, width uniformly about 3·5 cm. over a considerable part, but becoming less towards the apex and base. Pinnae about 20 mm. × 6 mm., usually crowded and in contact, their bases wholly concealing the rachis, arising at an angle of 70°–85°. Pinnae normally almost rectangular with obtuse apices and only slightly expanded auricles. Lower basal angle scarcely contracted, veins arising from lower half or three-fifths of base of pinna, veins of auricle parallel with rachis but scarcely crossing it. In upper part of leaf, pinnae becoming narrower; towards base of leaf pinnae becoming short and triangular.

Veins fine, traversing the lamina at a concentration of 40 per cm., forking at all levels, those on lower side of pinna nearly parallel with lower margin. Cuticle probably of medium thickness. (Upper cuticle unknown.) Lower showing stomata in strips between the veins and placed in about two rather irregular files. Apertures usually transverse. Epidermal cells along veins elongated with coarsely sinuous walls and very prominent papillae. Cells of stomatal files similar but shorter and less regular. Stomata sunken in oval pits, margins of pits somewhat constricted by very prominent papillae of adjacent cells. Subsidiary cells small, thick walled, not papillate. Trichomes absent.

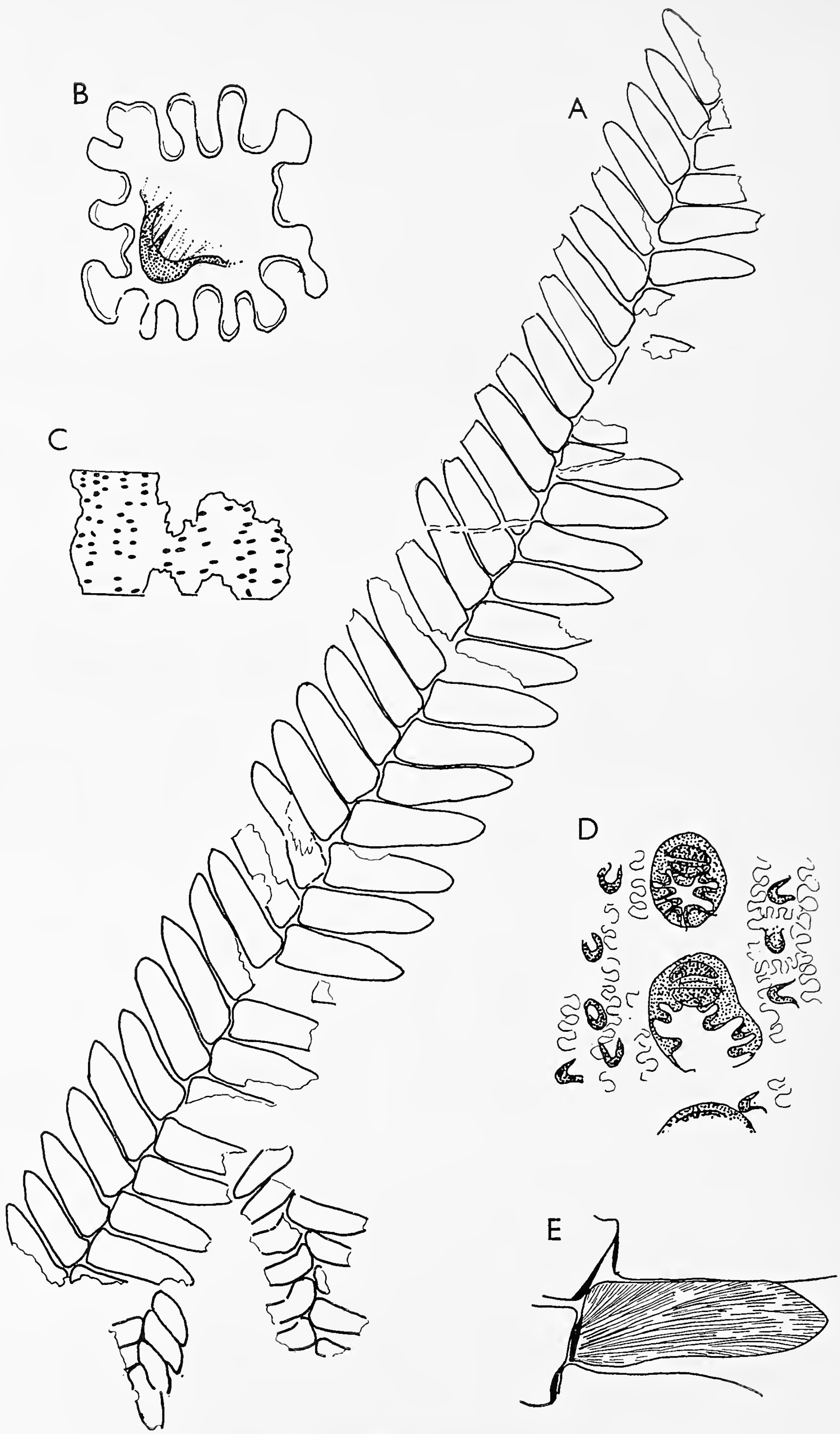

Fig. 14. **Otozamites parallelus** Phillips

A, specimen K.219 Leckenby Collection, Cambridge. The cuticle preparations were made from the large specimen. The small fragment at the right, bottom is distorted, $\times 1$. B, a cell from near a vein, lower cuticle, $\times 800$. C, distribution of stomata in a strip up to 1 mm. wide, $\times 20$. D, lower cuticle, $\times 200$. E, venation. Many of the veins are obscure and some of those shown may be wrong, but their direction and concentration is correct. The region of attachment (which forms an open hole) is shown in black, $\times 2$.

Holotype. Specimen figured by Phillips (1875, p. 221, lign. 47).

Discussion. This account is based on specimens K.218 and K.219 at Cambridge. These specimens are unlocalised but I think they are from the classic Haiburn locality near Tyndal Point since they are preserved in a hard, sandy ironstone and the rock has on it some barnacles which show that it is from the upper part of the tidal zone. This is the only place I know where the rock has this character. It is in the upper part of the Lower Deltaic.

Although the figured specimen (K.219) is impressive its fine details are poorly shown. Some rather poor preparations of the lower cuticle were made but the upper cuticle has vanished as often happens in poorly preserved *Otozamites* leaves.

A few specimens in old collections have been given the name *O. parallelus*. Some of these are fragments of *O. simpsoni* or *O. graphicus* and others are too poorly preserved to be determinable.

The specimens figured here may have been identified by Leckenby and I accept the identification with Phillips' holotype (which I have not seen). The pinnae agree fairly well in shape, but Phillips shows the veins arising at a greater angle and more widely spaced. Phillips however was usually careless with the veins and nearly always showed too few when they were crowded.

Comparison. *O. parallelus* differs from *O. simpsoni* in its larger pinnae and in its very different cuticle; *O. simpsoni* having exposed stomata and numerous trichome bases. It differs from *O. graphicus* (which it resembles in cuticle) in its short, obtuse pinnae.

Occurrence. *O. parallelus* is evidently a rare species though it must have been locally common at the point where the Leckenby specimens occurred. I have never collected it, nor are there any specimens in the Hamshaw Thomas Collection. Phillips' holotype is from 'near Whitby' and I think the Leckenby specimens are from Haiburn, both localities being Lower Deltaic.

Otozamites simpsoni sp. nov.

Text-figs. 15, 16

1949 *Otozamites feistmanteli* Zigno; Harris, p. 280, text-figs. 3 A, D, E, 4. (Figures repeated here.)

See p. 37 for discussion of *O. feistmanteli* Zigno and other similar forms.

Diagnosis. Leaf typically about 30 cm. long and 1·0–2·3 cm. wide, tapering towards both ends. (Petiole not known.) Pinnae uniform over most of the leaf, shape triangular with a rounded base and obtuse or subacute apex or rounded in smallest pinnae. Distal margin usually somewhat convex but sometimes straight and sometimes concave near the auricle; adaxial margin convex, straight or very slightly concave in its middle region. Pinnae typically 10 × 4 mm. — 5 × 3 mm., but smaller towards ends of leaf, rather crowded and usually overlapping by about 1 mm. Margins of pinnae distinctly thickened and projecting downwards, but not recurved. Upper surface of pinna often convex. Pinnae arising at an angle of 70°–85°, occasionally less, proximal margin lying over the middle of the rachis but scarcely crossing it. Auricle not or only slightly expanded.

Pinnae attached by an oval region occupying the adaxial half of the proximal margin, veins radiating from this region, forward veins (in region of auricle) usually diverging from

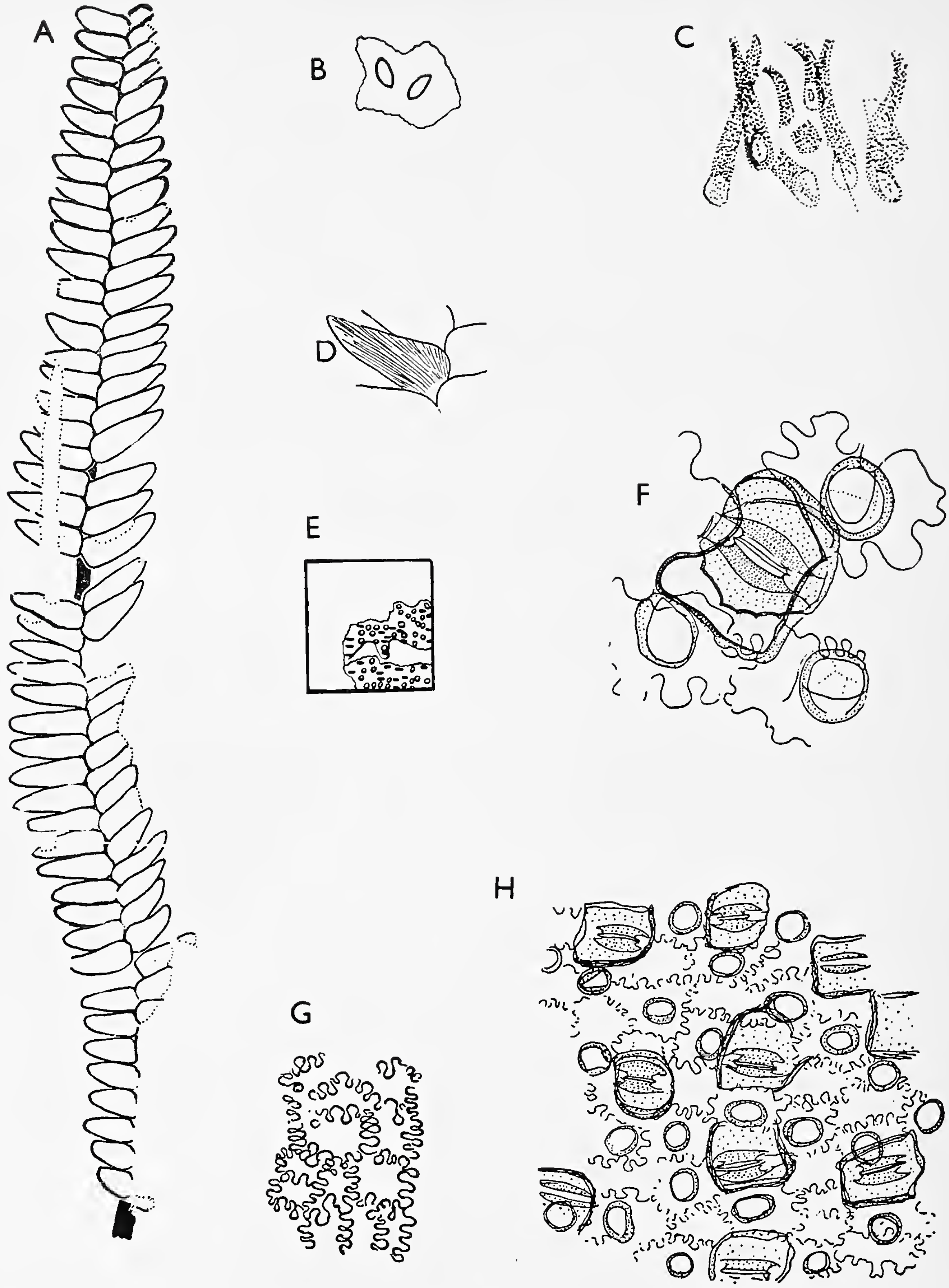

Fig. 15. **Otozamites simpsoni** sp. nov.

(**O. feistmanteli** auct. angl.)

A, Whitby Museum leaf, ×1. B, fragment of rachis cuticle showing holes where two pinnae were attached, V.53252, ×5. C, hairs, of rachis, V.53253, ×100. D, veins in one of the upper pinnae of A, ×2. E, fragment of lower cuticle showing stomatal apertures and trichome bases (rings). The square is 1 sq. mm., V.53252. F, stoma of Whitby leaf, ×500. G, upper epidermis of Whitby leaf, ×200. H, lower epidermis of Whitby leaf, ×200.

A, D, F–H are from Harris (1949). Specimens in B, C, E are from a fallen block between Widdy Head and Gnipe Howe, Hawsker.

the rachis or at most parallel, not crossing it. Veins indistinct, embedded in the thick substance of the lamina, traversing the lamina at a concentration of 40–50 per cm.

Cuticle of moderate thickness, 1–2μ on both sides, or upper rather thicker but fragile. Rachis rather thickly cutinised, showing straight walled rectangular epidermal cells and narrow hypodermal cells; originally hairy but hairs usually lost. Upper cuticle of lamina glabrous, showing uniform epidermal cells, veins probably not marked, stomata and trichomes absent. Over most of lamina cell outlines very ill marked, but strongly sinuous, cell surface flat. Towards margin cuticle becoming more coherent, cell outlines becoming well marked, cells elongated, folds of anticlinal walls very strongly marked often forming three-quarters of a circle. Surface of cell flat, not papillate, sometimes sculptured with small granules. Stomata and trichomes absent. Lower cuticle showing a marginal zone resembling the upper marginal zone but with a few trichome bases and sometimes marked off by a slight fold, and a broad inner region with stomata. Inner region divided into broad stomatal bands and narrow bands along veins without stomata, or vein zones almost unrecognisable. Epidermal cells of irregular shapes but tending to form rows along veins, often as broad as long; anticlinal walls strongly sinuous but often ill-defined; margins of cell often marked by a strong fold (as though an originally convex surface had collapsed). Surface smooth, not papillate. Trichome bases very numerous, occurring on half or more of the epidermal cells, both those along veins and between veins; consisting of a strongly cutinised ring 25μ wide; ring usually open (or closed by a very delicate cuticle); free part of trichome missing from cuticle and normally lost before preservation but occasionally retained as a covering of fine longitudinally pointing hairs 150μ long. Stomata numerous, rather evenly spaced in the interstitial zones, not forming files but transversely orientated. Whole stomatal apparatus of guard cells and subsidiary cells slightly sunken and surrounded by compression folds but margins not usually overhung to any considerable extent. Subsidiary cells rather smaller and more thickly cutinised than other epidermal cells, no papilla or other extension present over the guard cells. Guard cells not very thickly cutinised.

HOLOTYPE. Specimen in Whitby Museum, figured Harris (1949, text-figs. 3 A, D, E, 4).

DISCUSSION. My description in 1949 was based on a single imperfectly localised specimen in the Whitby Museum which may have come from Whitby. Since then I have collected a few more specimens and there are others in the Hamshaw Thomas Collection. All these are from the Lower Deltaic and it is interesting that all occur in a sandy matrix, some at least full of water worn plant fragments. Possibly the species grew inland and has been transported some distance, but against this is the fact that fragments are locally frequent at one locality (Widdy Head, Hawsker).

COMPARISON. *O. simpsoni* is sharply distinguished from all other Yorkshire *Otozamites* species by its cuticle, which is indeed like that of the very different leaf *Zamites gigas*. In form, however, it may be like *O. mimetes* though its pinnae are usually more acute.

In other floras there are narrow *Otozamites* leaves which are more or less comparable and I had identified the holotype with Zigno's *O. feistmanteli*, but Dr. Wesley who has shown me numerous new photographs has convinced me that they are distinct. Zigno's specimens have larger auricles in which the innermost veins run distinctly across the rachis. Its pinnae are also broader and blunter. Unfortunately the cuticles of the Italian specimens could not be prepared.

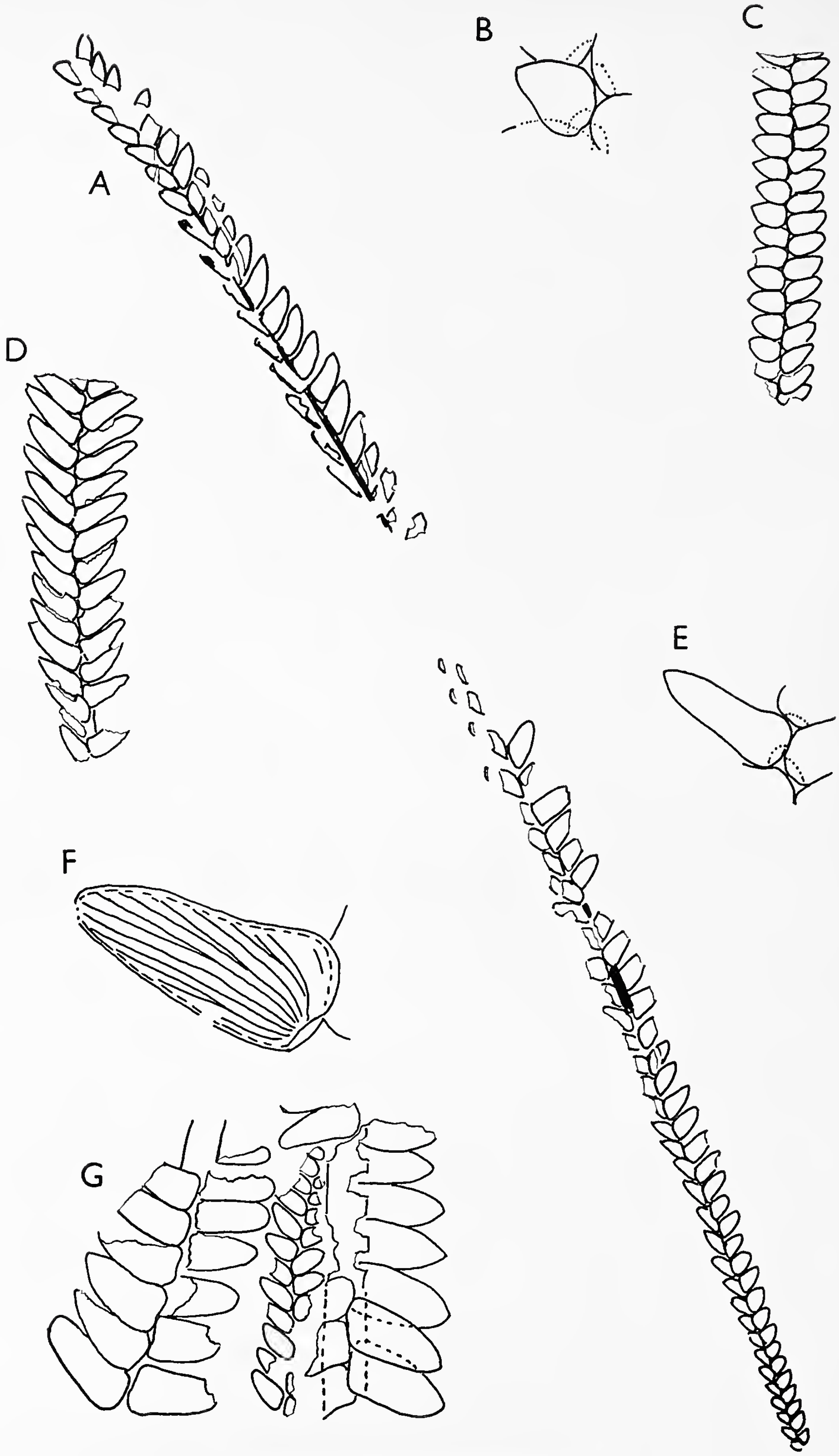

Fig. 16. **Otozamites simpsoni** sp. nov.

A, nearly complete leaf (the rock has broken away in the middle and the left side is compressed obliquely, V.52935, ×1. B, one pinna of C, ×2. C, leaf with short pinnae, V.52943, ×1. D, leaf with rather long pinnae, V.52938, ×1. E, one pinna of D, ×2. F, one pinna of a leaf from Widdy Head, V.52940, ×4. G, fragments of three adjacent leaves, V.52942, ×2.

A, F, G, fallen blocks, Widdy Head, Hawsker. C, fallen block, Gnipe Howe, Hawsker. D, Roseberry Topping.

Seward (1900, p. 221) mentioned various other species which he considered very like *O. feistmanteli*, a species which he then took broadly. Most of these are, however, more similar to one of the Yorkshire species, but some specimens of *Palaeozamia bengalensis* Oldham & Morris 1863 (now usually placed in *Otozamites*) do look rather similar, although the pinna apex is usually sharper and more forward-pointing. The Yorkshire specimen which Seward (1900) included in *O. feistmanteli* is now included in *O. falsus.*

The specific name commemorates Martin Simpson who had charge of the original specimen when he curated Whitby Museum.

OCCURRENCE. *Otozamites simpsoni* has been found in the following Lower Deltaic localities:

Roseberry Topping, in upper sandstone. (Hamshaw Thomas Collection.) Whitby (?). Whitby Museum and Hamshaw Thomas Collection. (Specimens not securely localised.)

Hawsker, fallen blocks near Widdy Head.

? Marske Quarry (V.12866) but determination not secure as the cuticle is not preserved. It is impossible to say whether the specimen from Marske figured by Thomas & Bancroft (1913) as *O. feistmanteli* (stomata only) belongs to *O. simpsoni.*

Otozamites anglica (Seward)

Pl. 1, fig. 5; Text-fig. 17

1900 *Nageiopsis anglica* Seward, p. 288, text-fig. 51. (Form.)
1949 *Otozamites anglica* (Seward) Harris, p. 275, text-figs. 1, 2. (Discussion, cuticle.)

DIAGNOSIS (taken from Harris 1949). Leaf rather small, estimated length 6–10 cm., width 2·5–3·5 cm. or less. Shape of leaf as a whole oblanceolate, apex being more or less rounded, base tapering. Petiole rather short, slender, smooth. Pinnae arising at an angle of about 90° over most of the leaf, but a smaller angle above; pinnae mostly separated by 1–2 mm., shape elongated-triangular in the lower part of the leaf, becoming parallel-sided above, apex obtusely pointed. Pinna attached over the lower half of the proximal border; auricle moderately developed, partly crossing the rachis, less developed in upper pinnae. Veins rather distant, fine, concentration typically 15 per cm., branching at all levels. Auricle provided with one or two forward running veins which then curve and end on the upper margin near the auricle. Substance of the lamina thin, flat margins not recurved.

Cuticle (imperfectly known) thin (less than 1μ) on both sides. Upper showing rather large cells, with finely marked outlines showing large rounded sinuosities. Papillae absent; other details unknown. Lower cuticle showing stomata sparsely, but almost evenly scattered, not forming files. Orientation rather varied. Cell outlines very indistinct but showing large sinuous folds, papillae absent. Guard cells fairly large and well cutinised, probably exposed; subsidiary cells probably represented by an oval thickened area around the guard cells. Trichome bases probably represented by occasional round thickened cells, chiefly along the veins.

HOLOTYPE. Whitby Museum No. 2503.

DISCUSSION. The specimens are almost exactly alike except for a little variation in width and all agree in being delicate; the lamina in fact seems thinner than in any other Yorkshire species and the cuticle is exceptionally thin. Certain naturally oxidised specimens

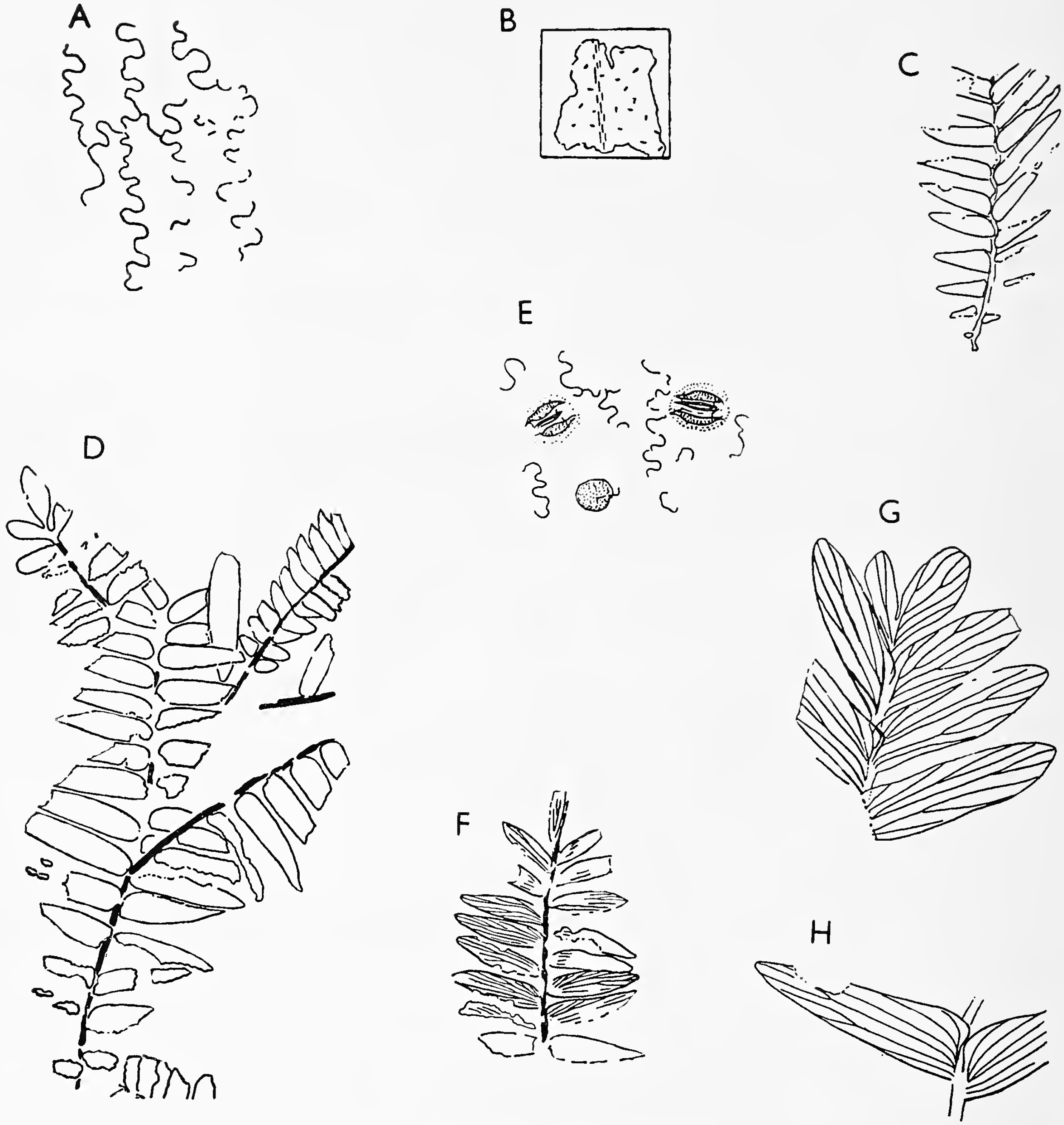

Fig. 17. **Otozamites anglica** (Seward)

A, upper cuticle of holotype, ×200. B, distribution and orientation of stomata, the square is 1 sq. mm., V.27657*a*. C, V.27657, ×1. D, second specimen in Whitby Museum, leaves simulating conifer shoots, mentioned by Seward, ? No. 2377, ×1. E, lower cuticle of holotype showing two stomata and a possible trichome base, ×200. F, holotype specimen, Whitby Museum, No. 2503, ×1. G, leaf apex, transfer preparation, V.27658, ×2. H, veins of one of the lower pinnae shown in C, ×2.

All the specimens are from the Whitby Plant Bed and the figures are from Harris (1949).

show a few isolated fibres up to 3 mm. long between the veins. The matrix of a specimen examined under xylol gave no evidence of any trichomes.

COMPARISON. *O. anglica* seems constant and is well distinguished from other species by the small size of the leaf; spreading pinnae; delicate texture of the lamina; rather widely spaced veins and thin cuticle with exposed stomata. The Yorkshire *O. penna* has pinnae of rather similar size, but they are more crowded, arise at a smaller angle, have much more crowded veins, a thicker cuticle and protected stomata.

A new specimen is figured here (Pl. 1, fig. 5) in which the auricles are small and the bases of the pinnae are almost symmetrically contracted (that is attachment is by a very small region just below the middle of the base). Such a specimen approaches the genus *Zamites* but the more normal form has a distinctly asymmetric pinna base.

OCCURRENCE. *Otozamites anglica* is rare. A single specimen is known from Saltwick, all the others are from Whitby. A specimen which seems to be No. 2377 in the Whitby Museum shows several overlapping leaves and was taken by Seward to be a branching Conifer. I have collected a few specimens from the Long Bight Plant Bed and there is a good Whitby specimen at Stockholm.

Otozamites mimetes Harris
Text-fig. 18

1949 *Otozamites mimetes* Harris, p. 285, text-figs. 3 B, C, 5. (Description and figures repeated here.)

DIAGNOSIS (from Harris 1949). Leaf linear lanceolate, original length unknown, width nearly 2 cm. Pinnae contiguous at their bases but scarcely overlapping, arising at an angle of about 70° to the rachis. Pinna about 10 mm. long, 5–6 mm. wide (rather less in the upper part of the leaf). Margins sometimes tapering so slightly as to be almost parallel, sometimes tapering distinctly. Apex varying from rounded-truncate to rounded-obtuse. Basal lobe (auricle) either almost undeveloped or feebly developed. Veins arising from the whole base of the pinnule apart from the auricle, diverging slightly; fairly distinct; traversing the lamina at a concentration of 3 per mm. Margins not thickened but surface of pinna distinctly convex. Region of attachment of pinnae strongly depressed.

Cuticle showing uniform (so far as is known) square or rectangular cells with strongly sinuous walls, sinuosities by no means reaching the middle of the cell. Cell surface flat, not papillate. Cell outlines fairly narrow and distinct.

Lower cuticle showing stomata in rather narrow but ill-defined bands between the veins. Epidermal cells rectangular to irregular, cell outlines strongly sinuous, marked by a very narrow and rather indistinct outline. Cell surface usually showing a distinct, thickened papilla, but not otherwise bulging. Stomata rather irregularly placed but nearly all transverse to the veins, tending to occur in 1–3 short longitudinal files but irregularly spaced in their files. Guard cells and subsidiary cells sunken in a cutinised pit which is overhung by enlarged papillae of surrounding epidermal cells (details not fully known).

Trichome bases represented by very occasional ring-like thickenings.

HOLOTYPE. Specimen in Yorkshire Museum, figured Harris (1949, text-figs. 3 B, C, 5).

COMPARISON. *O. mimetes* looks very like the Yorkshire *O. falsus*, in fact the two are scarcely to be distinguished without cuticle preparations. These distinguish them at once, for

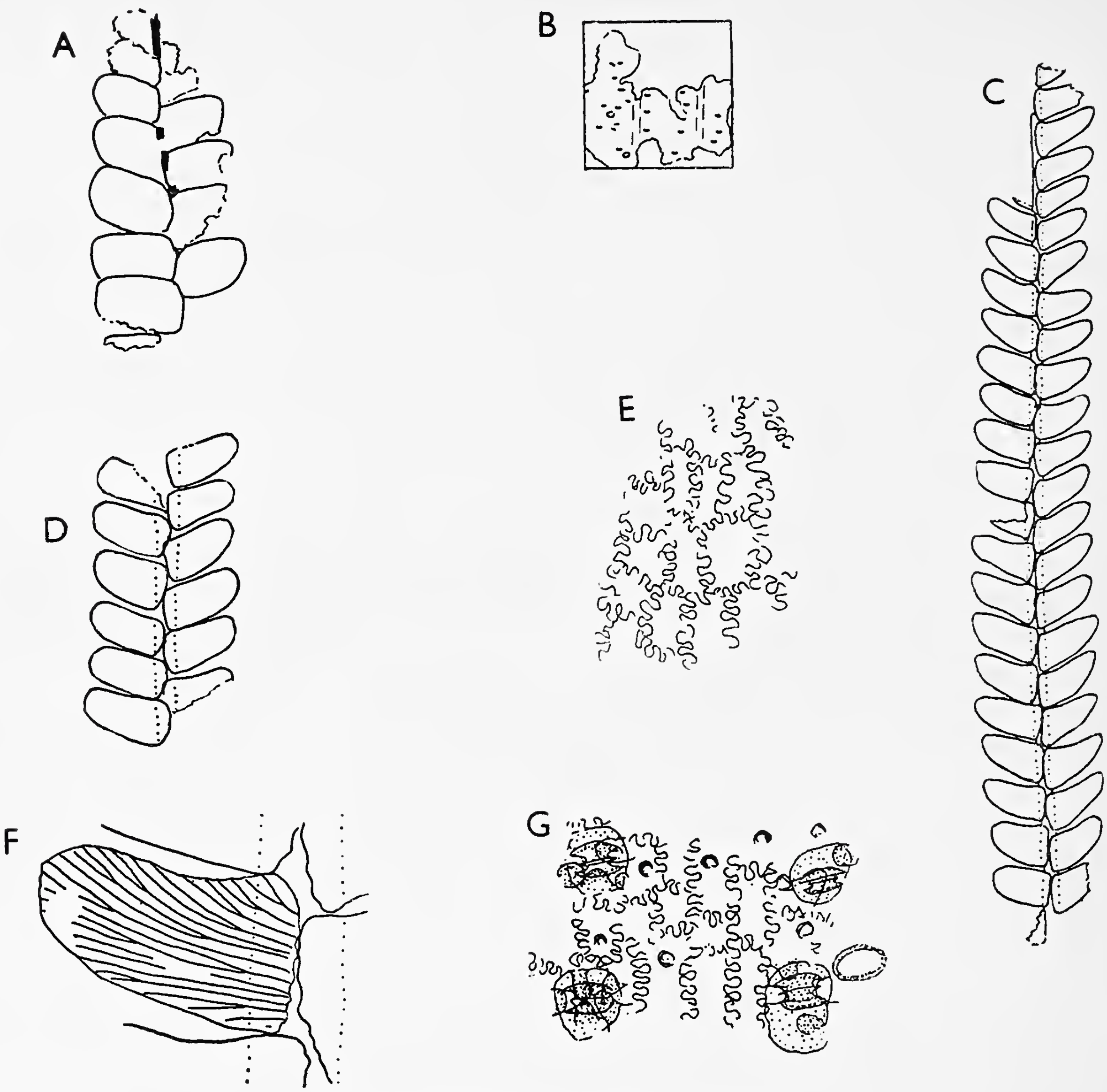

Fig. 18. **Otozamites mimetes** Harris

A, fragment from Cloughton Wyke, V.52919, ×1. B, distribution and orientation of stomata (black lines) and trichomes (rings) in a fragment of lower cuticle. The square is 1 sq. mm. C, larger fragment in Yorkshire Museum, ×1. D, smaller fragment in Yorkshire Museum, ×1. E, upper cuticle from specimen in C, ×200. F, one pinna of specimen in C, ×4. G, lower cuticle from specimen in C, ×400.

Fig. A is new, all the others are from Harris (1949).

O. mimetes has just occasional trichome bases while in *O. falsus* the lower epidermis is covered with bulging cells, much as in *Ptilophyllum pecten*. *O. simpsoni* is less similar, having smaller pinnae which are also relatively narrower and many more trichomes.

The Italian *O. mattellianus* Zigno (with which the Yorkshire Museum specimens had been identified) is distinguished by its longer and more pointed pinnae.

Occurrence. *O. mimetes* was based on two imperfectly localised specimens in the

Yorkshire Museum. A third (also figured here) was found lying loose at the foot of the Middle Deltaic cliff at Cloughton Wyke from which it had doubtless fallen. The matrix is a sandy shale and contains water-worn plant fragments; I do not recognise it as representing any known plant bed. The preservation is poor but it gave a cuticle preparation which was just adequate to confirm its identification. The original specimens were labelled 'Lower Estuarine Series near Scarborough' and I suggested they might be from Haiburn Wyke. All we know of its age therefore is that it is Middle Deltaic and very likely also Lower Deltaic; but labels of that kind are unreliable.

Otozamites falsus Harris
Text-figs. 19, 20

1900 *Otozamites feistmanteli* Zigno; Seward, p. 221. (Mention of present specimen.)
1949 *Otozamites falsus* Harris, p. 287, text-fig. 6 B–E. (Leaf, cuticle, figures repeated here.)

DIAGNOSIS (slightly emended). Length of leaf perhaps 20–30 cm., width in middle region 12–18 mm., but less towards apex and towards base. Rachis 3–4 mm. wide, smooth apart from longitudinal ridges. Pinnae almost concealing rachis, contiguous at their bases, not or only slightly overlapping, in middle region arising at an angle of about 70° to rachis, about 6 mm. × 4·5 mm. to 10 mm. × 6 mm., occasionally 14 mm. × 6 mm., shape nearly rhomboidal but tapering very slightly, apex rounded-truncate. Auricle scarcely developed, or very slightly expanded. Towards leaf apex, pinnae smaller and relatively narrower and more pointed, towards base of leaf pinnae becoming nearly square. Base of pinna not or only slightly contracted but uppermost two veins running upwards and outwards (i.e. where an auricle would be expected). Veins indistinct, concentration of veins about 30 per cm. Surface of pinna convex, margins entire, not marked off from the rest of the lamina; substance of lamina thick.

Cuticle of both sides moderately thick, but lower side of darker colour. Upper showing uniform more or less square cells in rows. Surface of cell flat, probably finely sculptured, non papillate. Lateral walls strongly sinuous, tending to form closed loops, interior of loop appearing thinner than rest of cell.

Lower cuticle showing a marginal region 200μ wide resembling the upper cuticle and an inner region with stomata and bulging cells; transition to margin rather sudden but no fold present. Inner region showing stomatal bands alternating with rather narrower bands along veins having no stomata. Stomata orientated transversely, irregularly spaced and not forming definite files. Epidermal cells short, often square, outlines unmarked or faintly marked and slightly sinuous. Cell surface bulging strongly to form a flattened mound with thick sides and sharply limited round or oval hole on top. Apical openings of longitudinal series of cells sometimes appearing continuous as a long slit. No trichome present to correspond to those holes in epidermal cells.

Whole stomatal apparatus sunken forming rectangular group overhung by neighbouring epidermal cells. Subsidiary cells small, without papillae. Guard cell thickenings well developed. Trichomes absent.

HOLOTYPE. V. 3683, figured Harris (1949, text-fig. 6 B–E).

COMPARISON. *O. falsus* has been compared with *O. mimetes* from which it is only reliably

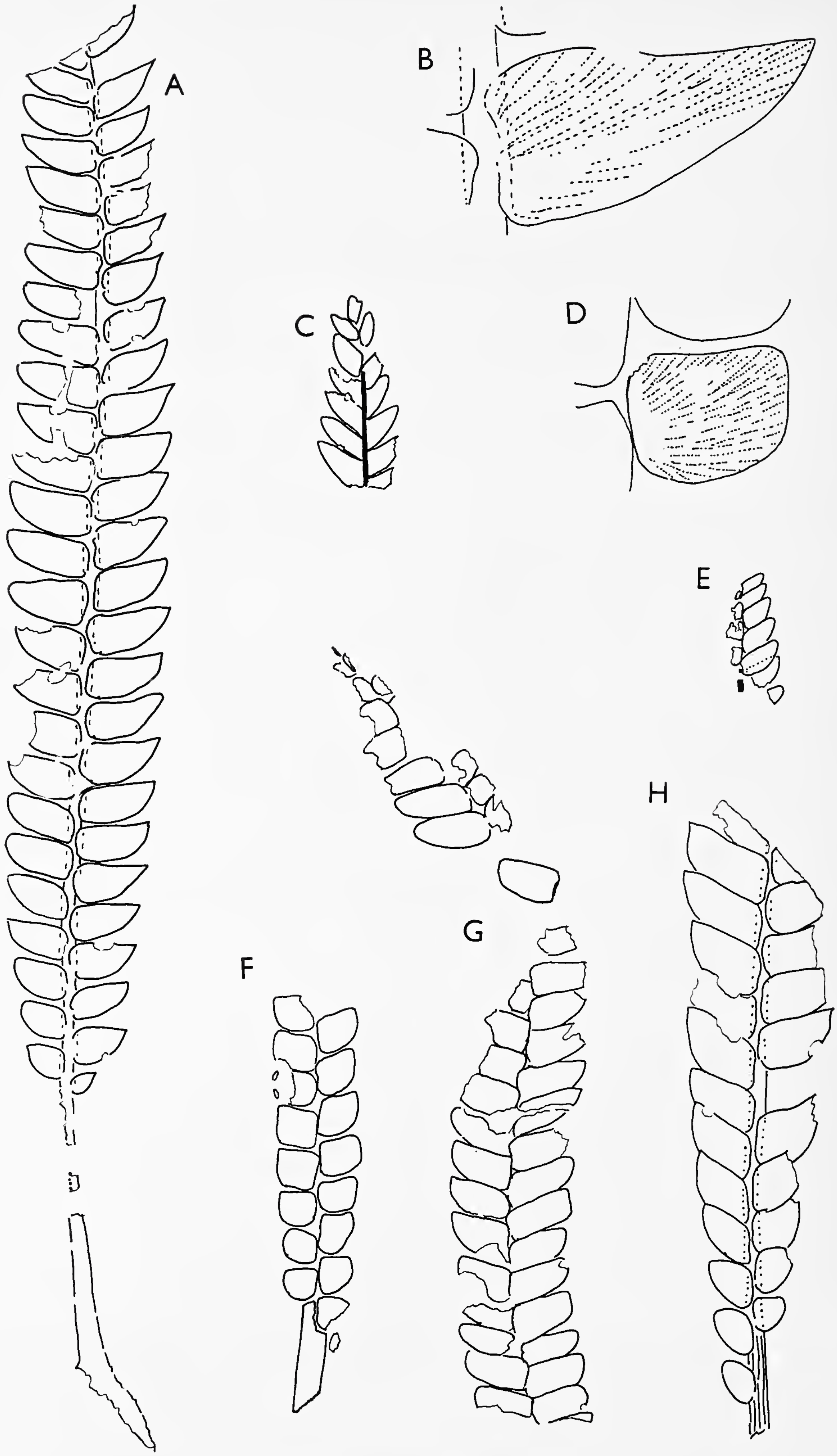

Fig. 19. **Otozamites falsus** Harris

A, nearly complete leaf, specimen labelled '*Otopteris acuminata*, Upper Shale Scarboro'. Specimen in Yorkshire Museum, ×1. B, a single pinna from A to show the veins, ×4. C, apex of leaf, V.52885, ×1. D, pinna from base of leaf, V.52883, ×4. E, apex of leaf, V.52882, ×1. F, base of leaf, V.52883, ×1. G, middle region of leaf (or possibly fragments of two leaves), V.52882, ×1. H, lower part of leaf, V.52886, ×1. The specimens in C–H are from blocks fallen from the cliff at Hawsker, High Whitby (54° 28′ 50″ N).

distinguished by its cuticle. It is also rather like *O. mandelshohi* as interpreted by Feistmantel (1890) and *O. seglei* as interpreted by Möller (1903), but in neither is the cuticle known. It is possible that when the cuticles of one of these older known species is described it may be identified.

The holotype had been named *O. feistmanteli* Zigno by Seward, but it differs in details both from the Italian originals and from the Yorkshire specimens I have called *O. simpsoni*. For instance the pinna is attached along almost the whole base, and *O. simpsoni* at least has a different cuticle. The stoma is fairly similar to that of some other species (e.g. *O. mimetes*) but the bulging epidermal cells are unlike those of other Yorkshire species but very like those of *Ptilophyllum pecten* and *P. hirsutum*. The stomata (in which the subsidiary cells lack papillae) are unlike those of *Ptilophyllum*.

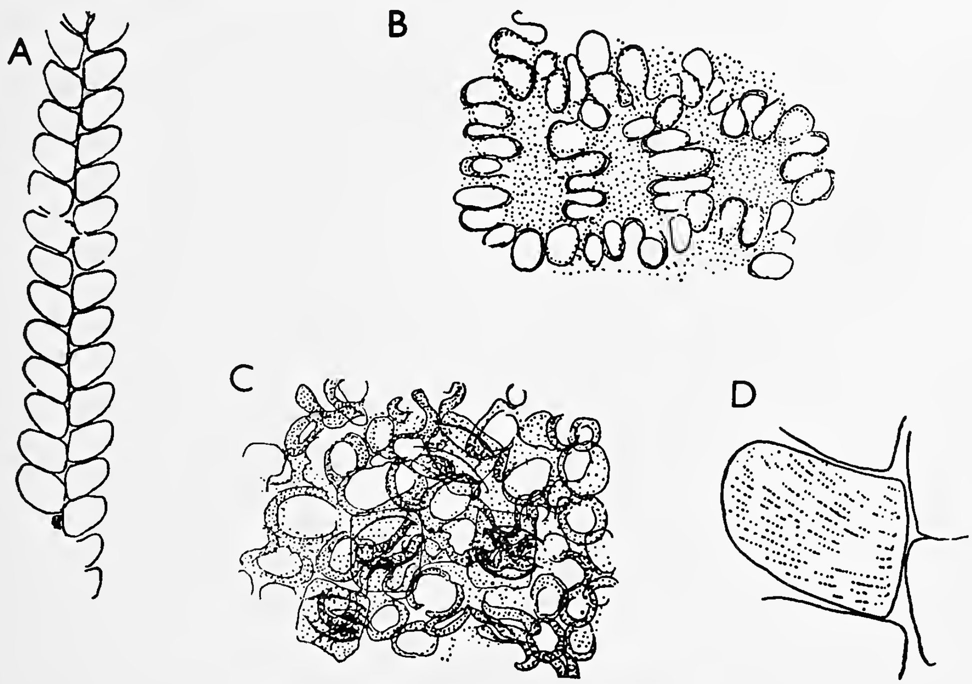

Fig. 20. **Otozamites falsus** Harris

A, leaf, ×1. B, upper cuticle, ×400. C, lower cuticle, ×200; both sides of the drawing represent cells along veins. D, outline of a pinna showing the veins (which are indistinct), ×4.

All the figures represent the holotype, V.3683. The figures are from Harris (1949).

O. falsus and *O. mimetes* are difficult to place in a genus being at the extreme limit of *Otozamites* as I would define it and bordering *Anomozamites* and perhaps *Ptilophyllum*. I have kept them in *Otozamites* however because the uppermost veins do suggest a vestige of an auricle and such a feature is quite foreign to *Anomozamites*. It is more doubtful what is their distinction from *Ptilophyllum*, and I have only preferred *Otozamites* because of the existence of a series of species linking them with more typical *Otozamites* leaves.

Cycadolepis pelecus (p. 117) possibly belongs to the same plant.

Ptilophyllum khargaense Kilpper 1965*a* from Egypt is closely similar to both *O. falsus* and *O. mimetes* in the form and venation of the pinnae, but is sharply separated from both by its cuticle which shows remarkable crenulate bulges on the lower epidermal cells. *O. mimetes* merely shows small round papillae, but *O. falsus* shows large but simple bulges. Kilpper discusses the difficulty in deciding whether *P. khargaense* should be placed in *Ptilophyllum* or *Otozamites*.

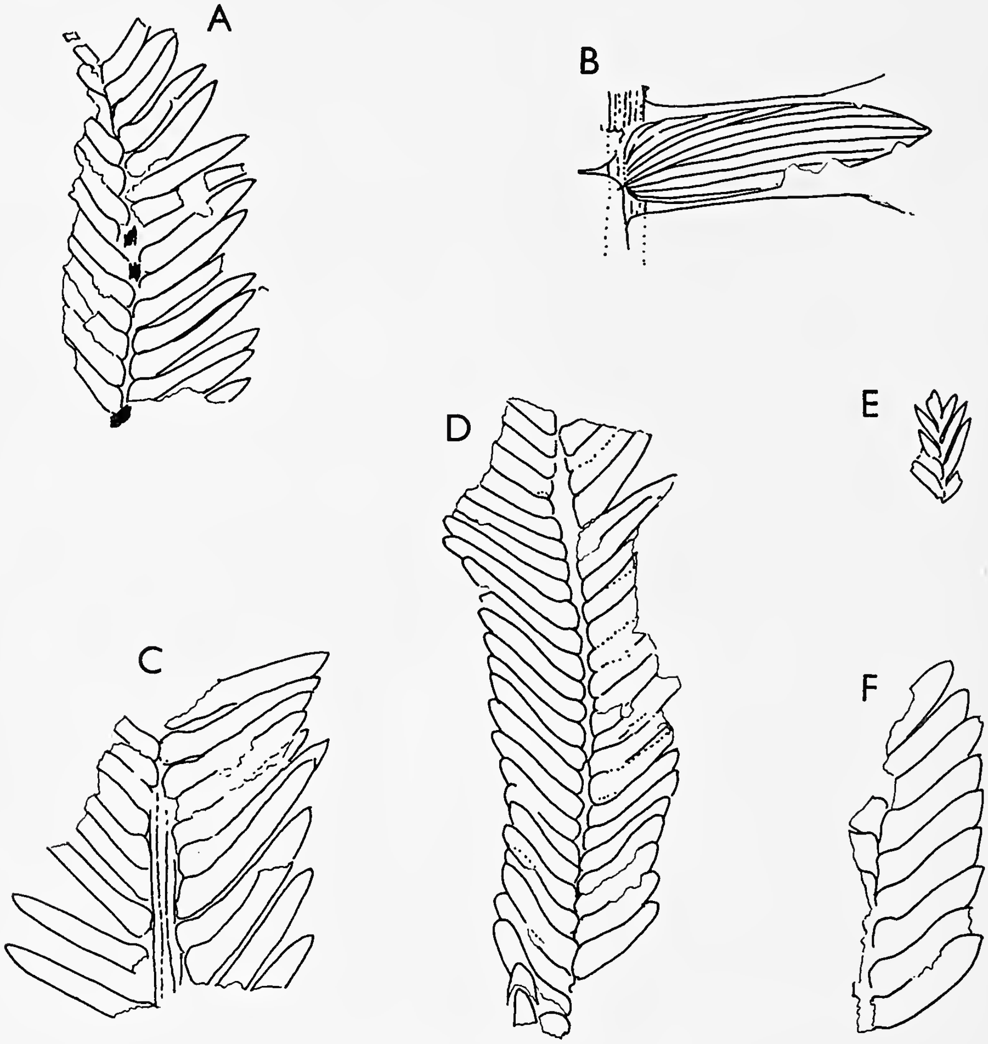

Fig. 21. **Otozamites penna** Harris

A, upper part of leaf, V.52923, ×1. B, pinna of V.52934*a*, ×4. C, D, middle regions of two leaves, V.52921 and V.52920, ×1. E, apex of a leaf, V.52932, ×1. F, middle region of a leaf, V.52931, ×1.

A, C, D are from Roseberry Topping (Lower Deltaic); B from Cloughton *Solenites* Bed; E, F, from Waif Garth, Goathland (Middle Deltaic).

Occurrence. *O. falsus* was based on the holotype alone and this was imperfectly localised. It has since been found repeatedly in fallen blocks representing a plant bed in the cliff near the High Whitby fog signal and the new specimens have made some addition to the diagnosis possible. In this bed it is the commonest species. It is also represented by two specimens collected by Hamshaw Thomas and labelled 'Whitby'. They are in a different matrix. All are from localities in the Lower Deltaic.

Otozamites penna Harris
Text-figs. 21–23

?1900 *Williamsonia pecten* (Phillips); Seward, in part, pp. 198, 200, pl. 3, figs. 5, 6 only.
1946 *Otozamites penna* Harris, p. 484, text-figs. 4 B, 6, 7. (Leaf, cuticle, figures repeated here.)

DIAGNOSIS (slightly emended). Leaf typically 15–20 cm. long × 1·5–3·0 cm. wide, widest leaves up to 4·0 cm. in middle region, tapering gradually towards base and apex. Petiole short, expanded basally but under 2 mm. wide in middle region of lamina, marked on both sides with 3–6 strong longitudinal ridges and with short transverse wrinkles. Upper surface of rachis usually partly exposed, margins overlapped by pinnae. Pinnae slightly

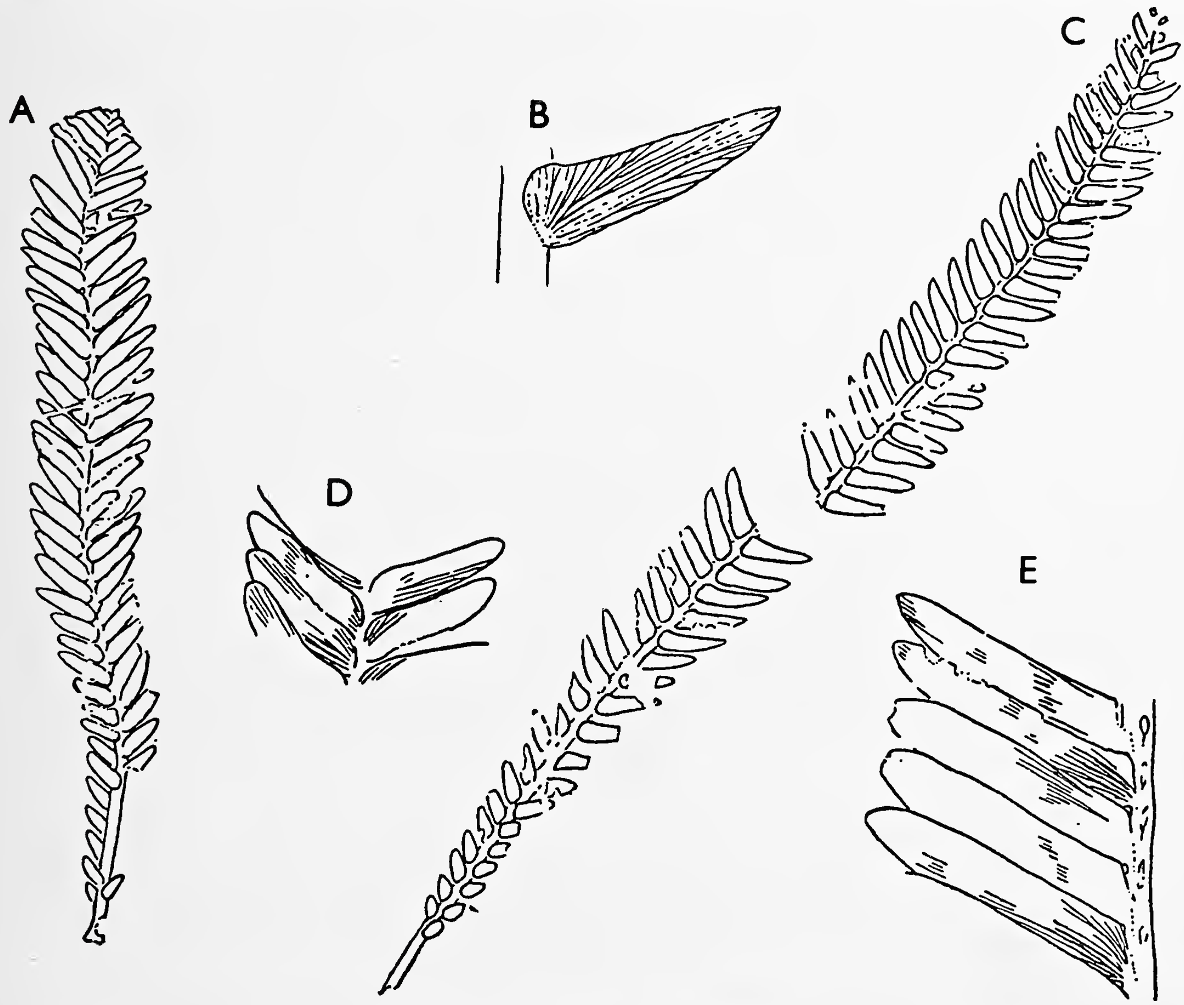

Fig. 22. **Otozamites penna** Harris

A, specimen 1134, Herries Collection, ×1. B, pinna of holotype, ×4. C, holotype, Herries Collection 2102, Saltwick, ×1. The break is due to a ripple mark in the sandstone. D, part of specimen 1134, ×4. E, part of broad specimen Herries 1159 (High Whitby) showing scars of detached leaflets, ×4.

All the figures are of specimens in the Yorkshire Museum and are from Harris (1946).

separated or touching or overlapping, arising at an angle of 60°–80°; length typically 13–17 mm. × 2·0–2·5 mm., largest 25 × 3·0 mm. Pinnae attached along lower half or third of proximal margin; basal angle slightly rounded, pinna contracting very slightly towards point of attachment. Upper basal angle either not expanded or expanded very slightly but never overlapping mid-line of rachis, even innermost vein usually diverging slightly from rachis. Pinnae straight, parallel-sided over most of their lengths then tapering to an obtuse or rounded point. Veins slender, traversing lamina at 4–5 per mm. Substance of lamina not very thick, margins unspecialised.

Both cuticles about 1μ thick (measured in folds). Upper showing neither stomata nor trichomes, consisting of rows of nearly uniform cells, veins scarcely indicated. Cells tending to be rectangular, walls finely but distinctly marked, sinuous; surface without any papilla or distinct sculpture.

Lower cuticle showing stomata in bands between veins, stomatal bands equalling vein bands in width. Stomata often in two indefinite files in each stomatal band, irregularly spaced, orientated more or less transversely. Epidermal cells rectangular or irregular, cell outlines sinuous, finely marked, often indistinct. Cell surface often flat, and uniformly thick, but sometimes showing thinner regions opposite sinuous folds and in some specimens showing a median thickening forming a solid or hollow papilla, but papilla never conspicuous. Surface sculpture of coarse mottling. Guard cells and subsidiary cells sunken in a pit, sides of pit overlapped to a considerable extent by large hollow papillae arising from surrounding epidermal cells. Subsidiary cells fairly small, thickly cutinised, without papillae of their own.

Many specimens without trichomes, but others with small numbers in stomatal bands, consisting of a more or less reduced and thickened epidermal cell bearing a cylindrical outgrowth of cuticle about 50μ × 25μ.

Holotype. Herries Collection, Yorkshire Museum No. 2102, figured Harris (1946, text-figs. 6 a, b, 7).

Description. This species was based on a series of specimens from one locality. It proves to be fairly widespread and common at a few points and the new specimens have led to a slight widening of the previous diagnosis. The changes are that a few rather broader leaves were found, that in some specimens the epidermal cells have no papillae and in some specimens the sac-like trichomes which were a characteristic of the original material are not seen.

The Hamshaw Thomas Collection provided over a dozen very similar leaves from Roseberry Topping. These showed that the variability is not of the ordinary random kind but has a local character and the range differs from that at the original locality, High Whitby. These differences are in cuticle only; and apart from one specimen mentioned at the end they do not affect the stomata.

The original material showed more or less perceptible papillae on the cells of the underside and also sac-like trichomes among the stomata. Most of the specimens from Roseberry show no papillae at all and no trichomes, but one shows very slight papillae but only under phase-contact illumination. Two only showed sac-like trichomes and these were very few. There is some variation in the stomata. In most specimens all those seen fall in the range covered by those previously figured but some showed more protected stomata, like those of *O. graphicus*, and as mentioned below one had unprotected stomata. Another general difference between the two sets of specimens is that the sinuous folds in the original specimens were rounded, but in nearly all the present ones they are closer and rather angular.

Other localities gave one or else two specimens only and it is unknown whether a special feature of cuticle is peculiar to this locality. For instance a leaf from Boulby Alum quarry has an exceptionally thick cuticle with deeply penetrating anticlinal walls. A specimen from the Cloughton Wyke *Solenites* Bed has an exceptionally thin cuticle and exposed stomata (in which however it agrees with one Roseberry specimen). While this kind of variation may

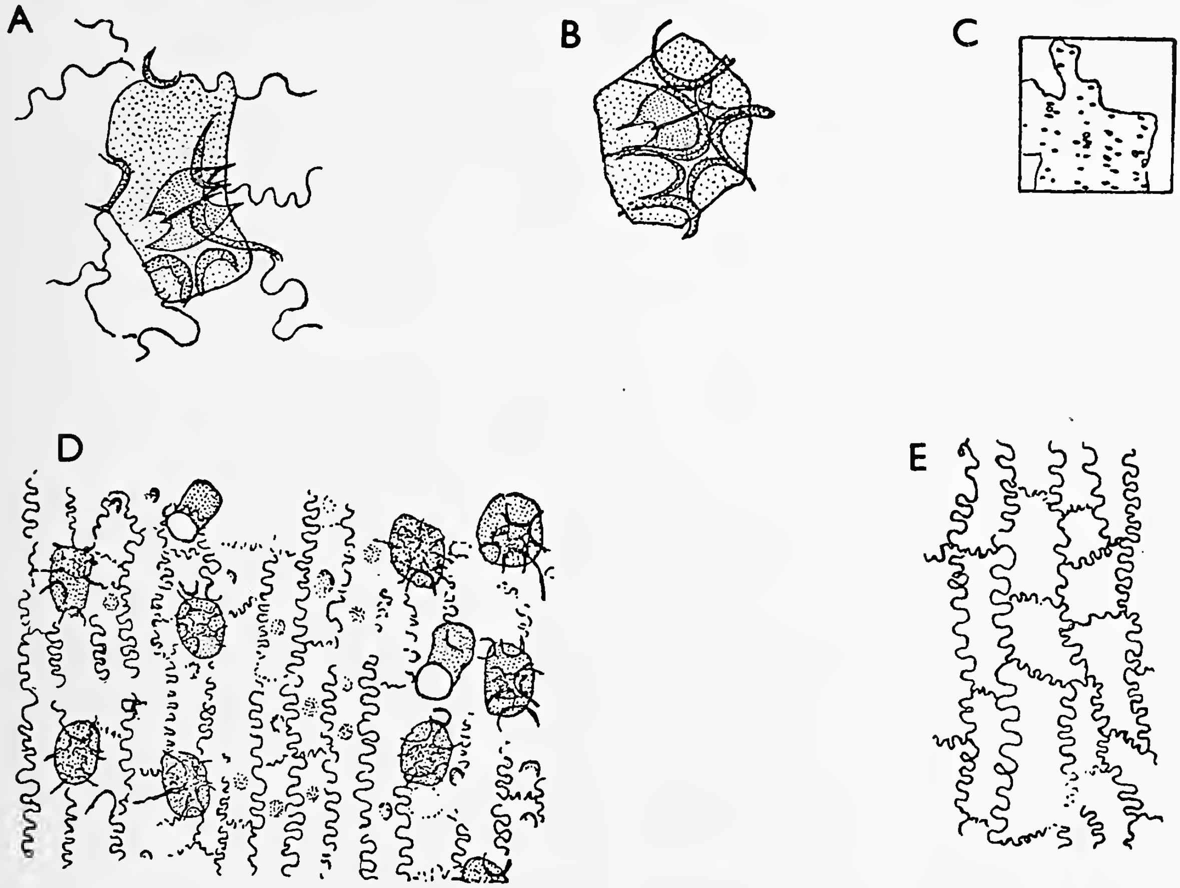

Fig. 23. **Otozamites penna** Harris

A, exposed stoma, ×500. B, stoma almost concealed by papillae of surrounding cells, ×500. C, fragment of lower cuticle showing orientation of stomata (black lines) and trichomes (rings), ×20. D, lower cuticle showing two complete stomatal bands and one vein, ×200. E, upper cuticle, ×200.

All the figures are of the holotype (Herries Collection No. 2102 in the Yorkshire Museum) and are from Harris (1946).

indicate the existence of unrecognised distinct species it seems best to disregard it and to regard *O. penna* as an inconstant and indeed difficult species of rather small stratigraphic value.

Occurrence. *O. penna* (or forms with a closely similar cuticle) occurs throughout the Deltaic Series but much more commonly in the Lower Deltaic. It is locally abundant at a point in the cliffs at High Whitby and in the basal black layer at Roseberry Topping (both

Lower Deltaic). Apart from imperfectly localised specimens in museums (which I suspect are all Lower Deltaic) its distribution is as follows:

Upper Deltaic	2 localities
Middle Deltaic Gristhorpe Series . .	2 localities
Millepore Series	1 locality
Lower Deltaic	12 localities

All the records above the Lower Deltaic are based on cuticle fragments only.

Otozamites tenuatus (Leckenby)
Text-fig. 24
(***O. bunburyanus*** auct. angl.)

The following are all Yorkshire specimens:

1864 *Otopteris tenuata* Leckenby *ex* Bean MS, p. 79, pl. 9, fig. 3. (Leaf fragment.)
1875 *Otozamites tenuatus* (Leckenby) Phillips, p. 221, lign. 46. (Name.)
1900 *Otozamites bunburyanus* Zigno; Seward, p. 211, pl. 2, figs. 4, 5. (Good leaf fragments.)
1917 *Otozamites bunburyanus* Zigno; Seward, p. 542, text-fig. 606B. (Drawing of Leckenby Coll. specimen K.232.)
1946*a* *Otozamites bunburyanus* Zigno; Harris, p. 366, text-figs. 4, 5. (Good fragments, cuticle. Figures and description repeated here.)

The relation of *O. tenuatus* to the specimens mentioned below is doubtful:

1879 *Otozamites Bunburyanus* Zigno; Feistmantel, p. 211, pl. 7, figs. 5–8; pl. 16, fig. 2. (Very narrow leaf.)
1891 *Otozamites Bunburyanus* Zigno; Saporta, p. 460, pl. 298, fig. 1. (Fairly good leaf. Bathonian; France.)
1901 *Otozamites Bunburyanus* Zigno var. *major* Roth, Kurtz & Burckhardt, p. 14, pl. 3, fig. 7. (Ill-preserved fragment. Lias; Argentine.)
1903 *Otozamites Bunburyanus* Zigno; Möller, p. 15, pl. 2, figs. 14, 15. (Leaf fragment. Middle Jurassic; Bornholm.)
1920 *Otozamites Bunburyanus* Zigno var. *indica* Seward & Sahni, p. 28, pl. 5, figs. 45, 46. (Very narrow leaf. Jurassic; India.)

The following are definitely distinct:

1868 *Otozamites Bunburyanus* Zigno, p. 9, text-figs. 4, 5. (Italian fragments.)
1881 *Otozamites Bunburyanus* Zigno; Zigno, p. 102, pl. 38, figs. 1–8. (Good Italian leaves.)
1932 *Otozamites* sp. aff. *Bunburyanus* Zigno; Carpentier, p. 7, pl. 2, fig. 3. (Structural material. Corallian; France. Re-described by Florin 1933*a*.)

Emended Diagnosis. Leaf linear, possibly 30 cm. long × 0·6–0·8 cm. wide. Petiole 7 mm. wide below but narrowed to 3 mm. at the base of the lamina, rachis marked with fine longitudinal ridges and densely hairy on the back. Pinnae nearly circular but with a very obtusely pointed apex, base truncate or slightly cordate; form nearly constant over the whole leaf. Region of attachment occupying about a quarter of the basal margin. Basal angles equal or upper one very slightly expanded; apex pointing at about 45° to the rachis. Rachis completely overlapped by pinna bases; pinnae on same side sometimes separate, sometimes overlapping.

Upper surface of pinnae strongly convex, substance very thick; under surface showing a prominent, smooth but not reflexed margin and a concave lamina covered with short, fine appressed hairs. Veins forming obscure ridges on upper side and hidden by hairs on lower side; concentration 5–7 per mm.

Cuticle moderately thick, about 1·5μ above (increasing to 4μ at the margin, rather less than 1μ on concave under surface). Upper cuticle of lamina nearly uniform, veins scarcely

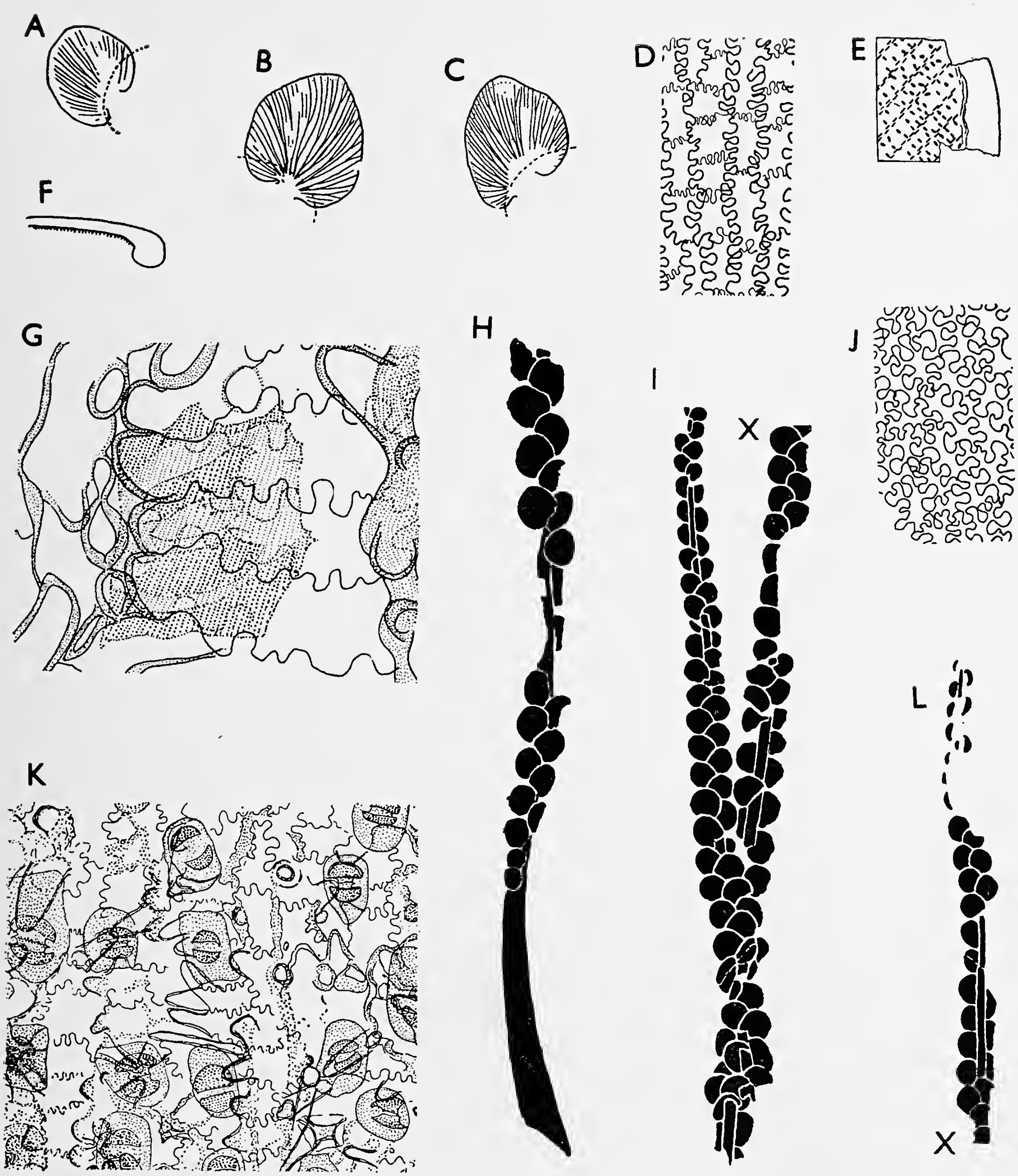

Fig. 24. **Otozamites tenuatus** (Leckenby)

A, pinna from 'L', ×4. B, pinna from 'H', ×4. C, pinna from 'H', ×4. D, upper cuticle, ×200. E, lower side and margin showing veins and stomata, ×20. F, imaginary section through lamina showing hairs and thick margin, ×10. G, stoma from outside; structures on surface shown by firm lines, structures below surface by broken lines; guard and subsidiary cells obliquely stippled, ×800. H, lower part of leaf, ×1. I, middle parts of leaves, one continued in L, ×1. J, cuticle of margin (underside), ×200. K, lower cuticle showing two veins and parts of three stomatal bands, ×200. L, top of right leaf in I, ×1.

The specimens are from Haiburn Wyke and are in the Yorkshire Museum. The specimens were figured as *O. bunburyanus* by Harris (1946).

shown but cells forming well marked rows parallel to veins. Lateral walls well marked, showing strong, rounded folds, end walls showing finer and closer folds. Cell surface flat, with thin areas in loops of folds. At margins of pinna, folds increasing in size and occupying most of surface.

Lower cuticle showing marginal region of uniform cells and consisting of inner region dividing into strips along veins separated by broader intervenal strips. Stomata numerous (100–120 per sq. mm.), confined to intervenal strips. Stomata often forming 1-3 longitudinal files or irregular, unevenly spaced in their files, orientated transversely as a rule. Epidermal cell outlines finely marked, often indistinct and confused by folds caused by collapse of bulging cell surface and by papillae. Most cells bearing a hollow papilla, papillae varying from a hemispherical bulge to a narrow conical hair 500μ long. Cells along veins similar to others. Stomata strongly sunken, guard cells and subsidiary cells being at bottom of a pit formed by surrounding epidermal cells and often further concealed by papillae pointing to mouth of pit. Mouth of pit sometimes to one side of stoma and reduced to narrow crack, sometimes rather widely open but guard cells still usually concealed by papillae. Occasional small oval cells (particularly along veins) possibly representing trichome bases, but trichomes not observed apart from long papillae of ordinary epidermal cells.

Discussion. *O. tenuatus* is evidently rare. A number of good specimens were collected long ago, but in more recent times there is but one fragment collected by Hamshaw Thomas. I have never found it. The best specimens are the ones in the Yorkshire Museum (some figured here) and there are ones which look typical in the Manchester Museum, the Hancock Museum, Newcastle, in the Leckenby Collection, Cambridge, in the Geological Survey & Museum (from Carlton Bank) as well as in the British Museum (Natural History).

Although rare it must be frequent in its main locality, and an unexplained fact is that leaves very often lie near one another in a manner suggesting origin from a single stem. This has been noted by Seward as well as by me (on many different blocks).

Comparison. *O. tenuatus* is only reliably determinable when its cuticle is available. Its form is indistinguishable from the Italian *O. bunburyanus* Zigno 1881 (at least on present knowledge).

Of other Yorkshire species *O. beani* is the most similar. It is normally distinguishable by its much larger pinnae which are also relatively longer. There are however a few very small leaves with rounded pinnae looking like those of *O. tenuatus* but with *O. beani* cuticle. I have determined them as *O. beani*. *O. falsus* has pinnae of similar size but with a wider region of attachment and a very different lower cuticle.

O. marginatus, a rather larger leaf with rounded pinnae, is distinguished by its sharply reflexed margin as well as by its cuticle.

O. tenuatus was identified with *O. bunburyanus* Zigno first by Zigno (1868, p. 9) and later by Seward (1900), and I agreed (Harris 1946) since the figures look just alike. *O. tenuatus* is now separated on information given me by Dr. A. Wesley. He tells me that the Italian specimens have a very different lower epidermis. In *O. tenuatus* the cell surface is flat apart from a hollow papilla occupying barely half of its surface. The papilla may be short or very long but is always thickly cutinised. *O. bunburyanus* has epidermal cells whose whole outer surface seems to bulge very strongly, the sides of the bulge are thickly cutinised but the top is thin or missing.

There is no intermediate form making a transition from the kind of epidermal cell of the Yorkshire leaf to that of the Italian leaf. This removes one of the very few remaining species of the Italian Upper Lias which seemed identical with one from the Yorkshire Lower Oolite.

It is useless to discuss the relation of *O. tenuatus* to the various leaves described as *O. bunburyanus* from countries other than Italy until their cuticles are known.

Occurrence. *O. tenuatus* has three localities all Lower Deltaic. These are the type locality Haiburn Wyke (perhaps in the beach); Howdale, Robin Hood's Bay (Hamshaw Thomas) and Carlton Bank (a specimen in the Geological Survey & Museum). Other specimens are unlocalised. A specimen from Goathland (not confirmed by cuticle) is probably from the Middle Deltaic Sycarham Series.

Otozamites marginatus Saporta
Text-fig. 25

1875 *Otozamites marginatus* Saporta, p. 168, pl. 109, fig. 1. (Leaf base. Bathonian; France.)

Diagnosis (Saporta 1875). *O. frondibus deorsum sensim angustatis, rachi tereti strictoque donatis, foliolis coriaceis racheos superficiem tegentibus, arcte contiguis imbricatisque, ambitu late ovatis, basi subinaequaliter rotundatis, marginibus subtus revolutis, nervulis ex insertionis loco ad margines undique divergentibus, pluries dichotome furcatis.*

Additional points from Yorkshire specimens:

Pinnae 9–13 mm. long, width about three-quarters of length, placed at acute angle to rachis below but at right angles above, attached on middle third of base, acropetal basal angle slightly expanded but scarcely forming an auricle. Margins sharply reflexed, overlapping by 100–200μ, entire, marginal rim about 0·7 mm. wide at apex but reduced towards base. Upper surface smooth, lower showing veins as obscure ridges crossing lamina at a concentration of about 50 per cm.; uppermost vein almost at right angles to lowest. Substance of lamina very thick.

Upper cuticle fairly thick (imperfectly known) probably composed of uniform, sinuous walled cells. Towards margin becoming very thick, composed of uniform cells with strongly sinuous walls, sinuosities often mushroom-shaped, cell surface mottled but not papillate, trichomes absent; on underside of margin cells similar (but often much modified by folds due to crushing).

Lower cuticle showing almost evenly dispersed stomata, course of veins often scarcely recognisable, but in parts distinguished as narrow tracts with few stomata but some trichome bases. Epidermal cells often nearly rectangular, walls rather thin but distinct, only slightly sinuous, cell surface flat not papillate but with small granular thickenings. Stomata numerous (about 200 per sq. mm.), transversely orientated to veins, sometimes in short longitudinal files but files inconspicuous. Whole stomatal apparatus often nearly round, subsidiary cell walls not sinuous, surface flat, not papillate. Guard cells not sunken. Cells adjacent to ends of stomatal apparatus often narrow. Trichome bases occasional, consisting of a somewhat thickened cell with a simple ring scar, free part missing.

Discussion. *O. marginatus* is represented by two specimens. One is a fragment collected by Hamshaw Thomas many years ago. Almost the whole of the rachis is missing (the last fragment was removed in cleaning). The lower surface of the pinnae is exposed and the specimen is indifferently preserved in sandstone. It gave poor cuticle preparations, the lower cuticle being fairly good, but the upper though thick has largely disintegrated and is disfigured by adherent organic matter. The specimen is labelled 'Cayton Bay Upper Beds' and is no doubt of Upper Deltaic age.

The second specimen is a single pinna obtained by bulk maceration of the Lower Deltaic

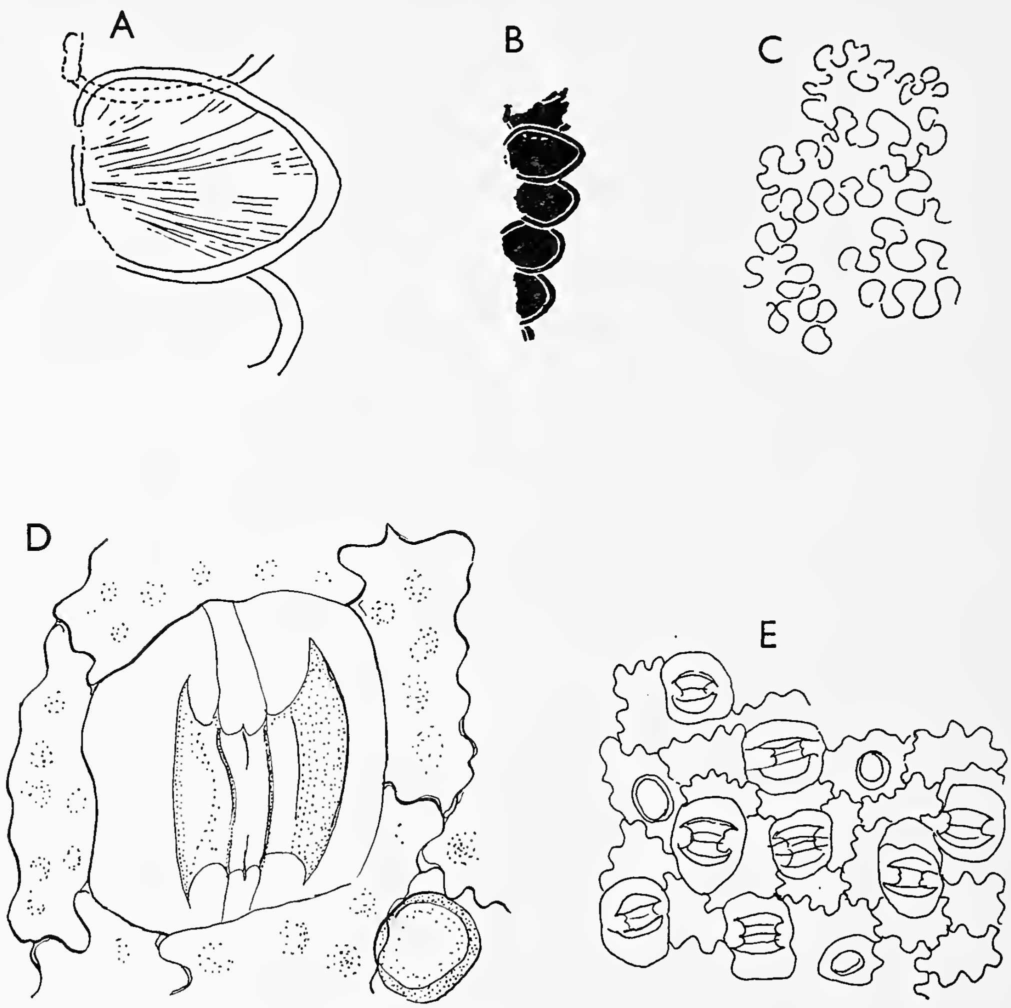

Fig. 25. **Otozamites marginatus** Saporta

A, upper pinna (from B), ×4. B, whole specimen; the uppermost pinna fragment was removed to expose the next pinna, V.52918, ×1. C, upper cuticle, from near margin, ×200. D, stoma and trichome base, ×800. E, lower cuticle, ×200.

The specimen is from 'Cayton Bay, Upper Beds'.

shale of Snilesworth, Wheat Beck loc. 3 (54° 20′ 37″ N, 1° 13′ 1″ W). This pinna is complete, but very small, being 4·0 × 2·5 mm. The margin is well marked and the details of both upper and lower cuticles are well preserved. The upper cuticle shows uniform cells in which the sinuosities cover the whole surface.

Saporta gives the age of *O. marginatus* as '? Bathonian'. Thomas' specimen is Bathonian but the Snilesworth one is Bajocian.

The holotype figured by Saporta (1875) is a rather better fragment of a leaf base but no fine details are known.

The fragments look very similar indeed and very few species have been described with which the Yorkshire specimens could be confused. The small rounded pinnae with a margin that is sharply marked off on the lower surface is unique. Saporta's figure shows fairly similar veins, though fewer of them; I suspect however that the artist left out about half of the crowded veins in many of the figures and I do not take this as a difference.

O. marginatus resembles exceptionally small leaves of *O. beani* in the size and shape of the pinnae, and also the normal leaves of *O. tenuatus* (Leckenby), *O. bunburyanus* Zigno and *O. trevisani* Zigno. In some of these at least the margin is smooth and thickened, but it has never been figured as reflexed as it certainly is here. The most similar (at least among Yorkshire leaves) is *O. tenuatus* but differences are that *O. tenuatus* has not a reflexed margin; the uppermost and the lowermost veins diverge in directly opposite directions and the lower cuticle shows tubular extensions of the epidermal cells which almost conceal the stomata. *O. bunburyanus* of Carpentier (1932), very similar in form to *O. tenuatus*, has still another type of cuticle, see p. 52.

Genus PTILOPHYLLUM Morris 1840, p. 327, expl. pl. 21

Diagnosis (emended). Leaf simply pinnate, pinnae attached to upper side of rachis, pinnae elongated, pointed, base of pinna asymmetric, basiscopic margin decurrent, acroscopic margin contracted and forming a rounded angle, but angle scarcely forming an auricle. Veins parallel arising from whole region of attachment, forking, ending near apex. Cuticle developed, stomata syndetocheilic with one subsidiary cell beside each guard cell; normally confined to under surface; cell walls normally sinuous.

Type Species. *Ptilophyllum acutifolium* Morris 1840, p. 327.

Remarks. Morris (1840, 1841) gave a vague definition of *Ptilophyllum* and later decided to drop the genus, but others took it up and used it though admitting that it is close to *Zamites*. Halle (1913, p. 374) tried to sharpen the distinction between the two by emphasising that in *Ptilophyllum* the pinna base is decurrent while in *Zamites* it is contracted. I accept this. *Otozamites* is distinguished from both by the enlarged auricle on the upper margin. Seward (1917, p. 512) while maintaining *Ptilophyllum* disagreed with Halle and rejected the character of the decurrent pinna base, but was as I believe mistaken. He based his arguments mainly on the type specimen (mistakenly called *Ptilophyllum cutchense*) in the British Museum (Natural History). He gave a figure (fig. 591) which shows rounded pinna bases, that is to say the lower angle is contracted. I have examined the specimen (V.20190) which is composed wholly of mineral and very obscure, but I agree that bases like the figure are visible. However it is figured badly, relief being reversed by illumination from below (the rachis is not a ridge but a deep furrow). The counterpart of this specimen (V.20192) has now been found and is a little clearer and suggests that the pinna bases may be decurrent after all. Of this I am sure, it is wrong to base much on the interpretation of such an obscure specimen.

Seward's argument was further confused by his accepting two figures of Thomas as '*Ptilophyllum pecten*' whereas they are *Otozamites gramineus*, and to add to the confusion one (fig. 593) is drawn upside down.

I have examined the pinna bases of many Yorkshire *Ptilophyllum* leaves. In nearly all the base is markedly decurrent but, rather often the pinnae are so crowded that the next pinna below hides the decurrent base until it is picked away. In a few leaves of *P. pectinoides* the pinna base is not at all decurrent but runs straight to the rachis and in a minute proportion it is very slightly contracted. This is the only example I have met of the trouble Halle foresaw when he proposed hard boundaries.

Much more difficulty arises in distinguishing *Otozamites* from *Ptilophyllum* for while a rudimentary auricle may occur in *Ptilophyllum*, there are leaves with round or oblong pinnae and scarcely more auricle which I have arbitrarily included in *Otozamites.* I have resisted the temptation to use the cuticle, for that would I believe change minor difficulties into major ones.

Kilpper (1965) has given a full review of *Ptilophyllum* in relation to *Palaeozamia.*

Field Key to the Yorkshire species of *Ptilophyllum*

The dimensions are of pinnae in the middle region of a normal leaf. A few leaves are exceptionally small.

1	Pinna under 10 mm. long	*P. pecten*
	Pinna over 10 mm. long	2
2	Pinna up to 3 mm. wide	*P. pectinoides*
	Pinna over 4 mm. wide	*P. hirsutum*

Other characters: *P. pecten* and *P. hirsutum* are strongly papillose beneath the lamina, *P. pectinoides* nearly smooth. *P. hirsutum* differs from the other two by its relatively as well as absolutely broad pinnae (length about five times width instead of about ten times).

There are probably further species but only represented by cuticle fragments.

Ptilophyllum pectinoides (Phillips)

Pl. 1, figs. 4, 9; Text-figs. 26, 27, 53 K

The following are Yorkshire specimens:

1829 *Cycadites pectinoides* Phillips, p. 125, pl. 10, fig. 4.
1841 *Ptilophyllum pectinoideum* (Phillips) Morris, p. 117. (Name.)
1873 *Zamites Phillipsii* Zigno, p. 46, pl. 32, figs. 1, 2. (Large leaves.)
1875 *Pterophyllum pectinoideum* (Phillips) Phillips, p. 226, pl. 10, fig. 4.
1900 *Williamsonia pecten* (Phillips); Seward, in part, p. 190, pl. 3, figs. 2–4, text-fig. 34 only.
1900*a* *Williamsonia pecten* (Phillips); Seward, p. 20, pl. 3, fig. 6.
1913 *Ptilophyllum pectinoides* (Phillips); Halle, p. 378, pl. 9, figs. 2–5. (Good leaves.)
1913 *Ptilophyllum pecten* (Phillips); Thomas & Bancroft, in part, p. 179, pl. 19, fig. 1; pl. 20, figs. 1, 2, text-fig. 27.
1920 *Ptilophyllum pecten* (Phillips); Seward & Sahni, p. 22, pl. 6, figs. 61, 62, text-fig. 2 B. (Cuticle, comparison with *P. acutifolium.*)
1933*a* *Ptilophyllum pecten* (Phillips); Florin, p. 11, text-fig. 4. (Stoma.)
1942 *Ptilophyllum caytonense* Harris, p. 568, text-figs. 1, 2. (Leaf of unusual form, cuticle.) Figures repeated here.
1946*c* *Ptilophyllum pectinoides* (Phillips); Harris, p. 392, text-figs. 1, 2. (Leaf cuticle.) Figures repeated here.
1953 *Ptilophyllum pectinoides* (Phillips); Harris, p. 36, text-fig. 1 K. (Leaf base figured and compared with *Cycadolepis hypene.*)

The following leaves from the Stonesfield Slate of the English Midlands look similar but are of unknown structure:

1823 *Polypodiolites pectiniformes* Sternberg, p. 36, pl. 33, fig. 1. (Refigured by Seward 1917, text-fig. 595.) This appears to be the earliest name.

1823 *Fuccides* (*Caulerpa*) *pennatula* Brongniart, p. 301, pl. 21, fig. 3.
1828 *Zamia pectinata* Brongniart, p. 49. (*Nomen nudum.*)
1835 *Zamia pectinata* Brongniart; Lindley & Hutton, p. 61, pl. 172.
1836 *Zamia taxina* Lindley & Hutton, p. 67, pl. 175.
1871 *Palaeozamia pectinata* (Brongn.) Phillips, p. 169, diagr. 30, figs. 2, 3.
1871 *Palaeozamia taxina* (L. & H.) Phillips, p. 169, diagr. 30, figs. 4, 5.
1904 *Williamsonia pecten* (Phillips); Seward, p. 106, pl. 9, fig. 6; pl. 12, fig. 8.
1912 *Williamsonia pecten* (Phillips); Krasser, p. 908, text-fig. 15. (Leaves from Middle Jurassic; Sardinia.)
1917 *Ptilophyllum pecten* (Phillips); Seward, p. 523, text-fig. 595. (Sternberg's specimen of *Polypodiolites pectiniformis* photographed.)

Seward (1904) gives other references to Stonesfield Slate specimens without figures.

Diagnosis (from Harris 1946 with slight addition). Leaf typically about 20 cm. long, 2 cm. wide. Larger leaves occasionally up to 4 cm. broad, but leaf rarely exceeding 4 cm.; smaller leaves occasionally 1 cm. but rarely less. Lamina as a whole of even width in middle region, tapering gradually below and rather more quickly to the apex. Pinnae in middle of leaf arising at an angle of about 60° to the rachis, separated by gaps of 0·5 to 1·5 mm. Width of pinnae in normal sized leaf about one-tenth its length, that is about 1·5–1·8 mm., width in largest leaves about 3 mm., width in smallest leaves about 1·0 mm.; pinnae near base and apex of leaf shorter but scarcely less wide. Pinnae straight or very slightly falcate, apex acute. Upper basal angle of pinnae rounded, as a rule not expanded, occasionally very slightly expanded but never forming a definite auricle. Lower basal angle normally distinctly decurrent but often concealed by the pinna below, very rarely basal angle rounded. Substance of lamina rather thick, often concealing the veins. Upper surface showing fine longitudinal grooves about three times as numerous as the veins. Veins arising from whole base of pinna, nearly parallel but uppermost and lowermost veins diverging slightly. Veins rather seldom branched, occurring at a concentration of 2–4 per mm.

Cuticle moderately thick; thickness (measured in folds) of upper about 1·5μ, of lower nearly 1μ. Upper cuticle without stomata or trichomes, showing rows of uniform rectangular cells. Walls distinctly marked, thrown into very strong sinuous folds with rounded loops reaching nearly to the middle of the cell. Distance between adjacent loops about 13μ. Surface of cell flat, without any papilla, veins scarcely or not at all marked. Lower cuticle showing stomata in bands between the veins, stomatal bands about equalling the vein bands. Epidermal cells forming longitudinal rows, cells often square or slightly broader than long, walls distinct, strongly sinuous but folds rather smaller than on upper side. Surface of most cells flat and non-papillate, surface of occasional cells (trichomes) bulging.

Stomata either scattered in their bands or forming two or three rather short longitudinal files in which they may be fairly evenly spaced, stomata seldom occurring close to one another. Nearly all stomata orientated transversely, very occasional ones oblique. Subsidiary cells small, outer margins often scarcely extending at all beyond the guard cell thickenings; surface rather thickened and walls only slightly sinuous. Each subsidiary cell bearing a papilla projecting over surface of guard cells. Papilla usually expanding from its base, apex rounded or flat and usually in contact with opposite papilla. Wall of papilla very thickly cutinised but interior hollow. Small encircling cells opposite subsidiary cells sometimes present in stomatal files.

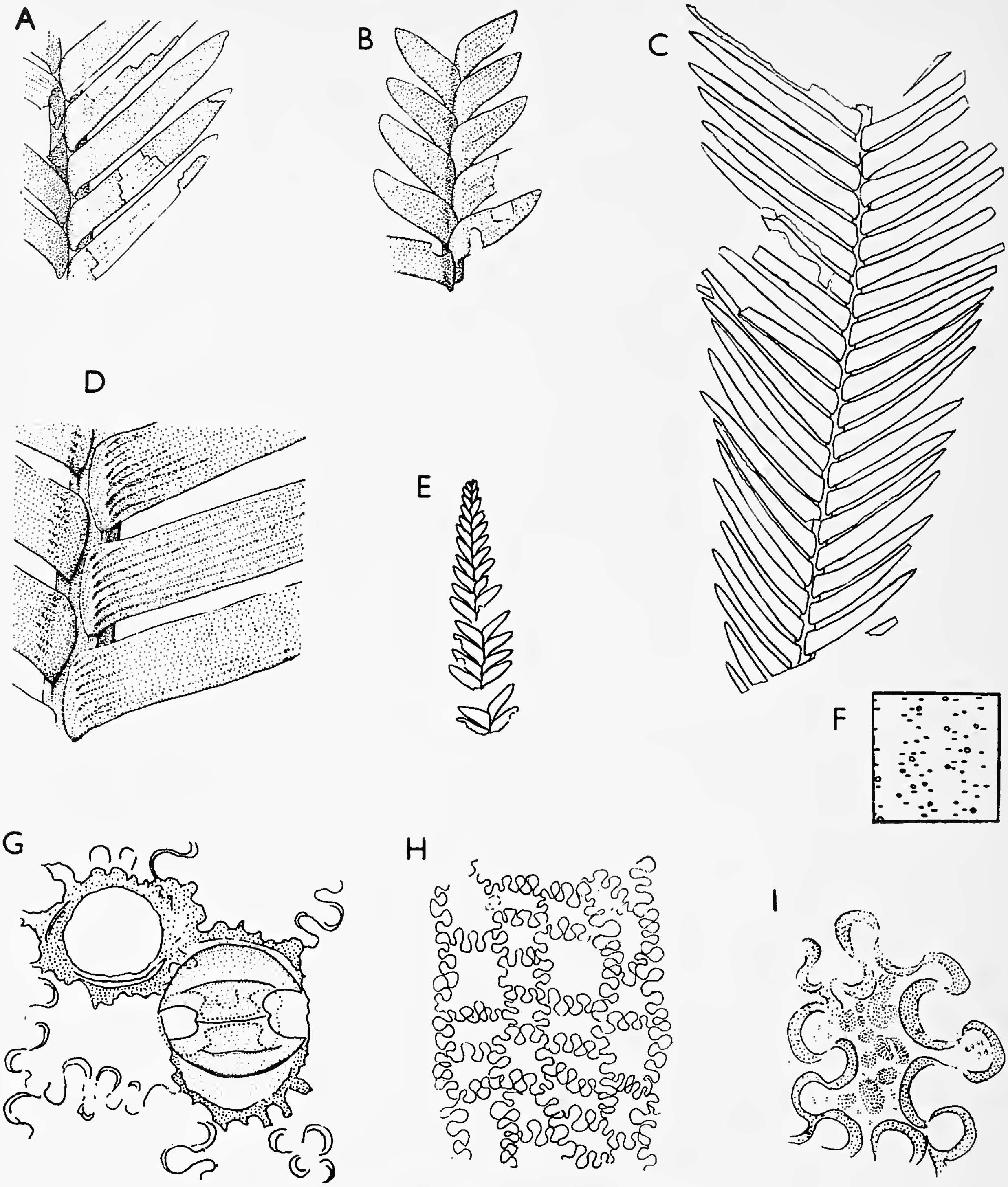

Fig. 26. **Ptilophyllum pectinoides** (Phillips)

A, specimen in Oxford Museum labelled E, ×3. B, part of E, ×3. C, lower part of large leaf, Yorkshire Museum, ×1. D, part of specimen shown in C, ×3. E, upper part of small leaf, Yorkshire Museum, ×1. F, one sq. mm. of lower cuticle of Oxford specimen labelled 'A', showing stomatal apertures (black lines) and bulging cells (rings). G, one stoma and one bulging cell of Oxford specimen 'A', ×500. H, upper cuticle, Oxford specimen 'A', ×200. I, one upper epidermal cell from specimen shown in C, ×800.

All the figures are from Harris (1946).

Guard cells sunken, aperture about 20–25μ, normally hidden by the subsidiary cell papillae. Crescent-shaped thickenings strongly developed, about 40μ long.

Trichomes (or bulging cells) occasional both along and between veins, consisting of an epidermal cell resembling other cells in shape and side walls, but whole surface somewhat thickened and bulging upwards in a hemisphere.

DISCUSSION. *P. pectinoides* is one of the most commonly exhibited Yorkshire Jurassic plants and is abundant at Whitby and many other Lower Deltaic localities. It is fairly uniform but among the very large number of specimens seen a few variants were noted. Apart from the size range given in the diagnosis, the most important is an occasional specimen in which the lower margin of the pinna is scarcely at all decurrent or even slightly contracted. This includes the form (Text-fig. 27) called *P. caytonense* (Harris 1942) which was based on a single specimen from the Gristhorpe Bed (where this species is very rare). A few similar specimens have now been found with many normal ones in certain Lower Deltaic localities. The slight peculiarities of the cuticle of the specimen of '*P. caytonense*' prove to be matched in *P. pectinoides* leaves of normal form, and I now regard it as merely an extreme form of this species. It is of interest in that it goes over the boundary into *Zamites* as defined by Halle. The specific diagnosis has been widened to include such specimens. I am convinced that there are local races in what I call *Ptilophyllum pectinoides* which differ in their lower cuticles. The leaves from many localities show cells with nearly flat surface walls and these are not or scarcely papillate. Nearly all specimens from certain localities, e.g. Marske Quarry, Whitby Haggerlyth, show bulging cells which have produced folds on collapse. Then in some localities the cells are more distinctly papillate, or instead of a small papilla there may be a large and considerably thickened area in the middle of every cell. Such forms show a slight approach to *P. pecten* and *P. hirsutum*. Possibly there may be races differing in gross form, for instance the leaves with constricted pinna bases are perhaps commoner at Gristhorpe than elsewhere. Intensive collecting would be needed to establish such differences beyond doubt, particularly as many localities gave intergrading or mixed populations.

Phillips recognised the difference between *P. pecten* and *P. pectinoides*, Seward (1900) united them together with certain species of *Otozamites* under *Williamsonia pecten*. In this he was followed by Thomas until about 1913 when Thomas began to recognise specific differences in the Yorkshire material as a result of his studies of cuticles. He published very little about this, though he proposed his new species in his (unpublished) Sedgwick prize essay. It was this work no doubt which later caused Seward to recognise that his *P. pecten* was composite, as we find indicated in Seward & Sahni (1920) where some study of the Yorkshire material was made. Curiously enough the name *pecten* was there applied to the larger leaves (correctly *pectinoides*) and the true *pecten* was regarded as an undescribed species resembling *P. hirsutum*.

I could not find the holotype of *P. pectinoides* in the Yorkshire Museum, a specimen has been labelled as the Type but it seems different. I feel sure that Phillips was dealing with the species here called *P. pectinoides* and certainly his own specimens at Oxford (refigured here) are what I call *P. pectinoides* (Phillips).

COMPARISON. As a result of Seward's union of *P. pectinoides* with various other species under *P. pecten*, the literature became considerably muddled. *P. pectinoides* has a general resemblance to most of the medium-sized *Ptilophyllum* leaves of other floras but there is as yet no proof that it occurs outside Yorkshire. Among the most similar are the specimens from the Stonesfield Slate of the English Midlands figured by Seward (1904) as *Williamsonia pecten* and by earlier authors cited by him under various names. They may be identical but as no cuticles are preserved this cannot be proved, and I consider that the best determination would be *Ptilophyllum* sp. cf. *pectinoides*. The age is similar to the Yorkshire Deltaics.

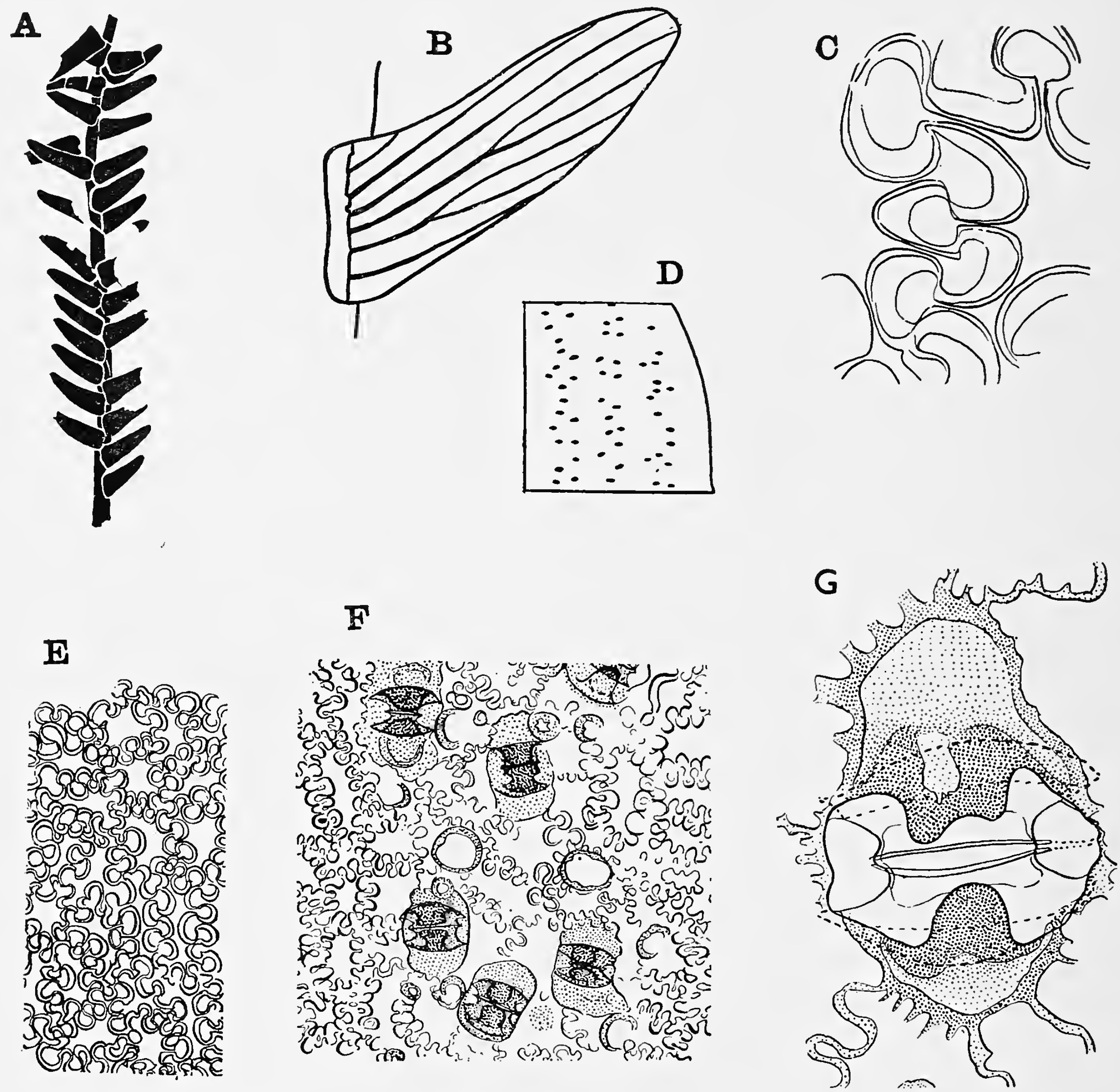

Fig. 27. **Ptilophyllum pectinoides** (Phillips)

A, leaf with contracted pinna-bases, ×1. B, one pinna, showing the veins, ×8. C, part of an upper epidermal cell, ×100. D, distribution and orientation of stomatal apertures, ×20. E, upper cuticle, ×200. F, lower cuticle, veins run along both margins, ×200. G, stoma, ×1000.

All the figures are from Harris (1942) and represent V.26756 which was then described as the holotype of *P. caytonense* Harris.

The following are among the most similar from other regions: Some of the leaves named *Ptilophyllum acutifolium* from India look similar; see for example Seward & Sahni (1920, pl. 6, fig. 54, 54*a*). It is clear, however, that some at least of the Indian specimens have a different cuticle, the stomata being far more crowded than in *P. pectinoides* (see Seward & Sahni 1920, pl. 6, fig. 62). *P. ukrainense* Doludenko (1963) also is of rather similar appearance to forms of *P. pectinoides* with close set pinnae, but its lower cuticle shows lines of hollow papillae, much as in *P. hirsutum*.

Ptilophyllum hislopi (Oldham) from the Jurassic of Argentina as interpreted by Menéndez (1956, pl. 4, text-fig. 2) differs in showing strongly prominent hollow papillae over the lower surface, but the subsidiary cells themselves lack papillae.

Occurrence. *Ptilophyllum pectinoides* is widespread and abundant throughout the Lower Deltaic. It is often the commonest leaf in a bed and it is well represented in museums. Notable localities are Whitby, Roseberry Topping and Hasty Bank. It is still common just above the Eller Beck Bed but then becomes rarer and is very rare in the Gristhorpe Series.

The species is distributed as follows:

Middle Deltaic Gristhorpe Series . .	3 localities
Middle Deltaic Sycarham Series . .	7 localities
Lower Deltaic . . .	about 40 localities

Other organs associated with and attributed to this species are as follows: Male flower, *Weltrichia whitbiensis*; female flower, *Williamsonia hildae*; scale, *Cycadolepis hypene*; stem not distinguished from that of *P. pecten*, *Bucklandia pustulosa*.

Ptilophyllum hirsutum Thomas & Bancroft
Text-figs. 28, 29

1837 *Filicites scolopendroides* Brongn.; Lindley & Hutton, p. 197, pl. 229. (*F. scolopendroides* Brongniart (1836) is different.)

1900 *Williamsonia pecten* (Phillips); Seward, in part, pl. 3, figs. 2, 6; text-fig. 34. (Leaves.)

1913 *Ptilophyllum* (*Williamsonia*) *pecten* (Phillips); Thomas, in part, text-fig. 3 B only. (Part of leaf.)

1913 *Ptilophyllum* sp. 'To be described later as *Ptilophyllum hirsutum*.' Thomas & Bancroft, p. 183, pl. 20, fig. 4. (Cuticle.)

1949 *Ptilophyllum hirsutum* Thomas & Bancroft; Harris, p. 290, text-figs. 6 A, 7, 8. (Form of leaf, cuticle, diagnosis, all repeated here.)

Diagnosis (from Harris 1949). Leaf rather large; length estimated at 20–30 cm., occasionally at least 40 cm., width over the middle leaf typically about 3·6 cm., occasionally 6 cm. Leaf tapering gradually to the base, apex variable.

Pinnae typically 5–7 mm. broad, nearly straight, apex obliquely truncate giving a rather acute point. Upper margin of pinna contracting slightly at the upper basal angle; lower margin either straight or very slightly contracted, not decurrent. Veins rather conspicuous, nearly parallel, but uppermost and lowermost diverging into the margins, traversing the lamina at a concentration of 30–35 per cm., branching occasionally at various levels, becoming finer and less clear towards the apex, most of them ending in the truncate distal margin.

Cuticle thick (2–3μ on both sides), tough. Upper lacking stomata, veins scarcely or not indicated, composed of more or less square cells with sinuously folded walls. About half to a third of the cell diameter unoccupied by folds. Cell surface flat, obscurely mottled; cell outlines usually well marked but sometimes rather obscure. Trichomes very rare. Lower cuticle showing stomata forming bands between the veins, and also a specialised marginal region with no stomata. Stomatal bands broader than vein bands. Stomata mostly orientated

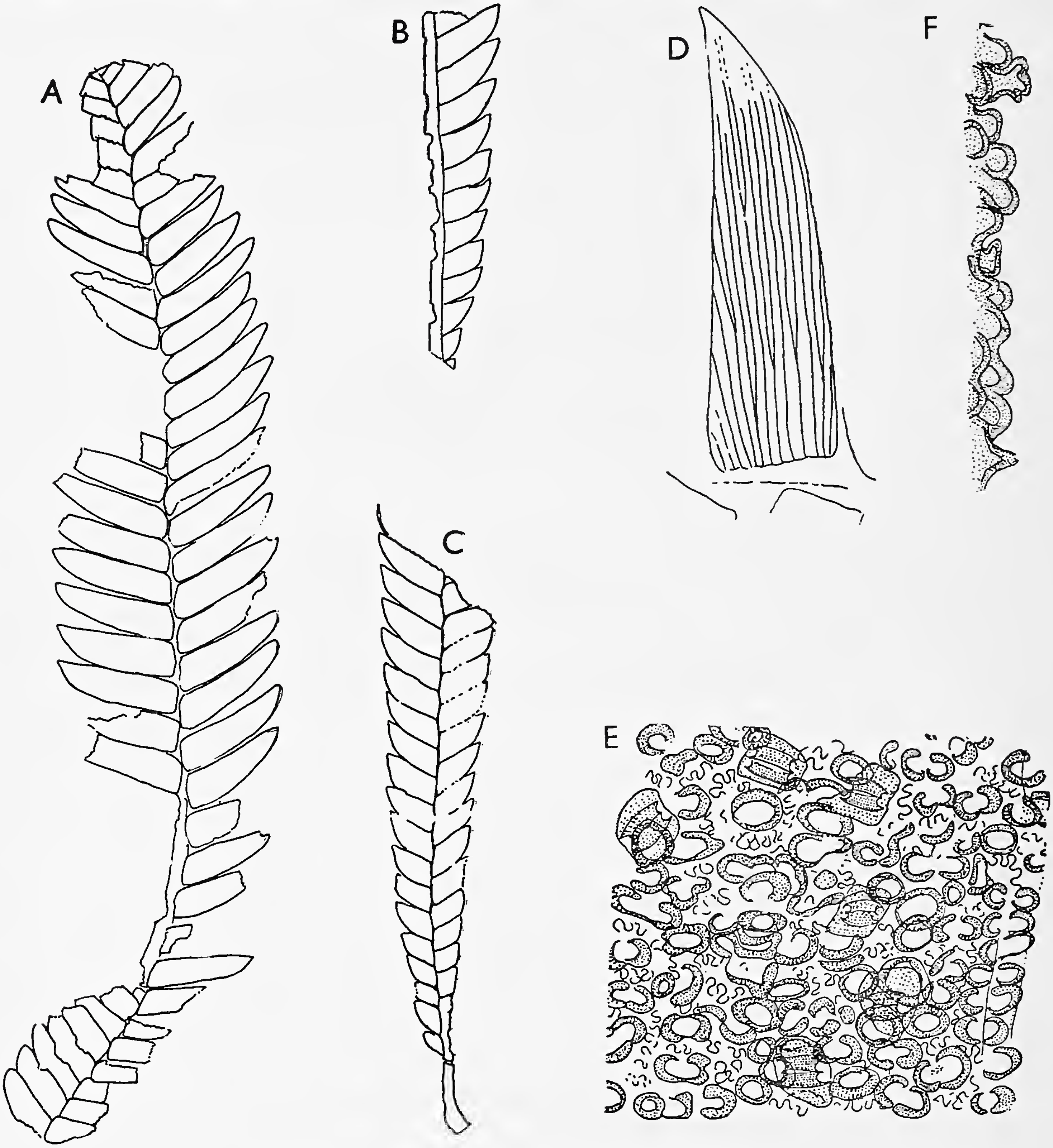

Fig. 28. **Ptilophyllum hirsutum** Thomas & Bancroft

A, specimen probably from Marske, V.27677, ×1. B, leaf base, Roseberry Topping, V.27676, ×1. C, leaf base, Beast Cliff, V.27680, ×1. D, venation of a pinnule from just below the middle of A, ×4. E, lower cuticle, V.27676*a*, ×200. F, fold in lower cuticle showing the papillae in side view, V.27683 (Saltwick).

All the figures are from Harris (1949).

transversely, not forming definite files but evenly scattered in the stomatal bands. Epidermal cells square to irregular, forming longitudinal rows; cell outlines sinuous as on the upper side; sometimes clearly marked but often rather indistinct and also much obscured by the cell papillae. Almost all cells bearing a large thickly cutinised hollow papilla, papilla usually dome shaped, but sometimes conical and sometimes mushroom shaped; very frequently divided into two equal domes. Papillae of cells of a longitudinal row often connected by strong longitudinal folds to form a corrugated ridge. Development of papillae rather variable; when strongly developed cell outlines are almost invisible, but where feebly developed, cell outlines are conspicuous. Cells along veins usually bearing exactly similar papillae, but when papillae are feebly developed, sometimes showing longitudinal striae.

Stomata almost concealed by overhanging cell papillae. Guard cells with well-developed curved crescent-shaped thickenings; partly concealed by broad, almost solid papillae of the subsidiary cells which usually meet over the aperture. Subsidiary cells probably not sunken below the general epidermal level (but overhung by papillae); subsidiary cells small, more

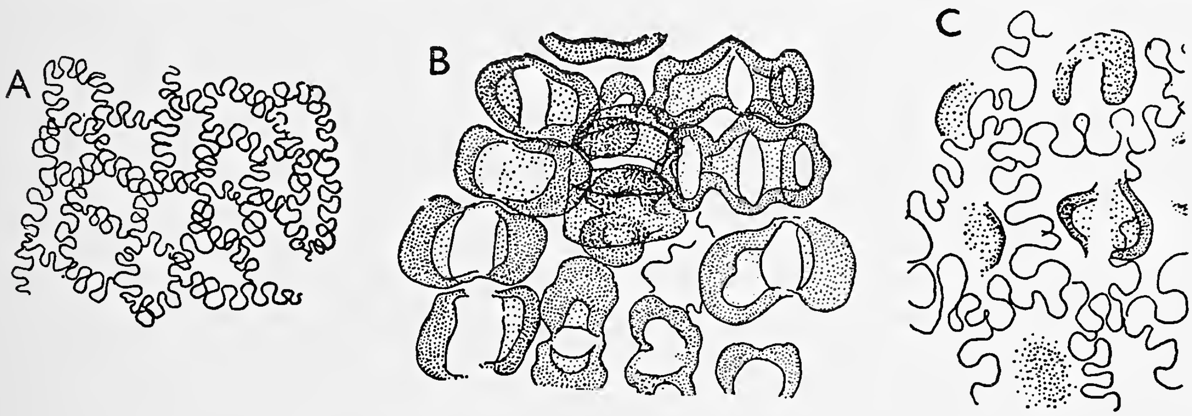

Fig. 29. **Ptilophyllum hirsutum** Thomas & Bancroft

A, upper cuticle, V.27676*a*, ×200. B, lower cuticle showing a stoma, V.27684, ×500 (Saltwick). C, transition from papillate to smooth marginal region showing cell outlines and feebly developed papillae, V.27676*a*, ×500. All the figures are from Harris (1949).

thickly cutinised than the rest of the cuticle. Marginal zone (without stomata) of lower side about 0·1 mm. wide. Cells resembling those of upper side in lacking papillae, but showing a gradual transition to those with normal papillae. Trichomes rare or absent.

Discussion. The leaf figured by Lindley & Hutton (1837, pl. 229) under the name *Filicites scolopendroides* Brongn. though roughly drawn agrees with *P. hirsutum* and nothing else known in Yorkshire. It is from Whitby but apparently not from the main Whitby Plant Bed. Lindley & Hutton supposed that it was the sterile leaf of the same plant as Brongniart's fertile *Filicites scolopendroides* (see Brongniart 1836, p. 388, pl. 137, figs. 2, 3). It is clear, however, that this is a wrong identification.

Ptilophyllum hirsutum must have been abundant at Marske Quarry, and many fine specimens collected by Lane are at Middlesbrough and there are others collected by him and by Hamshaw Thomas in the British Museum (Natural History). This locality is now overgrown. There are also some fine unlocalised slabs found by the old collectors elsewhere, but I have only collected scattered specimens from various points in the Lower Deltaic. One of the best specimens is the slab figured by Seward (1900, text-fig. 34) – a fragment 34 cm. long and originally perhaps 45 cm.

The name *hirsutum* which was given by Thomas & Bancroft (1913) to a figured cuticle preparation (without diagnosis) is inappropriate since it comes from a misinterpretation of the bulging cells of the lower epidermis. These were regarded as hair bases, but they never bear free hairs in any fossil specimen and I have seen no sign that any free part had been formed and dropped off early. They are complete organs with a cutinised top. Their size and form varies somewhat, the most characteristic appearance is given when the cells form very regular longitudinal rows and each papilla has two diverging domes with a thinly cutinised area between. The lower cuticle then shows a striking series of longitudinal dark and light bands. Cuticle fragments can be distinguished from the Middle Deltaic *P. pecten* by these papillae which in *P. pecten* are always rounded while in *P. hirsutum* they are commonly oval or bilobed. Another difference is that the folds of the cell walls of the upper epidermis extend nearly to the middle of the cell in *P. pecten* but leave a considerable area free in *P. hirsutum.*

No other kind of organ is specially associated with *P. hirsutum.* Such association might be expected at Marske but was not looked for when that quarry was being worked.

COMPARISON. The rather similar Yorkshire leaf described as *Zamites phillipsi* by Zigno (1873, p. 46, pl. 32, fig. 1) is more likely to be a *Nilssonia* than to belong to this species.

A few fossils from other countries more or less resemble *P. hirsutum.* The most similar is *P. ukrainense* Doludenko (1963) in which the cells of the lower epidermis also bear longitudinal rows of 2-domed papillae. These papillae are sometimes, however, of more elaborate form, each dome being subdivided and this is at best unusual in *P. hirsutum.* The leaves of the two species look very different, *P. ukrainense* having narrower and more crowded pinnae. In the form of its pinnae *P. hirsutum* looks more like *P. sokalense* Doludenko (1963), a leaf which also approaches *Otozamites parallelus* in form. The lower cuticle of *P. sokalense* is very different each cell having a small solid papilla while the stomata are like those of *Ptilophyllum pectinoides.*

OCCURRENCE. *P. hirsutum* is confined to the Lower Deltaic but occurs at all levels in that series. It occurs sparsely except apparently at Marske Quarry. It is known from 17 localities.

Ptilophyllum pecten (Phillips)

Text-figs. 30, 31

1829 *Cycadites pecten* Phillips, pl. 7, fig. 22. (Rough sketch.)
1834 *Pterophyllum pecten* (Phillips) Lindley & Hutton, pl. 102. (Good leaves.)
1841 *Ptilophyllum pecten* (Phillips) Morris, p. 117. (Name.)
1864 *Palaeozamia pecten* (Phillips) Leckenby, p. 77, pl. 9, fig. 4.
1873 *Pterophyllum pecten* (Phillips); Zigno, p. 15, pl. 29, figs. 1, 2.
1875 *Pterophyllum pecten* (Phillips); Phillips, p. 226, pl. 7, fig. 22. (As 1829.)
1900 *Williamsonia pecten* (Phillips); Seward, p. 191, in part; pl. 3, fig. 1 only.
1920 '*Ptilophyllum* sp. (the Cloughton Wyke form)' Seward & Sahni, p. 23; text-figs. 2 C, 3, 4. (Details of pinna, cuticle.)
1941 *Ptilophyllum gracile* Harris, p. 132, text-figs. 1–3. (Figures repeated here.)

EMENDED DIAGNOSIS. Larger leaves slightly over 20 cm. long and about 12 mm. wide, tapering at both ends. Pinnae in middle region arising at an angle of about 60°, usually in lateral contact. Width of pinna typically one-fifth of its length, about 1·0–1·5 mm. wide at its middle, wider below, length up to about 7 mm., apex obtuse; lower basal margin nearly always decurrent, very rarely running straight to rachis; upper basal angle often very slightly expanded. Substance of lamina very thick, concealing veins but upper surface showing ridges or grooves caused by fibres; lower surface showing a smooth border and papillate stomatal

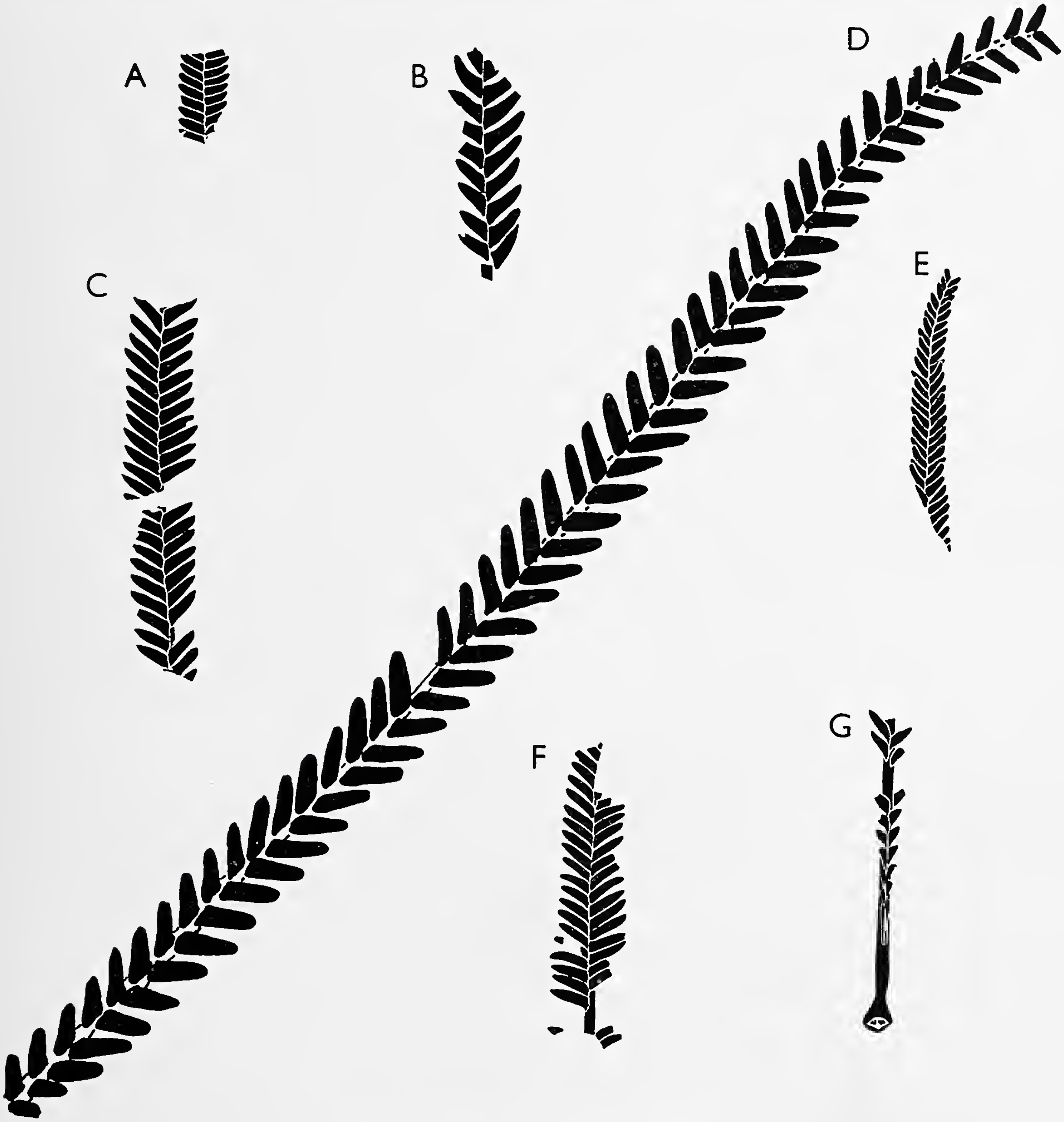

Fig. 30. **Ptilophyllum pecten** (Phillips)

A, fragment with overlapping pinnae, V.26751. B, V.26756. C, V.26755. D, Leckenby Collection Cambridge specimen 191 labelled *Williamsonia pecten* and *Ctenophyllum pecten*. E, upper part of leaf, V.26750*a*. F, V.26757. G, leaf base (see also Text-fig. 31), V.26758*a*.

All the figures are natural size and all except D are from Harris (1941). D is unlocalised but in a matrix resembling the Gristhorpe Bed, the rest were collected by F. M. Wonnacott from the Gristhorpe Bed.

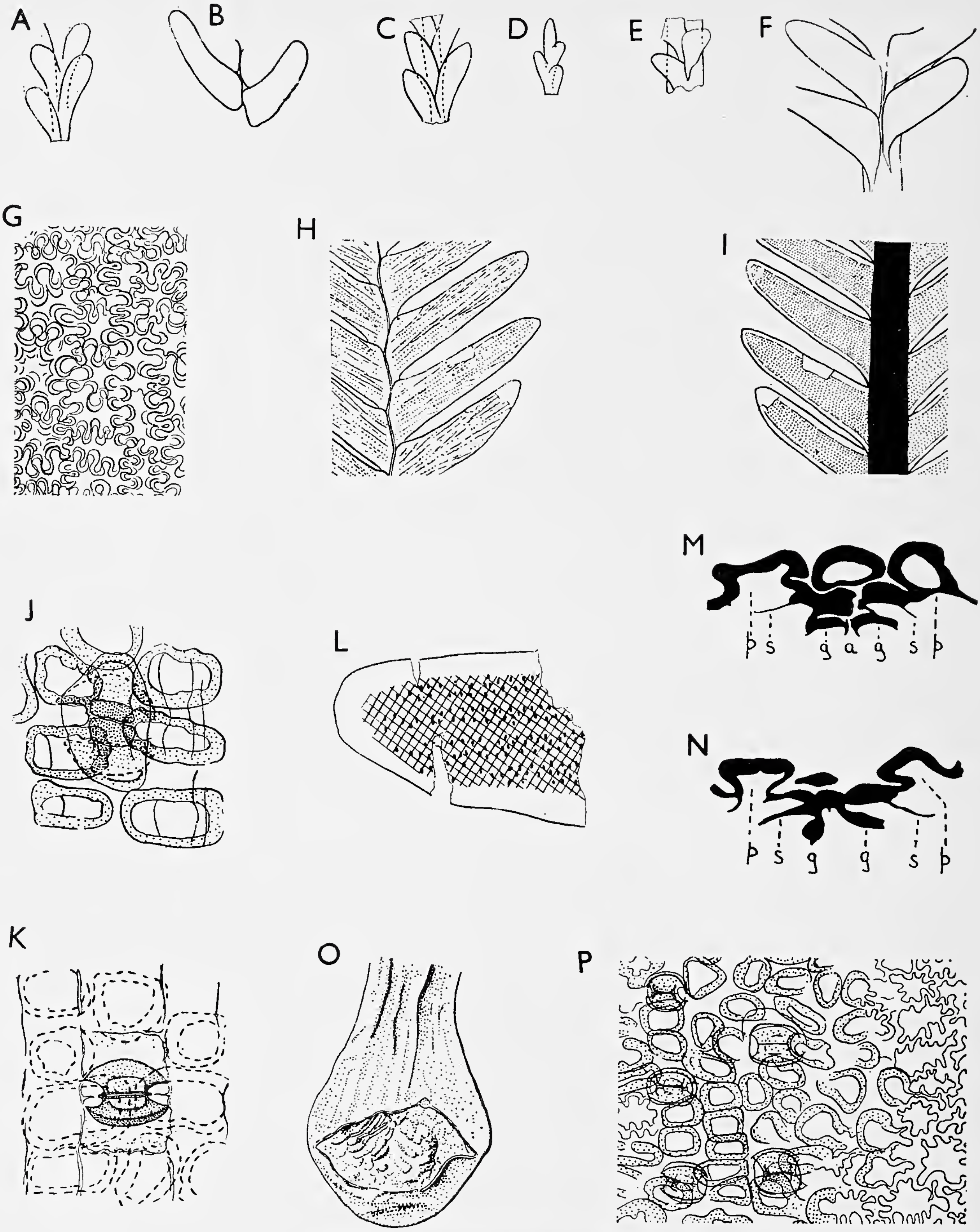

Fig. 31. **Ptilophyllum pecten** (Phillips)

A–F, details of pinnae, all ×4. A, C, D from V.26759; B, V.26750*a*; E, V.26762; F, V.26750; G, upper cuticle of lamina, V.26755*a*, ×200. H, upper surface of leaf showing furrows. I, under surface of same leaf showing papillate zones (transfer), V.26752, ×4. J, stoma (from outside) overlapped by papillae, V.26760, ×400. K, stoma (from inside), V.26755*a*, ×400. L, apex of pinna showing papillate region (cross hatched) and stomatal apertures, V.26753, ×20. M, N, adjacent microtome sections of cuticle; M, almost median; N, beyond the aperture. *p*, papilla; *s*, extension of subsidiary cell cuticle; *g*, extension of guard cell cuticle; *a*, aperture; V.26761, ×400. O, leaf base from specimen in Text-fig. 30G cleaned with HF, ×8. P, lower cuticle of lamina, margin to the right, V.26754*a*, ×200.
All the figures are from Harris (1941).

zone; veins (shown by lower cuticle) about 4 per mm. Rachis up to 1·5 mm. broad, smooth.

Cuticles 4–5μ thick. Upper showing uniform cells with very sinuous walls, curves of walls occupying nearly the whole surface. Lower cuticle divided into a marginal zone resembling upper cuticle and papillate stomatal region. Stomata usually confined to strips between veins, orientated transversely forming 2–3 irregular bands, whole stomatal apparatus sunken. Cells of stomatal region often nearly square and in longitudinal rows, outlines seldom visible but surface bulging to form a thickly cutinised hollow papilla 30μ across and 30μ high; papillae usually mushroom-shaped, the rounded top being broader than the stalk. Guard cells with well developed crescent-shaped plates; subsidiary cells small, bearing prominent blunt papillae meeting over the stomatal aperture. Trichomes absent (apart from papillae of lower surface).

Discussion. This species had an unfortunate history. The early collectors recognised the difference of *pecten* (of the Middle Deltaic) from *pectinoides* (of the Lower Deltaic). But Seward, studying mixed and imperfectly localised Museum material saw no reason to separate them and in fact included certain species of *Otozamites* as well under the name *pecten*. Later, as a result of Thomas' unpublished work on cuticles, distinctions between certain Yorkshire specimens were recognised but for some reason the name *pecten* was applied to the Whitby form (in fact *pectinoides*). Seward & Sahni (1920) were the first to figure the cuticle of true *pecten* and considered it a new species but they gave it no name. Florin (1933*a*) followed Seward in calling the Whitby leaf *P. pecten*, and so did I (Harris 1941), at least by implication, when I gave the new name *P. gracile* to the Middle Deltaic species of Seward & Sahni. Rather later it became possible for me to collect again and I soon realised my error.

Occurrence. The original specimens are from the Gristhorpe Bed where it is locally frequent and fragments are numerous at certain points. It is also abundant and well preserved in the Cloughton Wyke *Solenites* Bed. No good specimens are known from elsewhere, but there are small pieces of cuticle which resemble it from a few other Lower and Middle Deltaic localities. Their determination is not very secure and *P. pecten* must be regarded as of extremely local distribution. Cuticle fragments are known as follows:

Millepore Bed	1 locality
Middle Deltaic Sycarham Series . .	1 locality
Lower Deltaic	2 localities

The male flower *Weltrichia pecten*, the female *Williamsonia leckenbyi* and the scale leaf *Cycadolepis nitens* are attributed to the same plant, and the stem *Bucklandia pustulosa* is shared between this and *P. pectinoides*.

Genus NILSSONIOPTERIS Nathorst 1909*a*, p. 29

Diagnosis. Leaf falling from stem at maturity, petiolate, lamina simple, attached laterally to midrib, leaving part of upper surface of midrib exposed. Veins free, simple or forked, ending at margin.

Cuticle present, stomata syndetocheilic, having two lateral subsidiary cells, guard cells with crescent-shaped dorsal thickenings of cutin.

Type Species. *Taeniopteris vittata* Brongniart 1831.

Discussion. The history of *Nilssoniopteris* is as follows. The type species, *T. vittata*, was the type of Brongniart's genus *Taeniopteris*, and until 1909 when Nathorst studied cuticles of leaves of this appearance there was no reason to disturb the name *T. vittata*. In that year he attempted to study the cuticle of the Yorkshire leaf he had previously named *Nilssonia tenuinervis*. We now know that the cuticle of this is very delicate and hard to prepare and unfortunately he confused a specimen of *Taeniopteris vittata* with *N. tenuinervis*, and from this he did obtain a good cuticle which differed strikingly from the cuticles of all the other *Nilssonia* species he had studied. As its cell walls were sinuous he supposed it was a fern and described it under the new name *Nilssoniopteris tenuinervis*. Thomas later realised the mistake and I understand convinced Nathorst that his *Nilssoniopteris tenuinervis* was based on dissimilar specimens. Thomas & Bancroft (1913, p. 192) pointed out the mistake and advocated that *Nilssoniopteris* be abandoned. Seward (1917, p. 569) endorsed this.

Harris (1932) recognised the need for separate genera for Taeniopterid leaves with different kinds of cuticle, and since *Nilssoniopteris* seemed unsuitable proposed the new name *Taeniozamites* for Taeniopterids with a Bennettitalean cuticle. However the following year Florin (1933) revived *Nilssoniopteris* and reduced *Taeniozamites* to a synonym. Later (1933*a*) he defended this on the ground that *Nilssoniopteris tenuinervis* was based more on the cuticle of *Taeniopteris vittata* than on the form of *Nilssonia tenuinervis*. Since then Florin's usage has been generally adopted and the species *vittata* is taken as the type species both of Brongniart's genus *Taeniopteris* and of Nathorst's *Nilssoniopteris*. The legal position of *Nilssoniopteris* is not perhaps quite clear but its present circumscription is plain. It happens however that no formal diagnosis has been given, so I give one above.

Field Key to the Yorkshire species of *Nilssoniopteris*

1	Leaf length typically 4 × width	*N. major*
	Leaf length typically 10 × width	2
2	Margins appearing entire	*N. vittata*
	Margins sharply denticulate	*N. pristis*

In *N. major* the veins are more conspicuous than in *N. vittata* and often branch twice instead of once or not at all.

Nilssoniopteris vittata (Brongniart)

Text-figs. 32, 34 E

1. Yorkshire specimens:

1828 *Taeniopteris vittata* Brongniart, p. 62. (*Nomen nudum.*)
1829 *Scolopendrium solitarium* Phillips, p. 147, pl. 8, fig. 5. (Rough sketch.)
1831 *Taeniopteris vittata* Brongniart, p. 263, pl. 82, figs. 1–4.
1833 *Taeniopteris vittata* Brongn.; Lindley & Hutton, p. 175, pl. 62.
1835 cf. *Taeniopteris vittata* Brongn.; Lindley & Hutton, p. 71, pl. 176 B.
?1873 *Taeniopteris vittata* Brongn.; Saporta, in part, pl. 64, figs. 4, 5*a*, *b* only. (Poor figures, not typical.)
1875 *Taeniopteris vittata* Brongn.; Phillips, p. 205, pl. 8, fig. 5. (As 1829.)
1900 *Taeniopteris vittata* Brongn.; Seward, p. 157, pl. 16, fig. 1. (Leaf base.)
1909*a* *Nilssoniopteris tenuinervis* (Brongn.) Nathorst, p. 28, in part, pl. 6, figs. 23, 25; pl. 7, fig. 21 only. (Leaf and cuticle.) Pl. 6, fig. 24 and part of description refer to *Nilssonia tenuinervis*.
1910 *Taeniopteris vittata* Brongn.; Seward, p. 492, text-fig. 332. (Nearly complete leaf, base alone figured in 1900.)

1913 *Taeniopteris vittata* Brongn.; Thomas, p. 235. (Leaf and cuticle, no figure, p. 240; discussion of *Nilssoniopteris.*)
1913*a* *Taeniopteris vittata* Brongn.; Thomas, p. 199. (Locality.)
1913 *Taeniopteris vittata* Brongn.; Thomas & Bancroft, pp. 188, 192, pl. 19, figs. 10–12; pl. 20, figs. 5, 6. (Cuticle, discussion of *Nilssoniopteris.*)
1915 *Taeniopteris vittata* Brongn.; Thomas, p. 127, pl. 14, figs. 24, 26–28. (Good leaves, parent stem.)
1932 *Taeniozamites vittata* (Brongn.) Harris, p. 101, text-fig. 39 F. (Stoma.)
1933 *Nilssoniopteris vittata* (Brongn.) Florin, pp. 4, 15. (Name, comparison.)
1933*a* *Taeniopteris vittata* Brongn.; Florin, p. 12, footnote. (Reference to Nathorst's 1909 specimen.)
1933 *Williamsoniella coronata* Thomas (*Taeniopteris vittata* Brongn.); Zimmerman, p. 322, text-figs. 1, 2. (Attached leaves, restoration.)
1939 *Taeniopteris vittata* Brongn.; Darrah, text-fig. 175. (Leaf.)
1946*b* *Nilssoniopteris vittata* (Brongn.); Harris, p. 8, text-fig. 4 A, B, E, F. (Leaf and cuticle, comparison with *N. major.*) Figures repeated here.

2. The following leaves from other regions have been determined as *T. vittata* Brongn., but their cuticles are unknown:

?1823 '*Scitaminearum folium*' Sternberg, p. 42, pl. 37, fig. 2. (Poorly preserved leaf from Stonesfield in English Midlands.)
1835 *Taeniopteris vittata* Brongn.; Lindley & Hutton, pl. 176 B. (Sternberg's specimen refigured; identity held to be doubtful.)
1871 *Taeniopteris scitamineae-folia* ex Sternberg; Phillips, p. 171, diagr. 30, fig. 8. (Sternberg's specimen.)
1904 *Taeniopteris vittata* Brongn.; Seward, p. 91. (Reference to Sternberg's specimen.)
1905 *Taeniopteris vittata* Brongn.; Ward, p. 80, pl. 13, figs. 4–8. (Fragments, Jurassic; Oregon, U.S.A.)
1911 *Taeniopteris vittata* Brongn.; Seward, p. 45, pl. 3, figs. 30, 31. (Fragments, Dzungaria, Central Asia.)
1911 *Taeniopteris vittata* Brongn.; Thomas, p. 71, pl. 4, figs. 2, 3. (Fragments, Izium, Central Asia.)
1917 *Taeniopteris vittata* Brongn.; Arber, p. 47, pl. 4, fig. 4; pl. 6, figs. 2, 3. (New Zealand; questioned by Edwards 1934.)
1931 *Taeniopteris vittata* Brongn.; Gothan & Sze, p. 33, pl. 1, fig. 2. (Fragment, not typical, Sinkiang.)
1935 *Taeniopteris vittata* Brongn.; Toyama & Oishi, p. 67, pl. 4, fig. 4. (No details, Manchuria.)
1949 cf. *Nilssoniopteris vittata* (Brongn.); Carpentier, p. 13, pl. 11, fig. 8; ? pl. 10, fig. 10. (Fragments. Lias; France.)
1949 *Nilssoniopteris vittata* (Brongn.); Sze, p. 23, pl. 4, fig. 3 A. (Good leaves, China.)

DIAGNOSIS. Leaf of varied size. Full-sized leaf about 25 × 2·5 cm. (rarely 3·0 cm.), linear-lanceolate, middle region of even width, upper and lower parts somewhat narrowed. Apex obtuse or truncate, base tapering more or less quickly, lamina usually ending abruptly when reduced to about a quarter of its width. Petiole short, stout, without wrinkles, midrib smooth, appearing broad below, narrow above. Smaller leaves 1·0 cm. wide (rarely 0·5 cm.), shape linear, base tapering, apex tapering, acute. Substance of lamina thick, veins inconspicuous above, moderately conspicuous below, straight, arising at a concentration of 12–24 per cm., simple or once forked. Margin usually slightly recurved and forming a thickened, apparently entire edge in compressions; margin rarely flat and seldom showing the teeth in which the veins end. Upper side glabrous, lower side originally possessing a thin cover of stellate hairs usually shed before preservation.

Cuticles thick (upper about 5μ, lower 2–3μ). Upper cuticle without stomata or trichomes. Cells more or less rectangular, walls strongly marked, rather coarsely sinuous, with folds about 10μ apart, thickened ridges running from folds almost to middle of cell. Surface of cell flat, no papillae present. Cells along veins scarcely distinguished.

Lower cuticle with stomata in bands between veins, stomatal bands equalling or only slightly broader than bands along veins. Stomata typically about 40–50 per sq. mm., stomatal

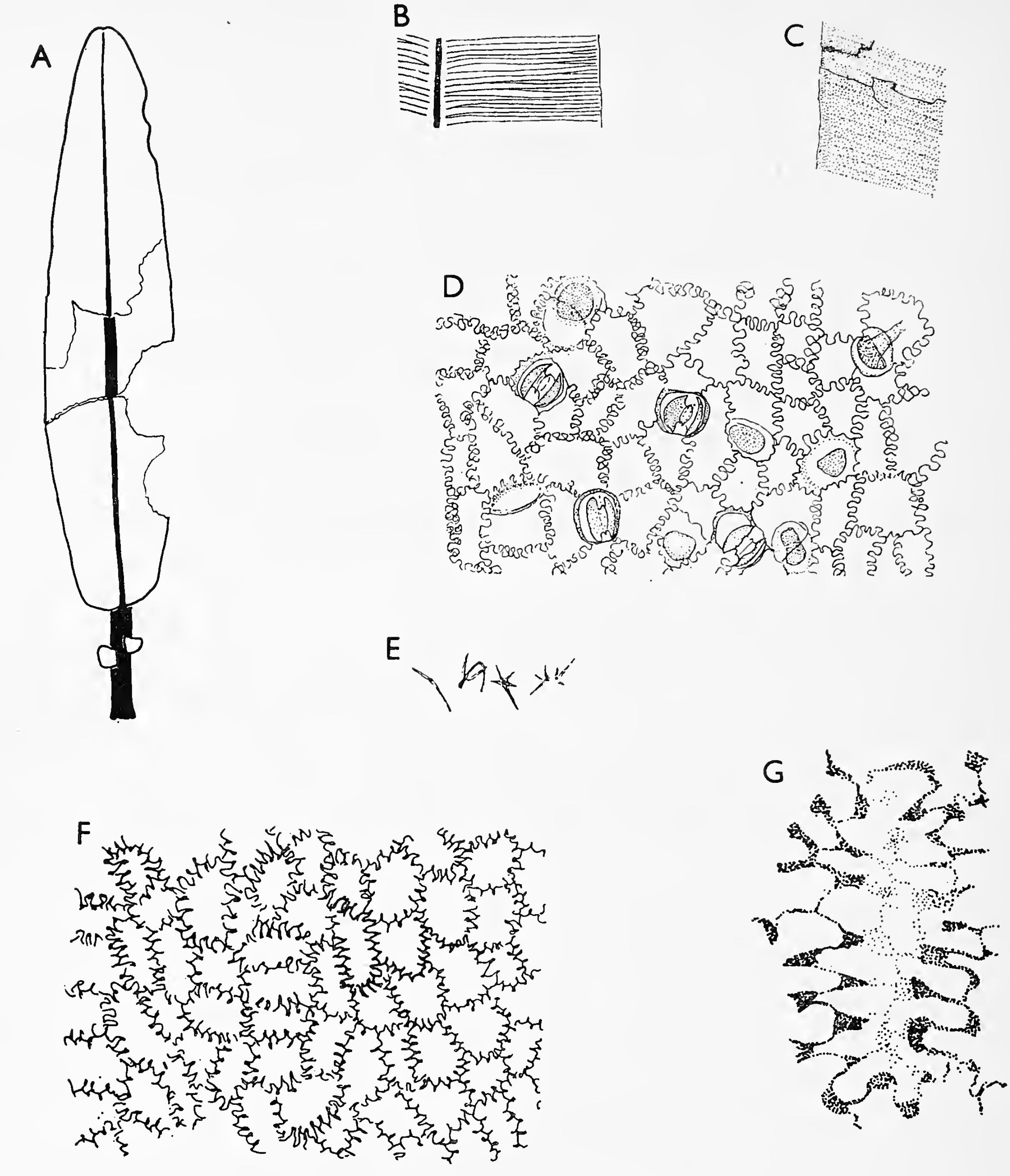

Fig. 32. **Nilssoniopteris vittata** (Brongniart)

A, unusual leaf with two basal segments, V.52860, ×1. B, veins of fairly large leaf, V.26922, ×2. C, edge of lamina, under surface, showing the thickened margin, V.25836, ×4. D, lower cuticle (vein on left), V.26922, ×200. E, hairs seen on rock impression of underside of lamina, V.29923, ×30. F, upper cuticle, V.52859, ×200. G, one cell of upper cuticle under phase contrast illumination, V.52859, ×800.

The specimens in A, C, F, G are from the Gristhorpe Bed, the others are from the Cloughton *Solenites* Bed. B–E are from Harris (1946).

index 7–10. Epidermal cells between veins polygonal, along veins rectangular but scarcely forming rows. Cell outlines strongly marked, very sinuous, but without ridges extending from folds, surface of cell flat, finely granular, not papillate. Stomata scattered, irregularly orientated, but often transverse to veins. Subsidiary cells small or very small, outer wall usually broad, thick, almost entire; inner wall usually bulging over guard cells. Guard cells well cutinised, aperture about 22μ long, usually sunken in a pit which may be rectangular, but is often constricted by ingrowths of subsidiary cells. Trichomes always present, but numbers varied; commonest along veins. Trichome base consisting of one or two cells, rarely more. Basal cell or cells rather smaller than other cells, outer walls thicker and less sinuous. Only part of trichome present in cuticle is a ring about 35μ wide on surface of basal cell or cells; free part of trichome bearing about four tapering branches up to 200μ long.

Discussion. The specific name *vittata* though long accepted is not the oldest. If we exclude Sternberg's (1823) designation as not intended as a binomial, Phillips' (1829) *Scolopendrium solitarium* is the oldest name supported by a figure. However, preference is given to Brongniart's (1828) nomen nudum, *Taeniopteris vittata*, and indeed Phillips himself accepted this.

N. vittata is very common and well represented in old collections, mostly from the Cloughton and Gristhorpe Beds. As the leaf of *Williamsoniella coronata* it belongs to one of the more fully known Yorkshire plants.

N. vittata varies greatly in width and the narrower leaves have simple veins, the wider ones forked veins. Segmented forms (Text-fig. 32 A) are rare. It is easy to confuse this leaf with *Nilssonia tenuinervis*. Forms of *N. vittata* which are both narrow and very long (and such leaves are frequent) often have almost all their veins simple and though the upper side of the midrib *is* exposed, it is hard to distinguish and its area is minute. However, *N. vittata* lacks the resin bodies between the veins, and the cuticle which is much thicker has entirely different structure. Ill preserved specimens of the two may thus be indistinguishable.

Each locality where *N. vittata* is common provided a similar series of leaves ranging from about 1 cm. to nearly 3 cm. broad and probably of equally varied length. This would agree with my suggestion that the series may come from different parts of the same stems (being produced at different seasons) as are the larger and smaller leaves of many herbs and trees, rather than as the result of favourable conditions of growth in one place, unfavourable in another.

Comparison. For comparison with Yorkshire leaves – see *N. major*, *N. pristis* and *Anomozamites nilssoni*.

Nilssoniopteris ajorpokensis from the Rhaetic of Greenland is very similar but differs in its strongly wrinkled rachis and midrib, its more delicate cuticle and less prominent cell outlines. Its stomata are less completely overhung by the subsidiary cell papillae.

N. glandulosa Florin (1933), which Florin has already compared with *N. vittata*, is only known from fragments. In *N. glandulosa* the lower part of the lamina tapers rather gradually. In *N. vittata* it is more commonly abruptly truncate but gradually tapering forms do occur. Florin states that the lamina (in *N. glandulosa*) almost meets over the rachis, but I believe there is no real difference here but rather a difference of preservation. It sometimes seems almost to meet in *N. vittata* and I have mistaken it for *Nilssonia tenuinervis* (as Nathorst did many years earlier). The epidermal cell outlines on both sides are less strongly sinuous and less extended by ribs onto the cell surface in *N. glandulosa* than in nearly all specimens of *N. vittata*. The most definite difference is in the hairs which in *N. glandulosa* have a base which may be composed of 1–6 cells and the free part is strongly cutinised and forming a mushroom-shaped upgrowth. In *N. vittata* it is composed of 1–2 cells and the free part is scarcely cutinised and forms a branched hair. *N. glandulosa* comes from the Lias of Bornholm.

Nilssoniopteris sp. A Lundblad 1950, a Rhaetic fragment, differs in its veins which make a smaller angle with the midrib while *Nilssoniopteris* sp. B Lundblad 1950 has less sinuous cell walls. *Nilssoniopteris taeniata* Samylina 1961 looks very similar but appears to have more 2-celled trichome bases. *Nilssoniopteris* aff. *ovalis* Samylina, Vachrameev & Doludenko (1961, p. 82, pl. 33, figs. 1–4; pl. 34, figs. 1–5) from the Upper Jurassic of Amurland is very similar. *Nilssoniopteris* sp. Vachrameev & Doludenko (1961, p. 83, pl. 35, figs. 1–6) is a similar looking leaf but with straighter cell walls.

Occurrence. Since the cuticle of *N. vittata* is rather like those of *N. major*, *N. pristis* and *A. nilssoni* the list of localities based on cuticles alone must be taken as imperfectly reliable. For this reason also I rejected some of my poorer cuticles.

Nilssoniopteris vittata is widely distributed in Yorkshire and is found throughout the Deltaic Series. It happens that all the hand specimens are from certain Lower and Middle Deltaic localities (Gristhorpe Series). It is rare in the Upper Deltaic (where it is represented by cuticle fragments in two localities).

Nilssoniopteris major (L. & H.)

Text-figs. 33, 34 A–D

1833 *Taeniopteris major* Lindley & Hutton, pl. 93.
1837 *Otopteris ovalis* Lindley & Hutton, pl. 210 A.
1875 *Taeniopteris major* Lindley & Hutton; Phillips, p. 204, lign. 15.
1900 *Taeniopteris major* Lindley & Hutton; Seward, p. 159. (Description.)
1913*a* *Taeniopteris major* Lindley & Hutton; Thomas, p. 236. (Locality and description.)
1913 *Taeniopteris major* Lindley & Hutton; Thomas & Bancroft, p. 189, pl. 19, fig. 9. (Cuticle.)
1933 *Nilssoniopteris major* (Lindley & Hutton); Florin, p. 5. (Name.)
1946 *Nilssoniopteris major* (L. & H.); Harris, p. 13, text-figs. 4 C, D, 5. (Form, cuticle, comparison with *N. vittata*. Figures and description repeated here.)

The following cannot be accepted until confirmed by further study:

1905 *Taeniopteris major* Lindley & Hutton; Fontaine *in* Ward, p. 79, pl. 13, figs. 1–3. (Jurassic; Oregon.)

Emended Diagnosis. Leaf of varied size. Full-sized leaf about 15 cm. long, 3–5 cm. broad, ovate-lanceolate; narrowing slightly from the middle towards the top, apex obtuse, truncate or retuse; narrowing slightly towards the base, and then lamina ending abruptly or slightly cordate. Petiole short, stout, smooth or slightly wrinkled. Smaller leaves often 1·5–3 cm. wide, shape lanceolate to linear lanceolate, lamina tapering almost to the petiole in the lower part and tapering to an acute apex above. Substance of lamina rather thin, veins fairly conspicuous above, very conspicuous beneath, arising at a concentration of 6–12 per cm., simple or once forked or twice forked. Margin usually flat and showing the minute teeth in which veins end. Upper side glabrous, lower side originally possessing a thin covering of stellate hairs which may be lost but are frequently retained.

Cuticles moderately thick (upper about 2μ, lower 1μ). Upper without stomata or trichomes.

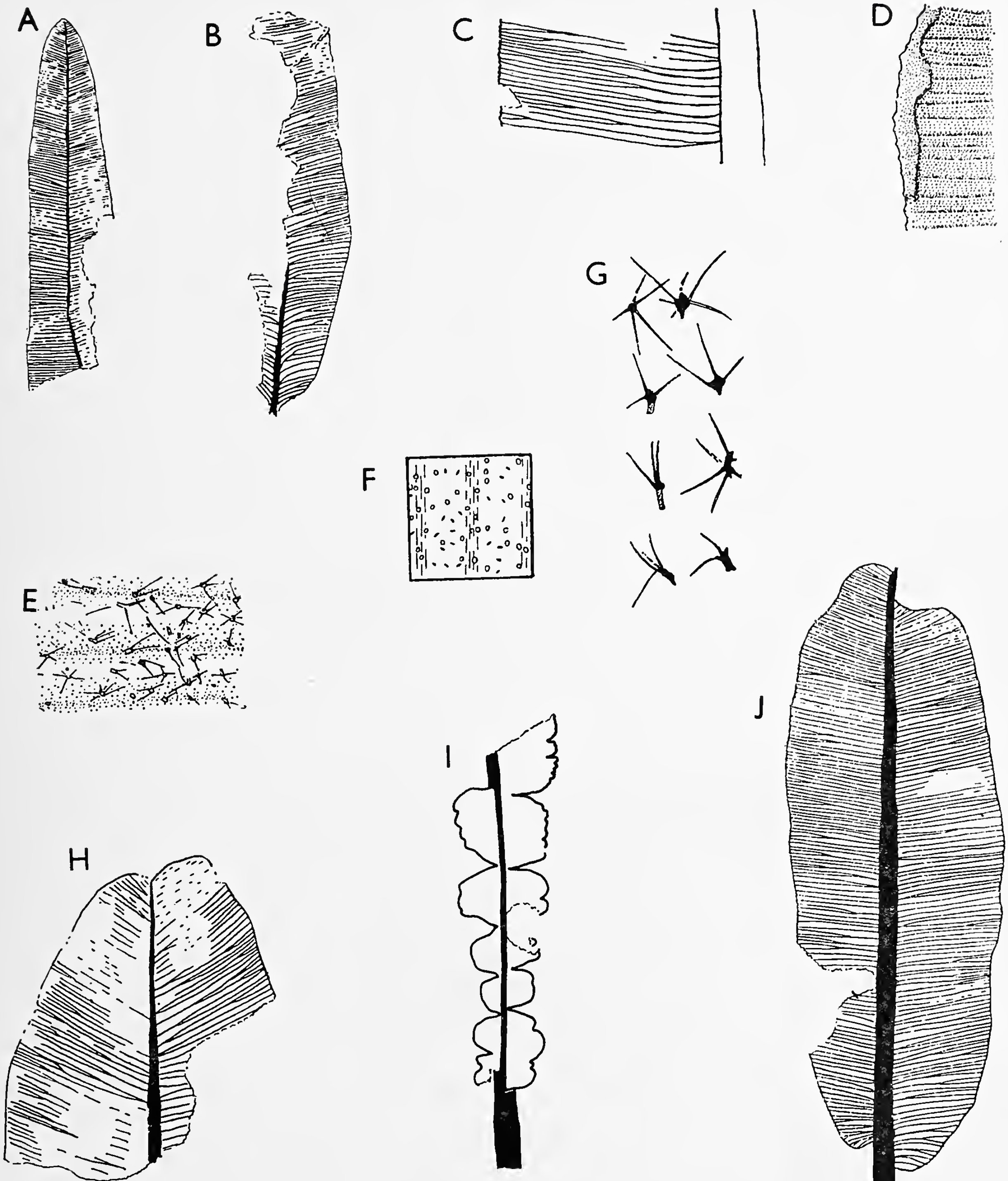

Fig. 33. **Nilssoniopteris major** (L. & H.)

A, apex of small leaf, V.26916, ×1. B, base of small leaf, V.26915, ×1. C, part of leaf showing veins and margin, V.26921, ×2. D, margin of Oxford Museum specimen and impression of underside, ×4. E, hairs on the rock impression of the underside, Oxford specimen, ×15. F, 1 sq. mm. of lower cuticle, circles represent trichome bases and black lines stomatal apertures, Oxford specimen. G, selected hairs of Oxford specimen, ×30. H, apex of large leaf, V.26920, ×1. I, abnormal (perhaps pathological) lobed leaf, V.52847, ×1. J, specimen in Oxford Museum, ×1.

The specimens in C, H are from the Gristhorpe Bed, the others from Whitby. All the figures except I are from Harris (1946).

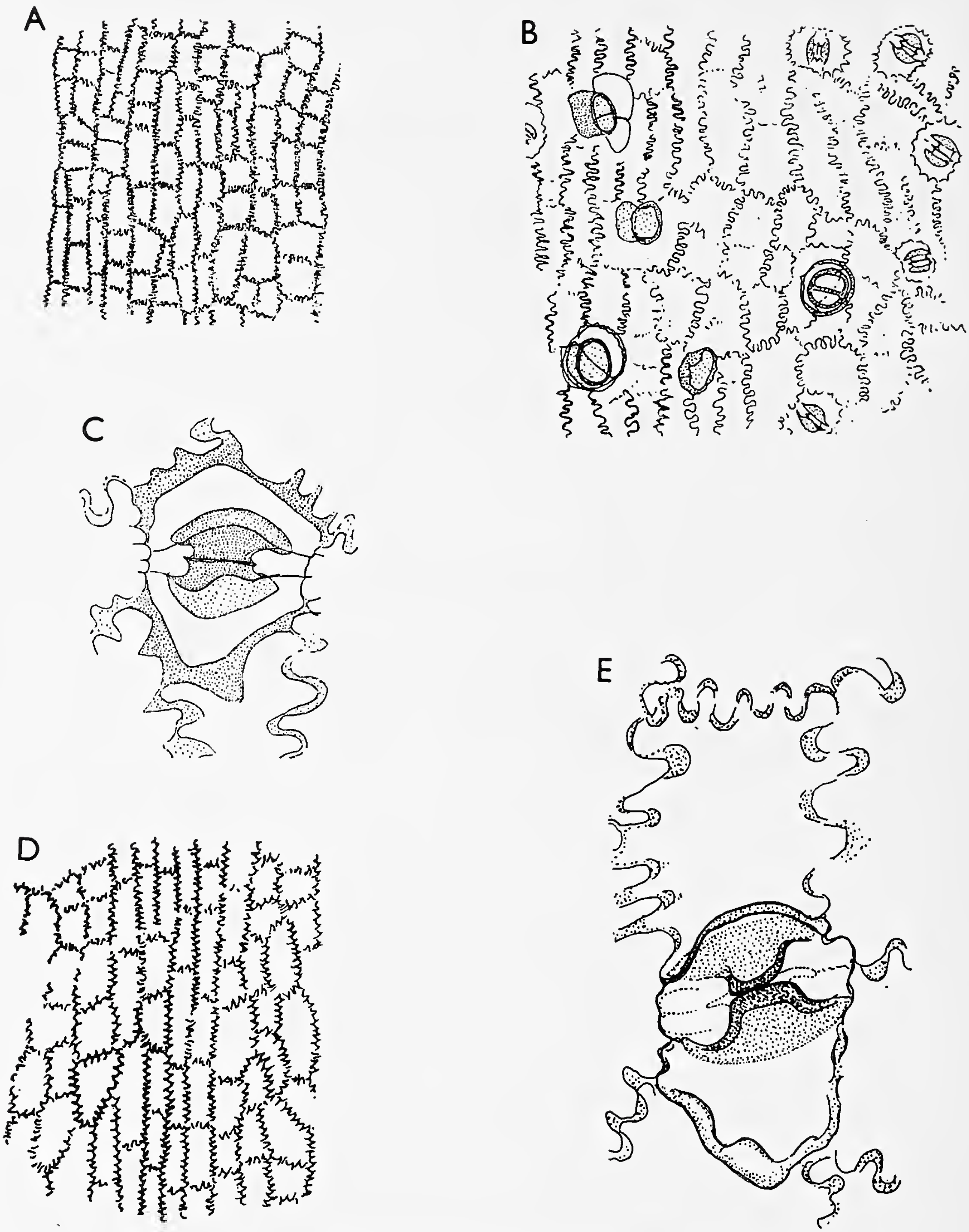

Fig. 34. **Nilssoniopteris major** (L. & H.), **N. vittata** (Brongniart)

A–D, *N. major*; E, *N. vittata*. A, upper cuticle, ×200. B, lower cuticle, ×200. C, stoma, ×800. D, upper cuticle showing a vein in the middle, V.53480, ×200. E, stoma of *N. vittata*, V.53481, ×800. A–C represent the specimen in Text-fig. 33J and are taken from Harris (1946). The original of D is from Whitby and that of E from the Gristhorpe Bed.

Cells more or less rectangular, slightly narrower along the veins. Cell walls rather finely sinuous with folds 6μ apart, short thickened ridges running inwards from the folds. Surface of cell flat, no papilla present.

Lower cuticle with stomata in bands between veins, stomatal bands considerably wider than bands along veins. Stomata rather sparse, typically about 30 per sq. mm., stomatal index about 5·4. Epidermal cells rectangular or polygonal, cell rows seldom obvious. Cell walls moderately distinct, thin, rather finely sinuous, cell surface flat, finely granular, not papillate. Stomata scattered and irregularly orientated. Subsidiary cells rather small, but usually considerably larger than guard cells. Outer wall of subsidiary cells broad and thick, with a few coarse tooth-like projections. Surface of subsidiary cells unthickened, not papillate, inner margin rarely bulging over guard cells to any extent. Stomatal aperture slightly sunken, about 18μ long, guard cells well cutinised. Stomatal pit usually widely open, rarely somewhat constricted by subsidiary cells. Trichomes always present, but numbers varied, commonest along veins. Trichome base consisting of 1–4 cells, usually smaller than other cells with thicker, less sinuous outer walls and a much thicker surface. Middle part of trichome consisting of a ring, 30–40μ wide, on top of basal cells, or occasionally a group of two or more of these rings and a more or less thick cuticle extending upwards from this basal ring, but then broken off. Free part of trichome an irregularly branched hair with 3–5 tapering points up to 300μ long.

COMPARISON. While most leaves of *N. major* and *N. vittata* differ sufficiently in size and shape, a considerable number of leaves of *N. major* are as narrow as typical forms of *N. vittata*, and exceptionally broad ones of *N. vittata* also occur. Thus a number of the old Museum specimens of each are in my opinion wrongly determined, and another consequence of the overlap in size range is that the two species appear generally associated in the field. They do sometimes occur together, but more often they are separate. Additional distinguishing characters are given below.

Comparison of *N. vittata* and *N. major*

N. vittata	*N. major*
1. Leaf linear-lanceolate (small ones linear).	1. Leaf elliptic-lanceolate (small ones linear-lanceolate).
2. Leaf 0·5–3·0 cm. wide.	2. Leaf 1·5–5·0 cm. wide.
3. Veins arise at 12–24 per cm., rarely conspicuous.	3. Veins in large leaves arise at 7–14 per cm., up to 25 in small ones, usually conspicuous.
4. Veins scarcely recognisable in upper cuticle.	4. Veins clearly recognisable in upper cuticle.
5. Margin usually thick and apparently entire.	5. Margin usually thin and denticulate.
6. Stomata larger, mean length of aperture about 22·5μ.	6. Stomata smaller, mean length of aperture about 18μ.
7. Stomata more frequent; index about 8 per cent.	7. Stomata less frequent; index about 5·4 per cent.
8. Subsidiary cells usually forming a pit with overhanging sides.	8. Subsidiary cells rarely overhanging guard cells.
9. Sinuous folds of upper epidermal cell walls coarser, about 10μ apart.	9. Sinuous folds of upper epidermal cell walls finer, about 6μ apart.

Occasional specimens of *N. major* have a partly segmented lamina. Such segmentation is always irregular and in the specimens figured here is so irregular and the lamina is so much curved as to suggest injury in the young bud. This idea is supported by the cuticle which is partly normal but shows marked malformation of the cells near the margin. Both *N. major* and *N. pristis* have a serrate margin, but the teeth of *N. pristis* are much sharper. As in *N. pristis*, the teeth alternate with the veins. *N. vittata* has minute marginal bulges also, but they are very short and are not seen in most specimens because the margin is curved downwards and when compressed, appears as a smooth marginal rib. The lamina must have been almost flat in *N. major*. It is very possible that the flower *Williamsoniella papillosa* Cridland belongs to the same plant as *Nilssoniopteris maior*, see p. 148.

Nilssoniopteris pristis sp. nov.
Text-figs. 35, 36

DIAGNOSIS. Leaf elongated (tapering gradually towards apex and towards base), margins parallel in middle region, width 1·0–3·0 cm. Midrib up to 3 mm. wide, prominent below but only about one-third of its width exposed above, surface often slightly marked with transverse wrinkles and bearing broken bases of trichomes on the back. Substance of lamina not very thick, veins prominent below, flat above but easily seen. Margins of lamina somewhat curved downwards but never reflexed; midrib sunken; margin bearing sharp teeth about 0·5 mm. long, teeth alternating with veins. Margin strengthened by a fibrous strand in which the veins end. Veins traversing lamina at a concentration of 15–25 per cm., almost transverse to midrib, mostly simple but a number forked especially in broader leaves. Lamina glabrous above and becoming glabrous below at time of preservation by loss of trichomes.

Cuticles about 2–3μ thick (measured in folds), upper cuticle showing nearly uniform cells, or those along veins slightly narrower and with thicker longitudinal wall. Trichomes absent. Cells rectangular in rather regular files, walls parallel with veins, coarsely sinuous (waves 25μ apart), end walls finely sinuous (waves 12μ apart). Cell surface flat, finely granular, not showing extensions from waves of lateral walls. Lower cuticle showing broad bands of cells without stomata along veins alternating with stomatal bands, stomatal bands often no broader than vein bands; crushing sometimes marked along sides of vein bands. Stomata scattered in their bands and variably orientated. Cells along veins more or less rectangular, and slightly elongated, all anticlinal walls coarsely sinuous. Cells between veins similar but isodiametric. Cell surface flat, finely mottled. Stomatal apparatus small, subsidiary cell group often nearly circular, anticlinal walls thick, not extending much beyond guard cell thickenings and often less extensive than guard cells. Guard cells sunken, whole region of aperture usually concealed by broad, flattish papillae of subsidiary cell, papillae very thickly cutinised.

Trichomes frequent along veins and some occurring between veins (free parts not observed, lost before preservation), consisting of a normal or small cell with a round scar.

The name is from *Pristis* the sword fish and denotes the resemblance of the lamina to the sword fish blade. (The classical *Pristis* is the name of any sea monster.)

HOLOTYPE. V.52855. Text-figs. 35 A, C, 36 C, D.

DISCUSSION. *N. pristis* is represented by about twenty fragments from the Cloughton *Solenites* Bed and three others. Most of the Cloughton fragments occur on three blocks and this suggests that it may be local, but it is easy to miss (for *N. vittata*) and may be more frequent. The marginal teeth may point downwards when they can only be seen with a microscope after careful preparation, and in certain specimens there are stretches of margin with no teeth at all alternating with regions well provided with teeth.

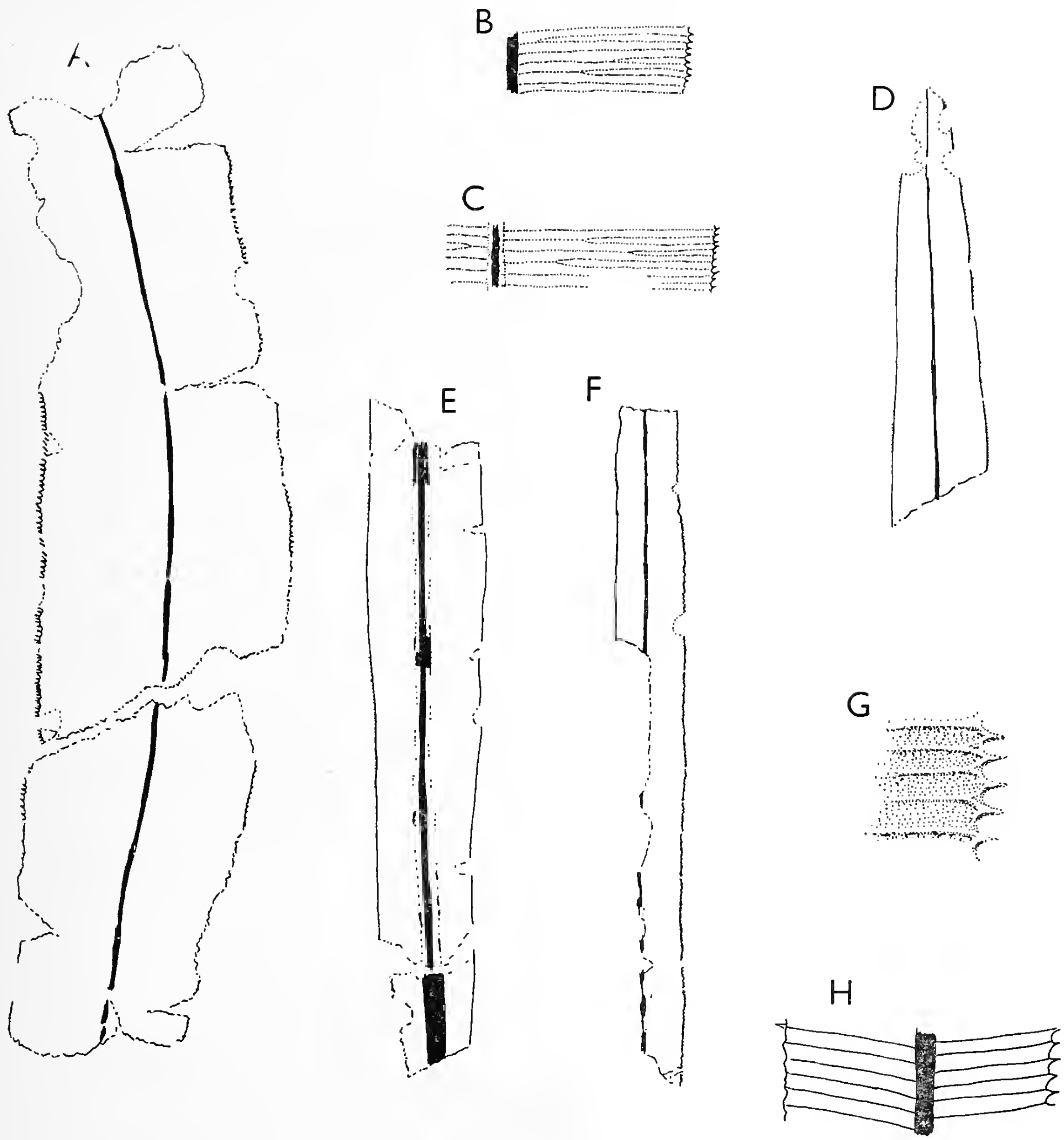

Fig. 35. **Nilssoniopteris pristis** sp. nov.

A, holotype (broadest leaf), V.52855, ×1. B, part of V.52854, ×2. C, part of A, ×4. D, upper part of leaf, V.52853, ×1. E, lower part of leaf, V.52853, ×1. F, narrowest leaf, V.52851, ×1. G, imprint of lower surface showing veins ending in marginal fibre band, V.52854, ×8. H, details of F, ×4.

The position of the teeth, alternating with the veins, is noteworthy. In a naturally cleared specimen the very slender vein (represented by a few narrow tracheids only) continues to 1 mm. from the margin where it is supplemented by more numerous narrow dark cells on either side, these are presumably fibres. The fibre masses then divide and one group swings forwards into the next tooth in front and the other back to the next tooth behind, but I could not see what happened to the tracheids of the vein. These fibres thus form a marginal band with a very sinuous course.

No specimen still bears the free parts of the trichomes on the under surface of the lamina. The lamina was searched both directly and in transfers and so was the rock imprint. On the midrib better developed trichome bases were seen in transfers. These consist of little cones about 40μ wide and 40μ high bearing at the top a broken stump of what may have been a

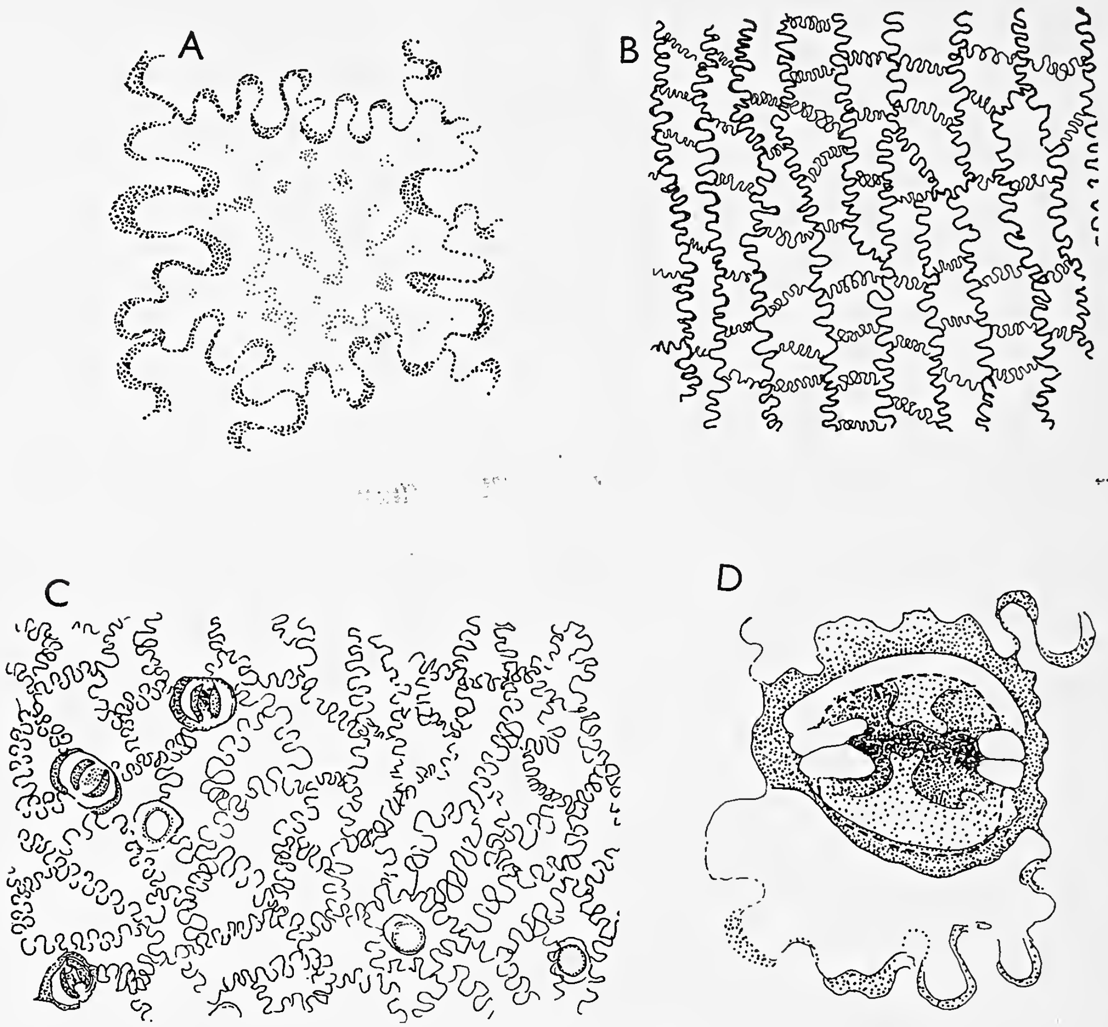

Fig. 36. **Nilssoniopteris pristis** sp. nov.

A, one cell of upper epidermis under phase contrast lighting, V.52856*a*, ×800. B, upper epidermis, a vein is on the left, V.52856*a*, ×200. C, lower epidermis of holotype, V.52855*c*, ×200. D, one stoma of holotype seen from outside. The guard cell thickenings are indicated by a broken line, ×800.

small, simple hair. In *N. vittata* and *N. major*, though most of the free hairs may be lost, a few at least of the branched ends can normally be found.

Comparison. *N. pristis* is distinguished from other species by its sharp marginal teeth, *N. major* merely has blunt vestiges of teeth and *N. vittata* normally shows no obvious trace of them, though there are slight bulges on the downwardly curved margin. The teeth are however often concealed, being curved slightly downwards when the leaf looks just like a specimen of *N. vittata* with unusually conspicuous veins. The cuticles of the two are fairly similar also, but *N. pristis* has smaller subsidiary cells and more protected guard cells. *N. pristis* is probably a longer leaf and much more attenuated towards both ends.

OCCURRENCE. Hand specimens are known from the Cloughton Wyke *Solenites* Bed and the Cloughton *Quinqueloba* Bed and probably the Gristhorpe Bed. Cuticle fragments identified by the leaf margin are known from the Gristhorpe Bed and from Lealholm (Glaisdale) Stonegate Beck at loc. 4 (57° 27′ 45″ N). The first three belong to the Middle Deltaic Gristhorpe Series, the last to the Sycarham Series. Nothing is known of any other part of this plant.

Genus ANOMOZAMITES Schimper 1870, p. 140

EMENDED DIAGNOSIS. Leaf abscissed at base of petiole, shape of leaf as a whole long-lanceolate, lamina divided to midrib into segments, segments broad, typically as broad as long, base of segments not constricted. Veins numerous and parallel, simple or forked, ending at distal margin. Midrib partly exposed on upper side of leaf. Cuticle present, stomata syndetocheilic, having two lateral subsidiary cells, guard cells with crescent-shaped dorsal thickenings of cutin.

DISCUSSION. Schimper's diagnosis deals only with naked-eye features and does not clearly distinguish it from *Nilssonia*. I give a brief emended diagnosis which includes the Bennettitalean features of the cuticle. I earlier (Harris 1932) listed some features of the cuticle in which most species of *Anomozamites* differ from most species of *Pterophyllum*, but I consider it wiser to drop these from the diagnosis. The sole distinction from *Pterophyllum* is in the shape of the lamina segment which in *Pterophyllum* are typically much longer than broad. Thus when a specimen is not satisfactorily placed on this character, the difficulty is obvious.

Anomozamites ranges from the Upper Triassic to the Lower Cretaceous but many of the species placed in it may belong to *Nilssonia*. It seems to decline in importance through its range, being for example more numerous and with more species in the Rhaeto-Liassic (e.g. of Greenland) than in the Bathonian and Bajocian of Yorkshire.

Field Key to the Yorkshire species of *Anomozamites*

Margin of segments minutely denticulate	*A. nilssoni*
Margin of segments entire	*A. thomasi*

Another difference is that in *A. nilssoni* the segments are mostly contracted a little above the base while in *A. thomasi* they are not contracted.

Anomozamites nilssoni (Phillips)
Text-figs. 37, 38

The following are Yorkshire specimens:

1828 'a fern,' Murray, pl. 5, fig. 1.
1829 *Aspleniopteris Nilsoni* Phillips, p. 147, pl. 8, fig. 4. (Phillips 1875, p. 227 redetermined this specimen as a form of *Taeniopteris major* but it seems to me more likely to be *A. nilssoni* as ordinarily understood. The figure is at two-thirds natural size and the lower part is omitted.)

1833 *Pterophyllum Nilsoni* (Phillips) Lindley & Hutton, p. 193, pl. 67, fig. 2.
?1833 *Pterophyllum minus* (Brongniart); Lindley & Hutton, p. 191, pl. 67, fig. 1. (Possibly *Nilssonia compta.*)
1864 *Pterophyllum Nilssoni* (Phillips); Leckenby, p. 76.
1864 *Pterophyllum minus* (Brongn.); Leckenby, p. 78, pl. 9, fig. 2.
1873 *Pterophyllum Nilssoni* (Phillips); Zigno, p. 22, pl. 29, fig. 3.
1873 *Pterophyllum minus* (Brongn.); Zigno, p. 23.
1875 *Pterophyllum Nilssoni* (Phillips); Phillips, p. 227. pl. 8, fig. 4. (Same figure as Phillips 1829.)
1875 *Pterophyllum minus* (Brongn.); Phillips, p. 228.
1900 *Anomozamites Nilssoni* (Phillips) Seward, p. 204, text-fig. 36.
1913 *Anomozamites* (*Wielandiella*) *Nilssoni* (Phillips); Thomas & Bancroft, p. 187, pl. 19, fig. 5; pl. 20, fig. 8.
1942*a* *Wonnacottia crispa* Harris, p. 577, text-figs. 1–3. (Specimen described as a microsporophyll but now considered to be a galled leaf.)
1943 *Anomozamites nilssoni* (Phillips); Harris, p. 506, text-figs. 1, 2. (Leaf, cuticle.)

The following is possibly identical:

1956 *Anomozamites dentatus* Vassilevskaia, p. 30, pl. 2, fig. 1. See p. 82.

The following is probably distinct:

1925 *Anomozamites Nilssoni* (Phillips); Kawasaki, p. 40, pl. 21, fig. 46. (Jurassic; Korea.)

EMENDED DIAGNOSIS. Leaf long lanceolate, typically 15 cm. × 3 cm.; width 4·5 cm.–0·5 cm.; range in length not known. Lamina divided into segments which may be square but may be uneven, some of them narrow, some of them broad and leaf apex often undivided. Lateral margins of segments usually contracted in basal 2 mm., but afterwards parallel or only slightly constricted, gaps about 2 mm. wide present between segments. Free margin of segments minutely denticulate (except sometimes in the smallest leaves), teeth blunt, each marking the end of a vein. Veins arising at right angles to rachis, some simple but most once forked, slightly prominent on lower side. Upper surface of lamina showing bulging cells, lower surface smooth. Margins scarcely thickened.

Midrib only slightly less exposed on upper side of leaf than lower, showing fine longitudinal striations but not transversely wrinkled. Petiole short, its base scarcely expanded.

Upper cuticle 2–3μ thick, lower 1–2μ. Upper nearly uniform but veins faintly shown by 2–3 files of narrower cells, stomata absent but a very few trichome bases present. Epidermal cells square or less regular but tending to form files parallel with veins, longitudinal walls moderately sinuous and with jagged thickenings, extending laterally, end walls less sinuous and less thickened. Cell surface appearing flat, not papillate, finely mottled.

Lower cuticle showing narrow, ill defined strips along veins with fewer stomata, trichome bases generally distributed over veins and between them, stomata occurring up to near margin but margin itself much thickened and with none. Cells square or irregular with more sinuous walls than on upper side, cell surface indistinctly mottled, never papillate. Stomata scattered in broad intervenal areas, not forming files, irregularly orientated but often transverse. Subsidiary cells rather small but extending beyond guard cells, outer wall often nearly semicircular, not sinuous. Surface not thickened, never forming a papilla over guard cells. Guard cell cuticle only moderately thick.

Trichome bases consisting of an ordinary or rather small cell, occasionally a pair of cells, bearing a single ring-shaped scar in the middle. Free part scarcely cutinised often retained at

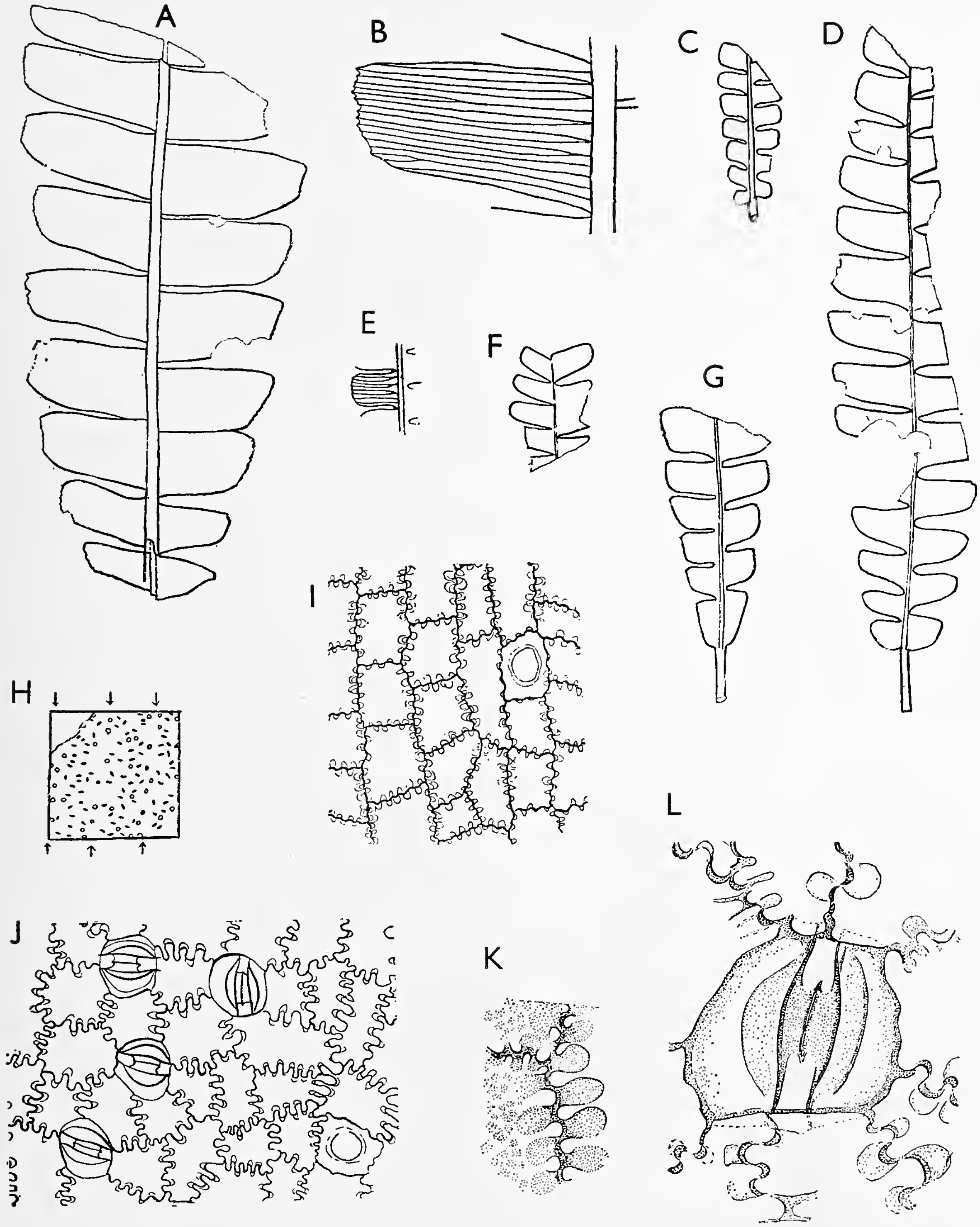

Fig. 37. **Anomozamites nilssoni** (Phillips)

A, large leaf, V.25893, ×1. B, segment of A, ×2. C, small leaf, V.26853, ×1. D, leaf with complete petiole, V.25845, ×1. E, segment of C, ×2. F, apex, V.26854, ×1. G, base and petiole, V.26856, ×1. H, stomata (black ovals) and trichomes (rings) in one sq. mm. of lower cuticle. The arrows mark the nearly vertical veins, V.26855. I, upper cuticle with a trichome base over a vein, V.26855, ×200. J, lower cuticle, V.26855, ×200. K, upper cuticle, V.26855, ×800. L, stoma, V.26855, ×800.

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

preservation, consisting of a short tube bearing about five pointed cells radiating from its apex. Trichomes more numerous and larger on midrib.

Discussion. Galled leaf. The specimen Harris (1942*a*) described as *Wonnacottia crispa* consists of a leaf 12 cm. long in which every segment of the lamina is more or less strongly curled and bears, on the abaxial side, numerous round pouches, formerly regarded as pollen sacs but now regarded as galls. The galls are very unevenly distributed. Where there are no galls the segments have the normal venation and cuticle of *A. nilssoni* (with which the specimen is accordingly identified) but near the galls the epidermis changes (on both sides of the leaf). The cuticle is much thickened and the cells become small, straight-walled polygons and there are very few stomata.

Trichomes become very numerous being borne on nearly every cell. The free part is short and simple and thinly cutinised. Inside the galls there was much resinous matter and a faint indication of straight-walled cells. Most of the galls macerated yielded no pollen but one (unfortunately) was found to give about a hundred grains, and on this fact I concluded that they were sporangia. The grains are monocolpate as usual in the Bennettitales.

Subsequently I found a few specimens which look like ordinary *A. nilssoni* leaves but bear just a few galls and these may be on the upper side as well as on the lower. The best example of this kind is a specimen (No. 40) at Manchester Museum. These made it hard to hold the view that the pouches were sporangia and when a specimen of *Nilssoniopteris major* was found bearing a few bodies looking just like *Wonnacottia* galls, the idea was abandoned. I conclude that the pouches are galls and the one containing pollen had acquired it through an accident. I imagine that the galled leaf was borne just beneath the flower and the pollen (which is all of one kind) entered through a hole in the gall. From the way the epidermis near the galls is changed I conclude that the attack was made early while the cells were still soft and growing. I would compare these galls with the little galls on the leaves of *Corylus*, *Acer* and other trees caused by the attacks of the gall-mite *Eriophyes*, though in these plants the galls all project upwards.

Apart from reinterpretation of *Wonnacottia*, the only material difference between the account given above and the description of Harris (1943) is that the trichomes on the under side were described as simple, but the finding of some better specimens proves that at the end of the basal cell the hair branches as a star.

Some variation was met in the stomata in a single preparation. About one stoma in twenty shows a small encircling cell, and in one this cell had divided transversely. Then a few examples were seen of what may be incipient stomata. Text-fig. 38 G shows a normal stoma, then one with a very small subsidiary cell below (or possibly none) followed by a cell which has divided transversely late in development. This cell, if an incipient and arrested stoma, supports Florin's theory of the ontogeny of the Bennettitalean stoma. Maheshwari has rightly pointed out that a rather similar arrangement (in the grasses for example) results from a different ontogeny and we have not yet demonstrated what really does happen in the Bennettitales.

Comparison. See *A. thomasi*, p. 87. The lamina of *A. nilssoni* is so irregularly divided that both Hamshaw Thomas and I have sometimes confused specimens of it in our field determinations with species of *Nilssonia*, *Nilssoniopteris* and other genera. These mistakes were only corrected when the cuticles of all specimens were examined as a routine.

Anomozamites dentatus Vassilevskaia 1956 from the Ferghana looks very similar and agrees

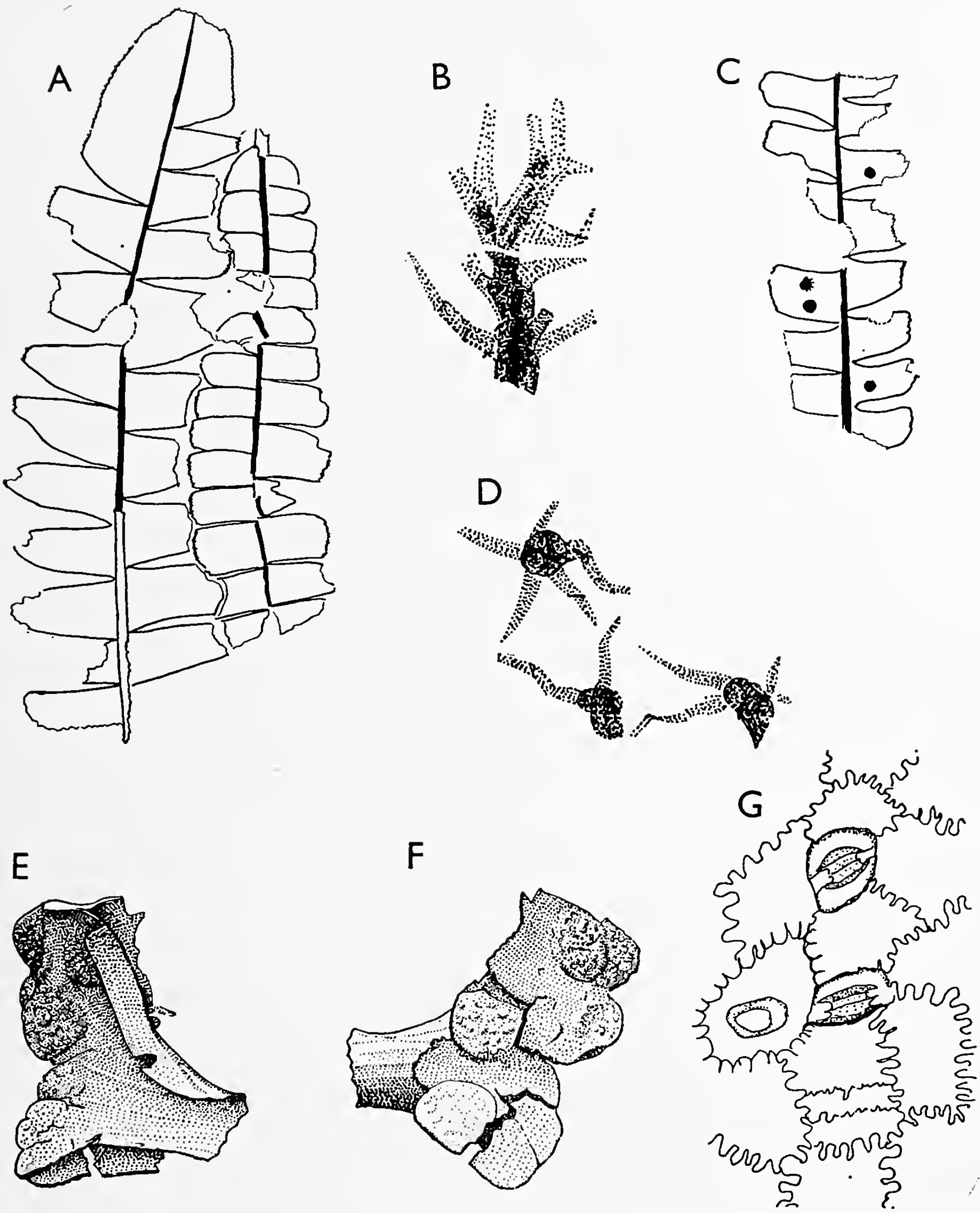

Fig. 38. **Anomozamites nilssoni** (Phillips)

A, two leaves; that on the left has the commonest form of apex, that on the right has unusually crowded and rectangular segments, some apparently nibbled at the margin early in life, V.52816, ×1. B, large branched hair on midrib, V.53278, ×100. C, leaf bearing a few '*Wonnacottia*' galls, V.52814, ×1. D, normal trichomes, V.53278, ×100. E, F, two sides of a galled pinna from V.25851, ×10. G, lower epidermis, the upper stoma is normal, the lower has either an unrecognisably small subsidiary cell below, or none; then there is a cell with late divisions suggesting an incipient stoma, V.53279, ×400.

All the specimens are from the Gristhorpe Bed except G which is from the 'Yons Nab Marine Series' just below the Gristhorpe Bed. E, F, are from Harris (1942*a*) by permission of the Oxford University Press.

in its minute marginal teeth, a feature missed in earlier accounts of *A. nilssoni.*

The only specimen outside Yorkshire determined as *A. nilssoni* is a leaf from Korea figured by Kawasaki (1925, p. 40, pl. 21, fig. 46). This agrees in segmentation but probably differs in the entire distal margin of the pinnae and probably also in the veins, which in the Yorkshire specimens branch at all levels while in the Korean one they branch regularly in the middle of the pinna. The two forms are most probably distinct.

OCCURRENCE. All the previously figured specimens of *A. nilssoni* were from the Gristhorpe Bed where it is frequent at certain points. *A. nilssoni* proves widespread in Yorkshire and is to be found in the spoil heaps of many Moorland coal pits as cuticle fragments and as leaves.

Its localities are distributed as follows:

Middle Deltaic Gristhorpe Series . .	22 localities
Millepore Bed	1 locality
Middle Deltaic Sycarham Series . .	1 locality
Lower Deltaic	9 localities

Many of these localities are based on cuticle fragments from macerations and only the best and most characteristic of these were accepted.

The scale *Cycadolepis stenopus* certainly belongs to the same plant and the flower *Bennetticarpus diodon* may also belong to it.

Anomozamites thomasi sp. nov.
Text-figs. 39, 40

DIAGNOSIS. Leaf linear lanceolate, length of larger leaves estimated at 20–30 cm., width in middle region typically 1·5 cm.; (range noted 1·0 cm. – 2·0 cm.) Lower part of lamina tapering very gradually but apex obtuse. (Petiole not observed.) Rachis showing numerous weak transverse wrinkles on both surfaces, width of upper surface about a third of width below. Segments of lamina almost uniform, typically slightly longer than broad (but shorter near leaf base), often at right angles to rachis or at an angle of about 80°. Lateral margins of segments straight or sometimes contracted very slightly in lower 3 mm. but afterwards expanding slightly and overlapping next segment; distal margin usually straight, occasionally slightly waved or hollowed but never toothed. Margins with a weakly developed thickening rib. Veins rather obscure on both sides, often sunken above, scarcely projecting below, parallel, simple or forked once at varying levels, concentration in middle of segment about 25 per cm. Under side of rachis and of lamina without free trichomes at time of preservation.

Cuticles 1–3μ thick but more at extreme margin. Upper rather uniform but showing veins as strips of narrower cells, stomata and trichomes absent. Epidermal cells often rectangular and forming files parallel with veins, longitudinal and end walls only moderately sinuous, curves of wall capped by a thickened crescent rather than by a ridge, interior of cell flat, occupied by small uneven thickenings making it coarsely mottled. Lower cuticle showing a border about 200μ wide resembling upper side in absence of stomata and absence of a papilla on cells, but cuticle thicker than on upper side.

Main part of lower cuticle divided into narrow strips along veins, lacking stomata and broad strips between veins with stomata, stomatal strips ill defined. Cells tending to be square and to form files, walls moderately sinuous, cell surface flat except for a more or less distinct hollow median papilla, rest of surface with obscure mottled thickenings. Stomata scattered or forming short longitudinal files, variably orientated but mostly transverse to veins. Subsidiary cells usually small but extending beyond guard cells, outer wall often semi-circular, broad and not sinuous. Surface of subsidiary cell without a papilla. Guard cell

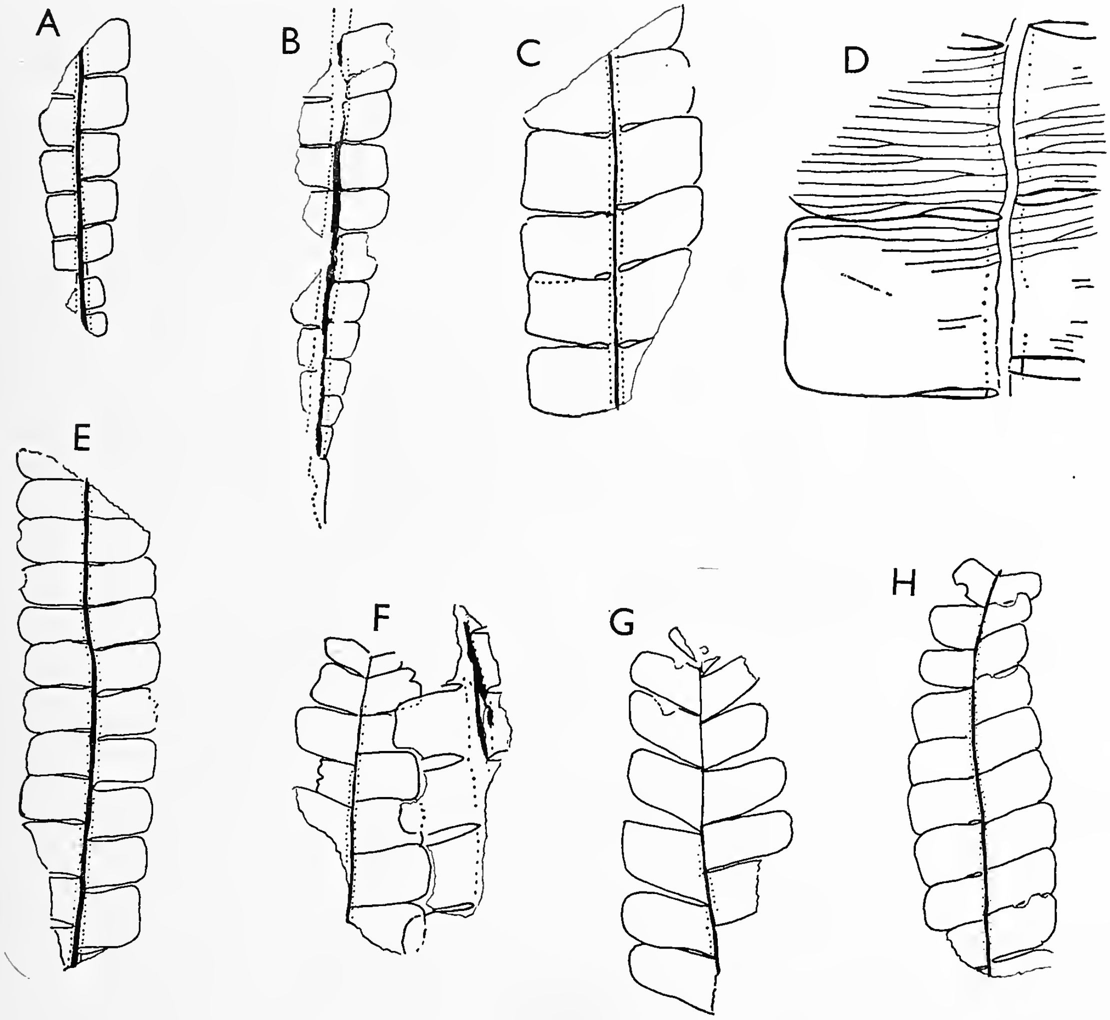

Fig. 39. **Anomozamites thomasi** sp. nov.

A, lower part of leaf, ×1. B, base of lamina, V.52818, ×1. C, V.52822, ×1. D, veins in upper part of C, ×2·5. E, holotype (also shown in Text-fig. 40), V.52824, ×1. F, V.52819, ×1. The fragment on the right has the widest midrib in the collection. G, upper part of leaf, V.52821, ×1. H, upper part of leaf, V.52823, ×1.

In all figures at ×1. The exposed upper side of the midrib is shown in black and the faint furrows caused by the margins of the midrib below the lamina are shown by dots.

thickenings only slight but with a ridge round the aperture, ridge forming a rectangle or more often two sides closed together. Trichome bases consisting of a small cell bearing a ring (very rarely two cells bearing a ring); rather few along veins and very few indeed among stomata. Trichomes present on midrib.

HOLOTYPE. V. 52824. Text-figs. 39 E, 40.

Discussion. *A. thomasi* is based on ten small hand specimens collected by Hamshaw Thomas at Roseberry Topping. They are in a dark, fragile shale and probably come from the lower layers which are no longer well exposed. These specimens bear numerous leaves of *A. thomasi* on one bedding plane and all the best of these are figured. As will be seen the specimens are remarkably uniform, in all the margin is entire. The estimate of leaf length is

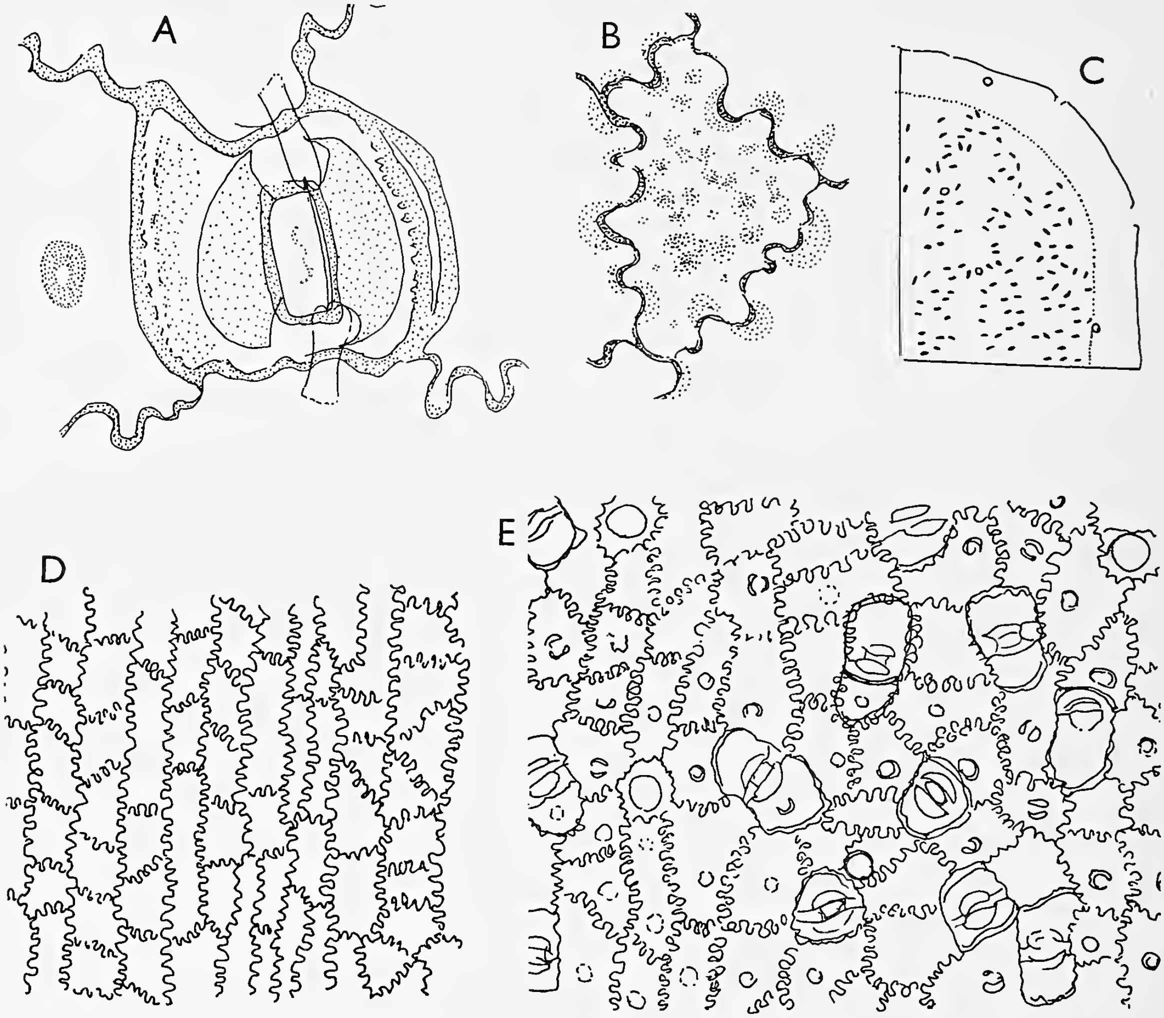

Fig. 40. **Anomozamites thomasi** sp. nov.

A, stoma of holotype, V.52824*a*, ×800. B, cell of upper epidermis of holotype, phase contrast lighting, V.52824*a*, ×800. C, margin of segment showing the zone of thicker cuticle, trichome bases (rings) and stomatal apertures, V.52824*b*, ×20. D, upper cuticle of holotype, V.52824*a*, ×200. There is a vein to the right of the middle. E, lower cuticle of holotype, V.52824*a*, ×200. There is a vein along the right edge and another with two trichomes near the left.

based on the very slight taper of the rachis. The various leaves proved to have a nearly uniform cuticle except that in some it is rather thin. In every specimen the hollow papillae can be seen on the epidermal cells of the lower side (more clearly with phase-contrast lighting), but while in some they are fairly conspicuous, in others they are very faint and would have been missed if not looked for.

A. thomasi is probably the same as the leaf from Marske mentioned by Thomas & Bancroft (1913) as differing from *A. nilssoni* in having 'spherical papillae' on the lower side: (they must have been hemispherical).

Unfortunately I found no Marske specimens of *Anomozamites* in Thomas' collection and Marske Quarry now needs much excavation before good material can be got from it. Though Thomas & Bancroft say that *Anomozamites* is known from Roseberry Topping they do not describe its cuticle.

COMPARISON. *A. thomasi* differs from *A. nilssoni* as follows: The leaf is probably longer and is certainly narrower and the base is more attenuated. It is much more regularly segmented and the segments are nearly always rectangular. The margin is slightly thickened and the distal margin is always entire, never denticulate as in *A. nilssoni*. Hairs are certainly less numerous on the under side and no specimen as preserved still retained the free hairs even on the midrib, but in *A. nilssoni* more than half retain them. The lower cuticle of *A. thomasi* is well distinguished from that of *A. nilssoni* by the hollow papillae of the epidermal cells, though these may be faint.

A. thomasi looks like *A. minor* of the Rhaetic of Sweden and Greenland. It is, however, distinguished by its cuticle which on the under side (in *A. thomasi*) has more numerous (closer) waves in the sinuous walls and papillae on the cell surface. These papillae distinguish it from all kinds of *Anomozamites* known microscopically.

OCCURRENCE. *A. thomasi* is known only from Roseberry Topping but may occur also at Marske. Both localities are in the Lower Deltaic.

Genus DICTYOZAMITES Oldham & Morris 1863, p. 37

Attention must be called to the confusion in *Dictyozamites*, as in *Otozamites* and *Zamites*, in the use of the term 'auricle' in describing the pinnae of this genus, see p. 2.

EMENDED DIAGNOSIS. Leaf simply pinnate, pinnae attached near upper margin of rachis, base of pinna contracted and usually asymmetric. Veins diverging from point of attachment, forking and anastomosing frequently. Cuticle developed, lamina normally hypostomatic, cell walls normally sinuous; stomata syndetocheilic with a subsidiary cell opposite each guard cell.

TYPE SPECIES. *Dictyopteris falcata* Morris (1863, p. 38).

Dictyozamites hawelli Seward
Text-figs. 41, 42

All the following are Yorkshire specimens:

1903 *Dictyozamites hawelli* Seward, p. 221, pl. 15, figs. 1–4. (Form and venation.)
1913 *Dictyozamites hawelli* Seward; Thomas & Bancroft, p. 186, pl. 19, figs. 6–8; pl. 20, fig. 7. (Cuticle.)
1913 *Dictyozamites hawelli* Seward; Thomas, p. 238. (Notes on occurrence and cuticle.)
1917 *Dictyozamites hawelli* Seward; Seward, p. 547, text-figs. 609 A (from Seward 1903), 609 C (from Thomas & Bancroft 1913), not 609 B which is *D. falcatus* (from Seward 1903).

EMENDED DIAGNOSIS. Leaf elongated (length unknown), width in middle region 6–8 cm. but narrowed towards both ends. Rachis up to 4 mm., marked with numerous, fine longitudinal ribs, bearing pinnae on its upper surface. Pinnae usually crowded and overlapping, occasionally just separate; in lower and middle parts of leaf pinnae arising at 75°–90° but angle reduced to 60° near apex. Pinnae in middle region of leaf 3–4 cm. × 8–11 mm.; straight or slightly curved forwards, widest near rachis and tapering almost evenly to an obtuse apex. Pinna attached by a small area on basiscopic side of middle of basal margin or near basal angle; basal margin nearly straight, neither basal angle expanded, distal angle not 'auriculate'. Veins in a full-sized pinna consisting of 5–6 nearly longitudinal strong ones running from attachment to apex and weaker ones curving out to margins and meeting margins at an angle of about 60°. Veins projecting strongly below forming meshes about 8 mm. × 0·4 mm. in middle of pinna, a line across pinna transverse to its long axis cutting 25–35 veins, occasionally 45. Towards margin, vein meshes remaining about 0·4 mm. broad but length reduced to 1 mm. Pinna margin thickened but not recurved.

Cuticles thin, upper about 2μ, lower about 1μ. Upper without stomata or trichomes, cells rather small, those between veins often square, and arranged in longitudinal files, anticlinal walls closely sinuous, the hollow loops conspicuously thinner than the rest. Cell surface becoming thicker towards middle of cell, thickening forming a number of separate patches or one central area but scarcely forming a definite papilla. Veins clearly indicated by narrower and more elongated cells in about three files, margin resembling a vein. Anticlinal wall of vein cell more evenly thickened than in intervenal cells.

Lower epidermis divided into strips along veins without stomata and intervenal areas with stomata; margins of vein strips often showing folds due to crushing. Cells along veins rectangular, forming about six files, surface unthickened apart from fine mottling, anticlinal walls moderately sinuous. Margin of pinna showing cells like those over a vein. Cells between veins isodiametric or irregular, tending to form longitudinal files, surface flat, as a rule without obvious thickenings but sometimes showing an indistinct median papilla. Papilla, if present, raised and hollow. Cells along veins without papillae.

Stomata moderately numerous in intervenal areas, scattered and not forming files, variably orientated but mostly transverse. Whole apparatus about as large as an ordinary cell; subsidiary cells semicircular, anticlinal walls scarcely sinuous, whole surface thickened. Each subsidiary cell usually bearing large flat papilla projecting over guard cell aperture. Guard cell thickenings well developed, aperture sunken and sometimes partly overlapped by epidermal cells adjacent to poles.

Trichomes present in intervenal areas but very few. Two kinds noted, (1) a single cell bearing an elongated sac of cuticle and (2) a cell showing a ring-shaped scar, the trichome being lost.

Discussion. Seward based *D. hawelli* on two fragments from the middle region of leaves and Thomas supplied some details of the cuticle, but nothing else has been published about this species. The Hamshaw Thomas Collection gave fragments of at least twenty leaves, mostly resembling those of Seward and evidently from the middle region, but there are two which seem to be from the top and the bottom of leaves (Text-fig. 41). One isolated pinna is distinctly curved, but the rest are nearly straight. Some of Thomas' specimens yielded good cuticles and it has been possible to give a fuller account of the species.

D. hawelli is recorded from Marske Quarry and from the neighbouring Upleatham Quarry, but both quarries are now so weathered as to require much excavation before collecting again becomes possible. I suspect that the two names may often refer to one quarry.

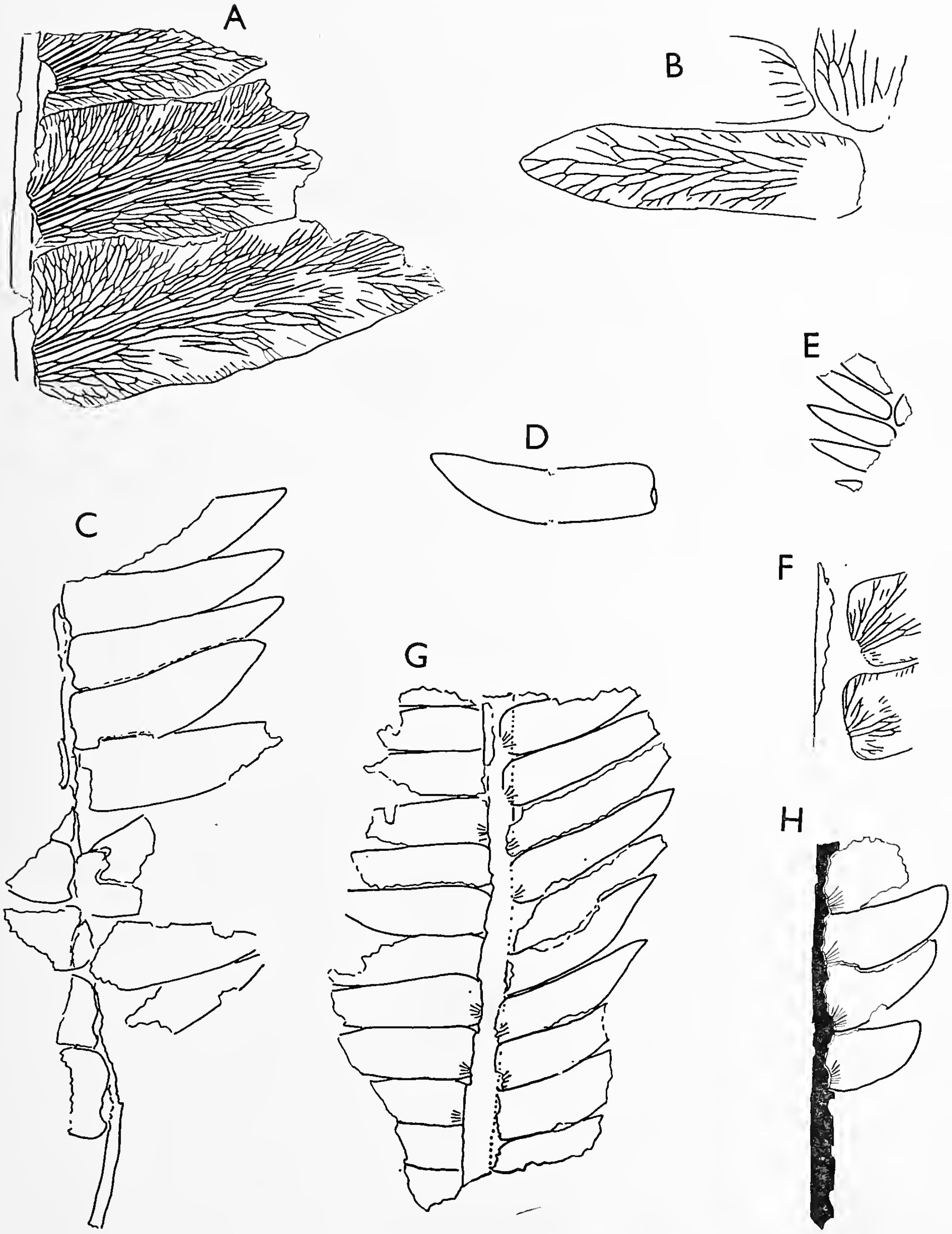

Fig. 41. **Dictyozamites hawelli** Seward

A, details of J. Hawell's specimen, V.53021, ×4. B, details of specimen in fig. E, ×4. C, fragment from middle region of leaf, V.53025, ×1. D, the most curved pinna seen, with attachment scar, V.53026, ×1. E, fragment from leaf apex, V.53023, ×1. F, details from G, ×2. G, fragment from middle region of leaf, V.53029, ×1. H, fragment from base of leaf, V.53027. Specimen in A labelled 'Upleatham Quarry', all the rest from Marske Quarry.

The specimens described here are in two very different rocks, a piece of hard ironstone, one of Hawell's originals and labelled J.H.1902, and the rest collected by Hamshaw Thomas and in a very soft rock varying from a grey clay to a slightly sandy and more shaley clay. In the ironstone the relief of the under surface is clearly shown but the plant substance has vanished, in the clays the substance is flattened and the veins are often hard to see but the cuticles are preserved. So far as I know no one has collected *D. hawelli* since about 1912. There are some good specimens in the Stockholm Museum.

Twenty different fragments yielded fairly uniform cuticles. Some, however, were very

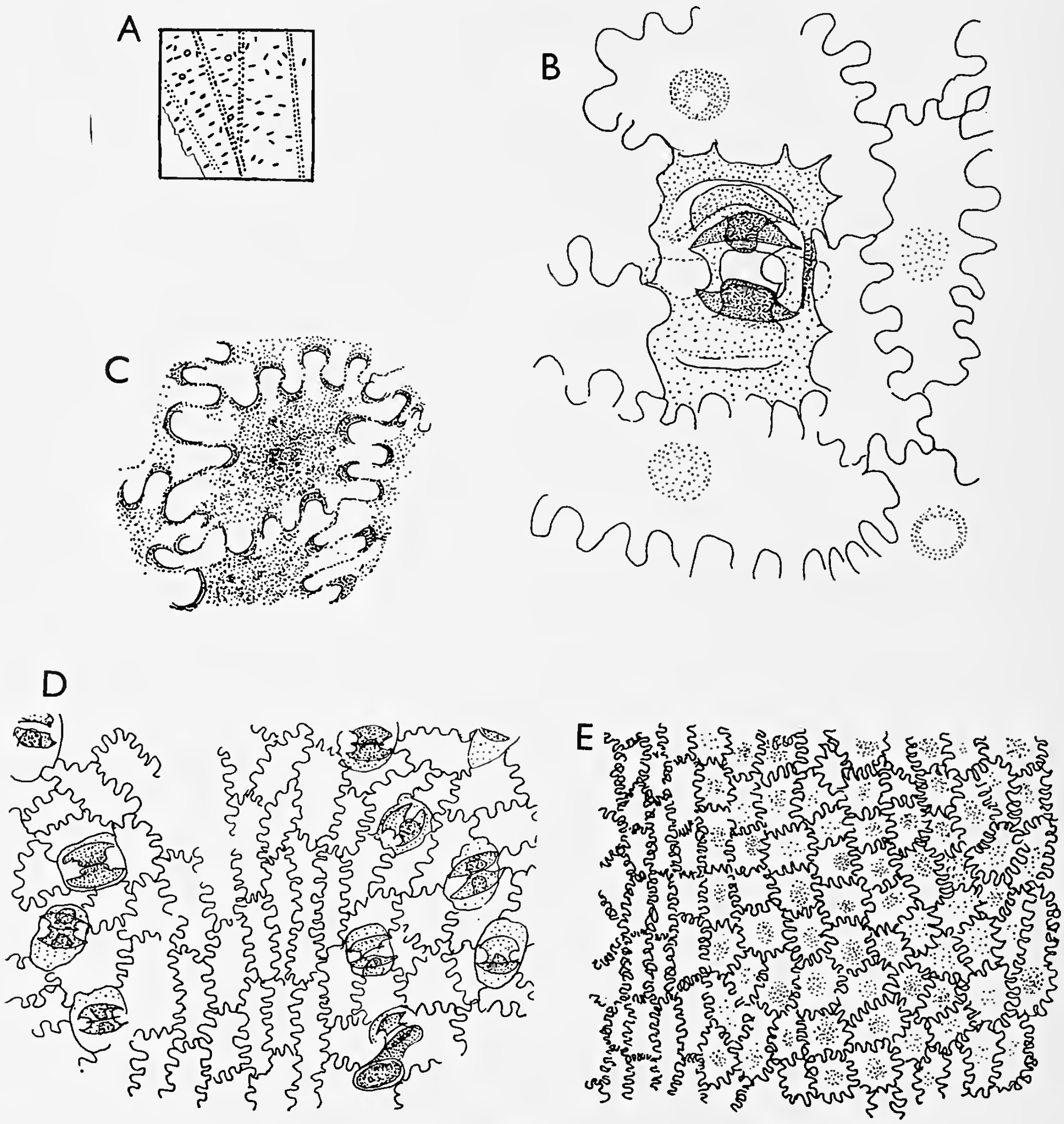

Fig. 42. **Dictyozamites hawelli** Seward

A, orientation of stomata in 1 sq. mm.; trichomes shown as rings, V.53028*a*. B, stoma from a specimen with unusually well developed papillae in epidermal cells, V.53024*a*, ×800. C, one cell from specimen in E, ×800. D, lower cuticle with a vein in middle and a trichome, bottom right, V.53022*a*, ×200. E, upper cuticle, vein to left. The cells are unusually well thickened, V.53022*a*, ×200.

thin and scarcely showed cell outlines on the lower side. Thomas commented on the lack of clear papillae on the cells of the lower epidermis. Three of my preparations, however, did show faint papillae on a good many cells and under phase-contrast lighting, papillae were to be seen in additional preparations or else there were a number of separate thickened areas on the surface of each cell.

The upper cuticle is often very characteristic, particularly in the leaves with thicker cuticles. The whole interior of the cell is thickened (and under phase-contrast lighting this may look like a papilla) and the margins of the cell formed by the sinuous loops forms a striking pale border.

No cuticle matching *D. hawelli* was found in any of my numerous macerations of shales and coals, but this is to be explained by its delicacy and the fact that it is hard to recognise at a low magnification. I was unable to recover the cuticle from macerations in bulk of waste rock from Marske.

No pinna is auriculate in the sense in which I use this word (see p. 2), though Seward giving it a different meaning describes the pinnae as slightly auriculate.

Most specimens show something of the mesophyll after maceration. Usually it is the palisade mesophyll which is seen as closely packed round cells just below the upper epidermis, the veins form pale streaks through this tissue. A few leaves show the lower layer of mesophyll which is a looser tissue of cells elongated transversely to the veins, no doubt like the transfusion mesophyll of Recent Cycads. This second layer also happens to be seen in the ironstone cast. No specimen shows any cells of the vascular tissue and there are no hypodermal cells.

COMPARISON. Rather few of the numerous species of *Dictyozamites* are known as whole leaves, and few also have details of the cuticle; they are distinguished on the size and shape of the pinnae and their venation, it being assumed that these pinnae are typical ones from the middle region of the leaf, an assumption which is reasonable. The veins differ mainly in their closeness and in the point where they converge to join the rachis.

D. hawelli has nearly straight non-auriculate pinnae 2·5–3·5 cm. × 0·7–1·0 cm.; they are attached just above the basal angle and the strong longitudinal veins in the middle of the pinna are up to six and at such a concentration that a line across the pinna crosses 3–4 per mm. These few facts distinguish it from all.

D. hawelli looks like many of the Indian leaves of *D. falcatus* (including some called *D. indica*, see Sahni & Rao 1933). There is a clear distinction, however, in *D. hawelli*; the pinnae are attached near the basal angle but in *D. falcatus* at the middle of the basal margin. Some specimens of *D. falcatus* (e.g. Feistmantel 1879, pl. 4, fig. 2) have weak auricles on both sides of the attachment, but no specimen of *D. hawelli* is auriculate. Another rather similar leaf is *D. asseretoi* Barnard 1960, but that has rather longer pinnae with distinct auricles on the acroscopic basal angle. In *D. asseretoi* the ordinary cells of the lower epidermis have clear papillae but the subsidiary cells have none. Trichome bases are frequent.

OCCURRENCE. The locality or localities (Marske and Upleatham Quarries) belong to the lower part of the Lower Deltaic Series.

Genus PTEROPHYLLUM Brongniart 1828, p. 25

The type species *Pterophyllum longifolium* Brongniart was a new name for *Algacites filicoides* Schlotheim 1822. Leuthardt (1903) gives good figures of this species.

Seward (1917, p. 548) discusses the early use of *Pterophyllum* which is confused. He rejects Brongniart's earliest use of *Pterophyllum* (1825*a*) for leaves subsequently called *Anomozamites*. It was Andrews (1955) who selected *P. longifolium* as type species.

The use of *Pterophyllum* has become more restricted (with the clearer recognition of *Nilssonia*, *Pseudoctenis* and other genera), but despite the very large number of times it has been used I cannot find any definition which approximates to the sense in which it is mainly used today. I therefore give an emended diagnosis below.

Emended Diagnosis. Leaf shed at maturity, leaf as a whole lanceolate, petiolate, lamina attached laterally and some of upper surface of rachis exposed, divided pinnately into segments, segments typically at least twice as long as broad, bases typically expanded (or at most slightly contracted) veins several, parallel, usually forked, not anastomosing, ending in or near distal margin. Cuticle present, stomata syndetocheilic having two laterally placed subsidiary cells, guard cells with crescent-shaped dorsal thickenings of cutin.

Discussion. The above diagnosis is designed to restrict the use to leaves agreeing with Bennettitales and where there is no knowledge of the cuticle its use is accordingly less secure. The distinction between *Pterophyllum* and *Anomozamites* is on the relative width of the pinnae and must be arbitrary and not always satisfactory.

It is distinguished from *Glossozamites*, *Sphenozamites* and *Zamites* by its expanded or scarcely contracted pinna bases, from *Ptilophyllum* and *Otozamites* by the shape of the pinnae which in those genera always have somewhat contracted acroscopic basal angles. From *Nilssonia* it is distinguished by its laterally attached lamina (as well as by cuticle) and from *Pseudoctenis*, in the sense in which that genus is used here, by its syndetocheilic stomata.

The genus thus restricted is first met in the Trias where it becomes abundant and gradually diminishes through the Mesozoic. It formerly included species in the Carboniferous, but Thomas (1930) showed that some at least of these have different cuticles, like *Pseudoctenis*.

All species of *Pterophyllum* (with known cuticle) belong to the Bennettitales but not one has yet been clearly related to a flower. However there is evidence which suggests that different species belong to the same plants as several considerably different kinds of Bennettitalean flowers, see for the example the diverse fructifications associated with *Pterophyllum* described by Harris (1932) and by Kräusel (1949). The genus is thus likely to be somewhat heterogeneous. I do not attempt to subdivide it into what may be more natural units (as Thomas for example did in 1930) because whatever the advantage of such units they are so difficult to apply that they would increase confusion.

Field Key to the Yorkshire species of *Pterophyllum*

1	Lamina as a whole oval (pinnae channelled, rachis hairy)	*P. fossum*
	Lamina as a whole elongated (pinnae flat, rachis smooth)	2
2	Pinnae typically 3–4 mm. wide	*P. thomasi*
	Pinnae typically 1–2 mm. wide	*P. cycadites*

Other species exist but are only represented by small fragments of cuticle.

Pterophyllum thomasi Harris
Text-figs. 43, 44

The following refer to Yorkshire specimens:

1900 *Dioonites nathorsti* Seward, p. 239. (Brief notes only.)
1917 *Pterophyllum nathorsti* (Seward); Seward, p. 556. (Discussion both of Yorkshire and of Scottish Kimmeridgian specimens.) Not *Pterophyllum nathorsti* Schenk 1883.
1930 *Leptopterophyllum nathorsti* (Seward) Thomas, p. 393, pl. 20, fig. 1; pl. 21, figs. 1, 2, text-fig. 5. (Form, cuticle, discussion.)
1952 *Pterophyllum thomasi* Harris, p. 618, text-figs. 3, 4. (New name, form, cuticle.)

The following from the Kimmeridgian of N.E. Scotland cannot be accepted as reliably identified without further evidence:

1911 *Pterophyllum nathorsti* (Seward) Seward, p. 694, pl. 4, figs. 60 A, 61, 61 A; pl. 5, figs. 79, 86, 86 A; pl. 9, fig. 36; pl. 10, fig. 44; text-fig. 13 A, B.

DIAGNOSIS (with slight additions to that in Harris 1952). Leaf usually large, probably elongated (length unknown), width typically 10–15 cm. (extremes noted 2 cm. and 17 cm.), shape oblanceolate, contracting rather suddenly above but tapered below. Rachis up to 8 mm. wide, mainly smooth but middle region with slight transverse wrinkles. Petiole up to at least 5 cm. long, widened below. Pinnae in lower part of leaf arising slightly above lateral margin of rachis, but closer in middle region and upper parts, arising on upper surface a short distance from mid-line, making an angle of 80°–90° to rachis but angle reduced near leaf apex. Pinnae in some leaves crowded and almost in contact laterally, in other leaves separated by 1–2 mm., straight or curving slightly forwards; width typically 3–4 mm.; width nearly uniform over much of their length but upper part tapering to give a rather acute apex; base slightly expanded, especially at lower angle. Margins slightly thickened but not recurved. Veins more or less distinct, parallel, some forked near rachis, but few or none branched at higher levels, ending in margins in apical region without causing protusions.

Substance of lamina fairly delicate.

Cuticles rather thin on both sides (about 1μ measured in folds). Upper cuticle composed of uniform cells, veins not indicated. Cells square or slightly elongated rectangles, mostly arranged in longitudinal rows. Margins sinuously folded. Cell outlines marked by broad, very ill-defined ridges. Cell surface flat, not papillose, surface sculpture of obscure mottling. Trichomes and stomata absent.

Lower cuticle showing stomata in interstices between veins, strips with and without stomata about equally wide. Epidermal cells along veins rectangular, those between veins rectangular or irregular and forming scarcely recognisable rows; walls sinuously folded. Cell outlines marked by fairly narrow and well-defined ridges. Cell surface flat, not papillose, obscurely mottled.

Stomata rather sparse in large leaves, fairly numerous in small ones; scattered in vein interstices, not forming longitudinal files, mostly nearly transverse in orientation but some oblique or longitudinal. Guard cells sunken, aperture exposed at bottom of small rounded or narrow pit formed by subsidiary cells. Thickenings of guard cells strongly developed. Subsidiary cells very small indeed, their outer margins often overlapped by guard cell thickenings; outlines ill-marked, walls not sinuously folded, surface not papillose, unthickened or

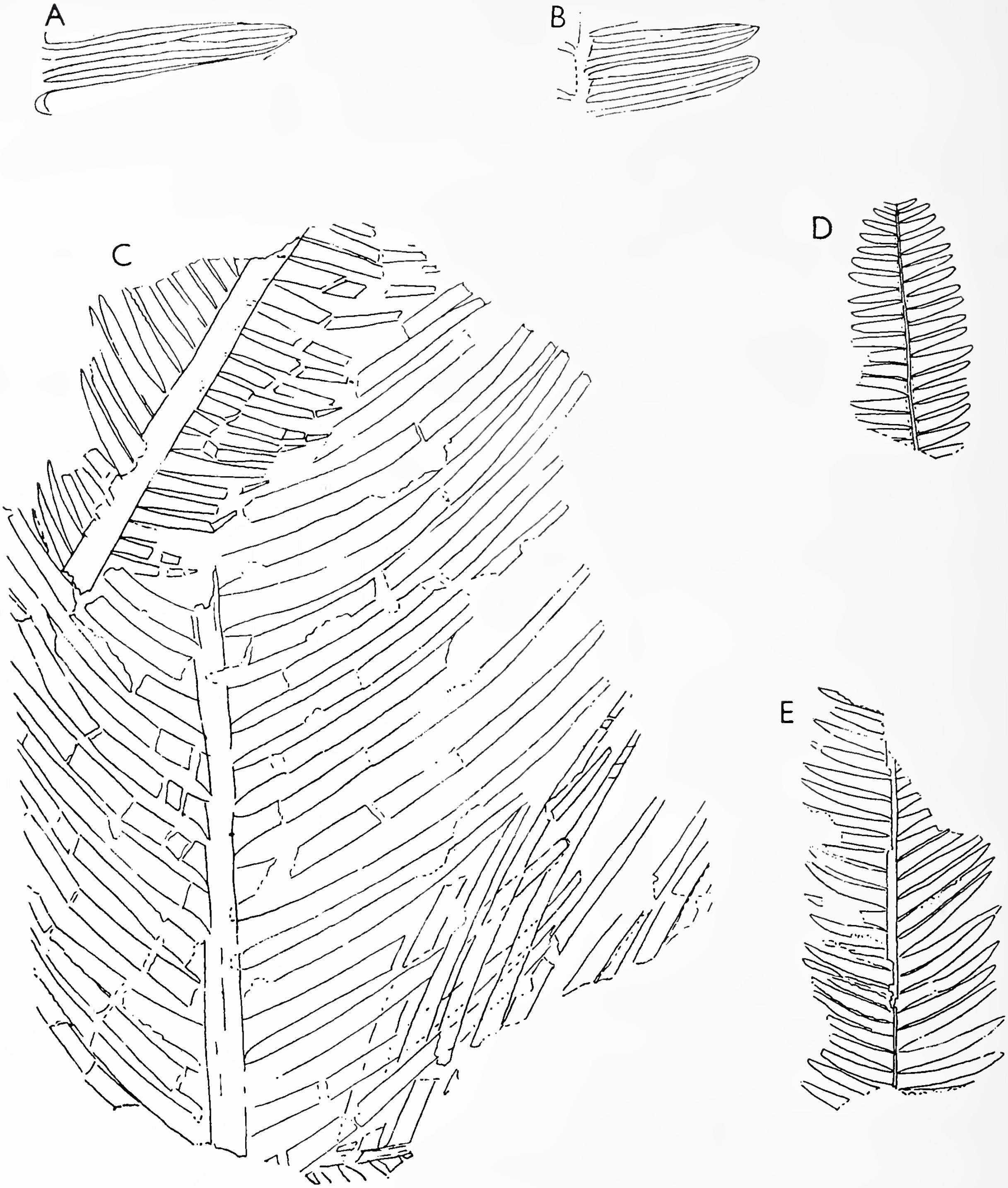

Fig. 43. **Pterophyllum thomasi** Harris

A, pinna of small leaf, V.29404, ×3. B, pinna from leaf in D, ×3. C, block in Yorkshire Museum showing fragments from lower, middle and upper parts of normal leaves, ×1. D, smallest leaf, V.29403, ×1. E, small leaf, V.29402, ×2. A, B, D, E are from Beast Cliff *Ptilophyllum* Bed, C is unlocalised. The figures are from Harris (1952).

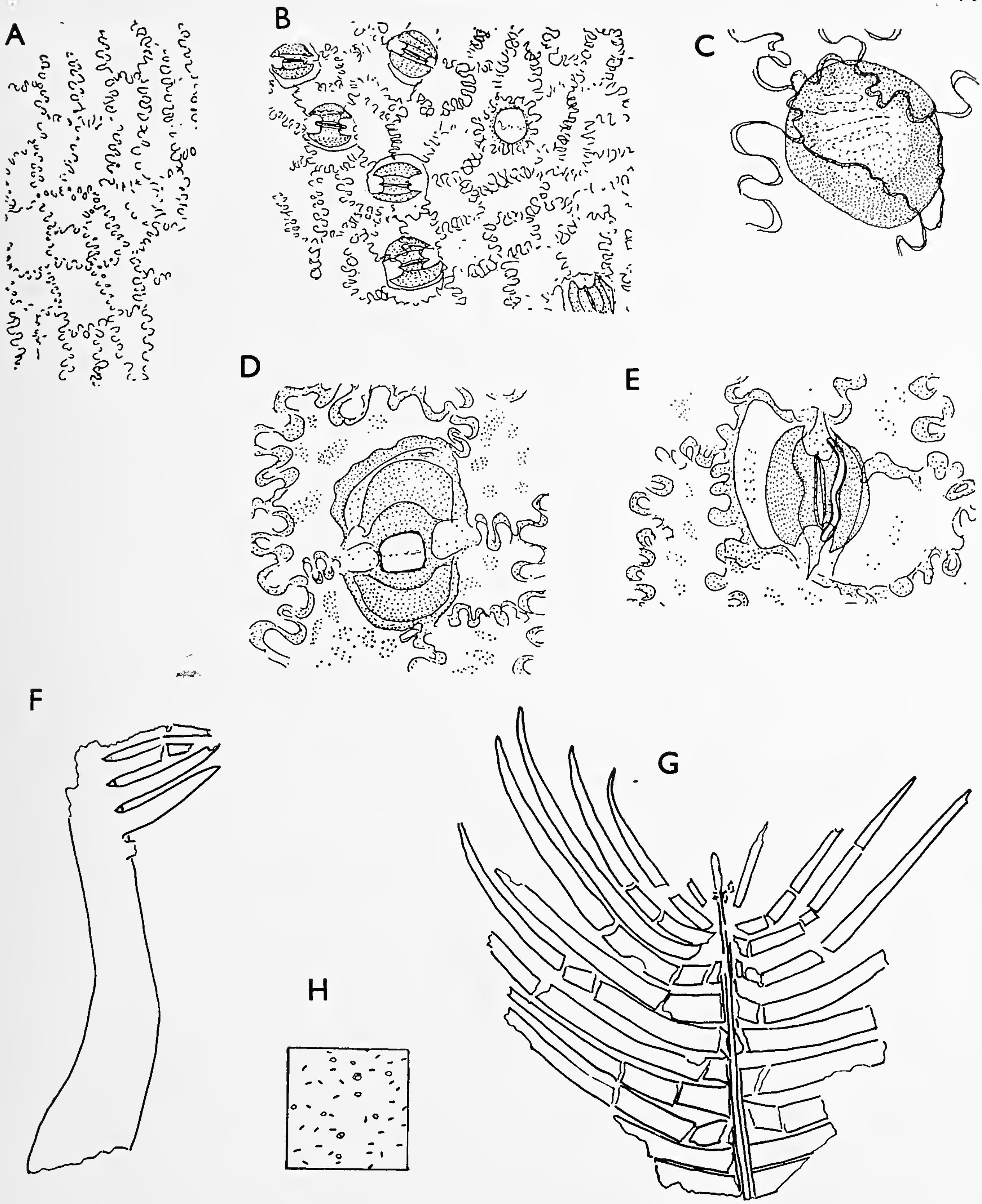

Fig. 44. **Pterophyllum thomasi** Harris

A, upper cuticle of specimen shown in Text-fig. 43D, V.29403*b*, ×200. B, lower cuticle of same specimen, a vein runs up the middle, V.29403*a*, ×200. C, trichome base from Leckenby Collection specimen K447, Sedgwick Museum, Cambridge, ×500. D, normal stoma of same specimen, the lower subsidiary cell is probably concealed, ×500. E, less usual form of stoma, V.29403*a*, Beast Cliff *Ptilophyllum* Bed, ×500. F, leaf base, V.52954, Gnipe Howe, Hawsker, ×1. G, apex of normal leaf (drawn from part and counterpart), V.52951 (Cloughton *Solenites* Bed) ×1. H, one square mm. of the lower cuticle, a vein runs along the left and another near the middle, V.29403*c*, ×20. All the figures except F and G are from Harris (1952).

moderately thickened. Encircling cells often present opposite one or both of the subsidiary cells similar in character to other epidermal cells.

Trichome bases frequent or occasional along veins, less frequent between them; best developed ones consisting of a round cell situated above junction of two or three ordinary or reduced epidermal cells. Outer parts of surface rather strongly thickened, but inner part thinner. Free part of trichome missing.

HOLOTYPE. Leckenby Colln. no. 222, Sedgwick Museum, Cambridge.

DESCRIPTION. *P. thomasi* is an uncommon species in the Yorkshire flora, but it is locally abundant at one point in the Cloughton Wyke *Solenites* Bed. This is 200 m. north of the salt pans and here it is about 3 m. above the high tide mark and difficult to collect in the cliff. It is associated with *Cycadolepis hallei* (*Cloughtonia rugosa*). We do not know whether Halle's material of *C. hallei* (which is also associated with *P. thomasi*) came from this point also. The new material from this locality and others agrees well with what had been figured earlier but includes the apex of a large leaf and also the petiole and base of a very large leaf.

Thomas (1930) gave the first useful description of this species and at the same time based the new genus, *Leptopterophyllum*, on it. Thomas's specimen lacked the upper cuticle – a rather frequent imperfection of Yorkshire Bennettitales but one without specific or generic significance. (Most of the present specimens have well preserved upper cuticles.) He gave various other distinguishing characters from *Pterophyllum* but none of them seems to me of sufficient importance to be used as a generic character, separately or in combination. The new specific name was needed because *Pterophyllum nathorsti* is a different fossil described by Schenk (1883).

P. thomasi very likely belongs to the same plant as *Cycadolepis rugosa*.

COMPARISON. *P. thomasi* differs from *P. fossum* in its much larger leaf, with flat pinnae, fewer stomata and usually more sinuous cell walls. From *P. cycadites* it differs in its wider pinnae, less evenly dispersed stomata and other slight differences of cuticle.

P. thomasi looks like a good many *Pterophyllum* leaves ranging from the Upper Triassic to the Lower Cretaceous, for instance forms of *P. jaegeri*, *P. subaequale*, *P. polonicum* as well as the Scottish Upper Jurassic leaves which, as mentioned above, Seward identified. These leaves are only satisfactorily distinguishable as species when the cuticle is available. *P. thomasi* is distinguished from nearly all the above by its very small subsidiary cells. Its trichome bases and the general characters of both cuticles give further specific characters.

OCCURRENCE. The holotype and certain other early specimens are unlocalised, but the matrix and associates suggest that they are from the Cloughton Wyke *Solenites* Bed like most of those described here.

Lower Deltaic:

Hand specimens are localised as follows:

Hawsker, fallen block below Gnipe Howe.
Beast Cliff *Ctenozamites* Bed.
Beast Cliff *Ptilophyllum* Bed.
Beast Cliff *Otozamites* Bed.
Haiburn Wyke; Phillips Colln. J23945 at Oxford.

Middle Deltaic Gristhorpe Series:

Cloughton Wyke *Solenites* Bed. (Locally abundant.)
Gristhorpe Bed.

Cuticle fragments matching *P. thomasi* are rather sparse. They are known from the following additional localities:

Upper Deltaic	1 locality (Scalby drifted plant bed)
Middle Deltaic Gristhorpe Series	2 localities
Middle Deltaic Sycarham Series	2 localities
Lower Deltaic	5 localities

Pterophyllum fossum Harris

Text-figs. 45, 46

1952 *Pterophyllum fossum* Harris, p. 624, text-figs. 5, 6. (Form and cuticle.)

DIAGNOSIS (considerably emended). Leaf as a whole ovate, width about 10 cm., length including petiole at least 12 cm. Petiole stout, tapering rapidly in the lamina; densely clothed on back with hairs 3 mm. long. Pinnae arising from lateral margins of rachis, separated by 1–3 mm., lower ones arising at an angle of 70°, upper ones at a small angle. Pinnae 1·5–2·0 mm. wide at base, increasing slightly in middle region, contracting slightly in upper third; apex truncate or rounded. Base of pinna not decurrent, unspecialised. Upper surface of pinna flat, lower surface slightly hollowed. Veins 6–8, parallel, rarely branched; only obscurely shown and often invisible on surfaces.

Cuticle fairly tough, 1–2μ thick (measured in folds). Upper showing no stomata and no trichomes or very few, composed of uniform polygonal cells arranged in short longitudinal rows. Veins usually not indicated at all, or occasionally suggested by a slight increase in thickness of cuticle. Anticlinal walls straight, prominent and conspicuous, usually with rather broad margins; very occasionally margins with slight jagged thickenings but never very sinuous. Periclinal walls flat, not papillate, usually decorated by about five thickened patches. Trichomes occasional or frequent.

Lower cuticle divided into marginal regions, 0·5 mm. broad, similar to upper cuticle and a thinner area with stomata. Transition region usually showing crushed folds. Stomatal region typically showing uniformly distributed stomata. Epidermal cells polygonal or rectangular, anticlinal walls clearly marked, straight, but usually with small jagged thickenings which occasionally amount to a finely sinuous wall. Periclinal wall usually bulging and on compression showing folds, not papillate, not sculptured. Stomata very numerous, mostly orientated transversely, evenly scattered and not tending to form longitudinal files. Subsidiary cells usually very small, surface flat, anticlinal walls thick, nearly straight. Stomatal aperture somewhat sunken, guard cell thickenings well developed. Aperture commonly concealed by thickened extensions from subsidiary cells. Trichome bases numerous both on and between veins, consisting of a ring on a small rounded cell or on a pair of cells. Similar trichomes occurring on marginal regions and on upper side.

HOLOTYPE. Leckenby Colln. no. K.223, Sedgwick Museum, Cambridge. Figured Harris (1952, text-fig. 5 A).

DISCUSSION. *P. fossum* was based on two old hand specimens in museum collections, one at Cambridge and one at Leeds. Both are imperfectly localised. Since then cuticle fragments which agree precisely with the original specimens have been found at a few localities.

On the other hand a rather varied series of cuticle fragments from various localities which were originally regarded as forms of this species are now regarded as of uncertain determination; this is because it is now clear that further species of *Pterophyllum* occur in Yorkshire, and we know too little about their range of variation for the determination of most of the cuticle fragments to be reliable. With the rejection of some of the cuticle fragments the diagnosis has been emended by cutting out much of the permitted variability.

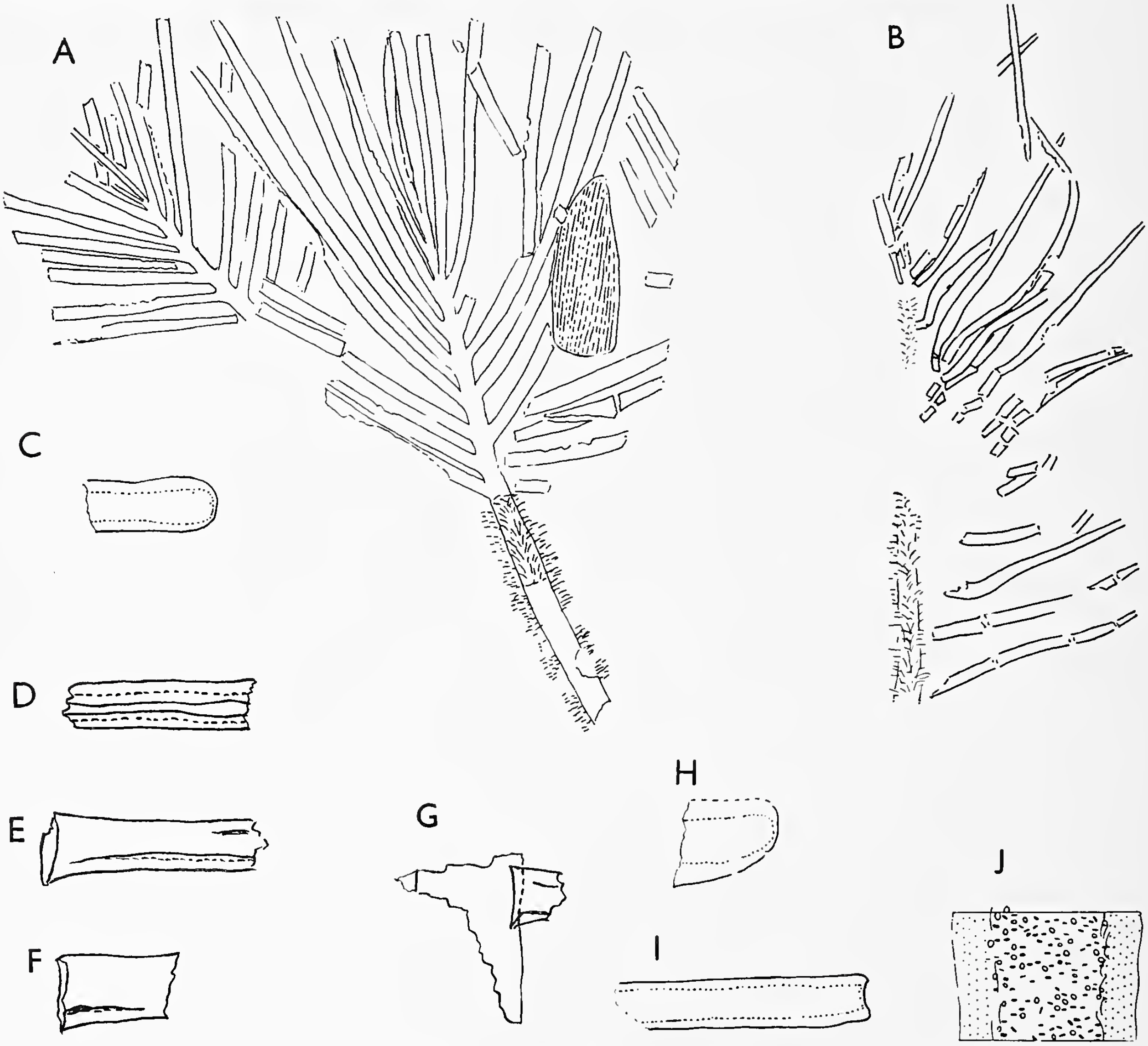

Fig. 45. **Pterophyllum fossum** Harris

A, holotype specimen and other fragments and a beetle elytron, Leckenby Collection K.223, Sedgwick Museum, Cambridge, ×1. B, specimen 64 in Leeds City Museum, ×1. In A and B the hairs on the rachis are not represented individually. C, pinna apex, Saltwick, V.29484, ×5. D–G, fragments from Marske Quarry, V.53323, all ×5. In D both margins of the stomatal groove overlap strongly; in E and F (both pinna bases) with a fold below but none, or only a slight one above. G, rachis and pinna base. H, pinna apex, V.29485, ×5. I, pinna with marginal folds, V.29483, ×5. J, distribution and orientation of stomatal apertures (short black lines) and trichome bases (rings), and marginal folds, Saltwick, V.29484, ×20.

All figures except D–G are from Harris (1952).

P. fossum approaches *Pseudocycas* in having the stomatal surface sunk in a groove. A few specimens have pinnae with a deep groove with margins that overhang and indeed nearly meet (Text-fig. 45 D) as in a typical *Pseudocycas*, but this is unusual. More commonly there is only slight overhang on one side, or no overhang but merely one or two wrinkles as though a steep wall had been crushed, and very often there are not even wrinkles but there is always a broad non-stomatal border. The flatter forms which are much commoner are better placed in *Pterophyllum* than in *Pseudocycas*.

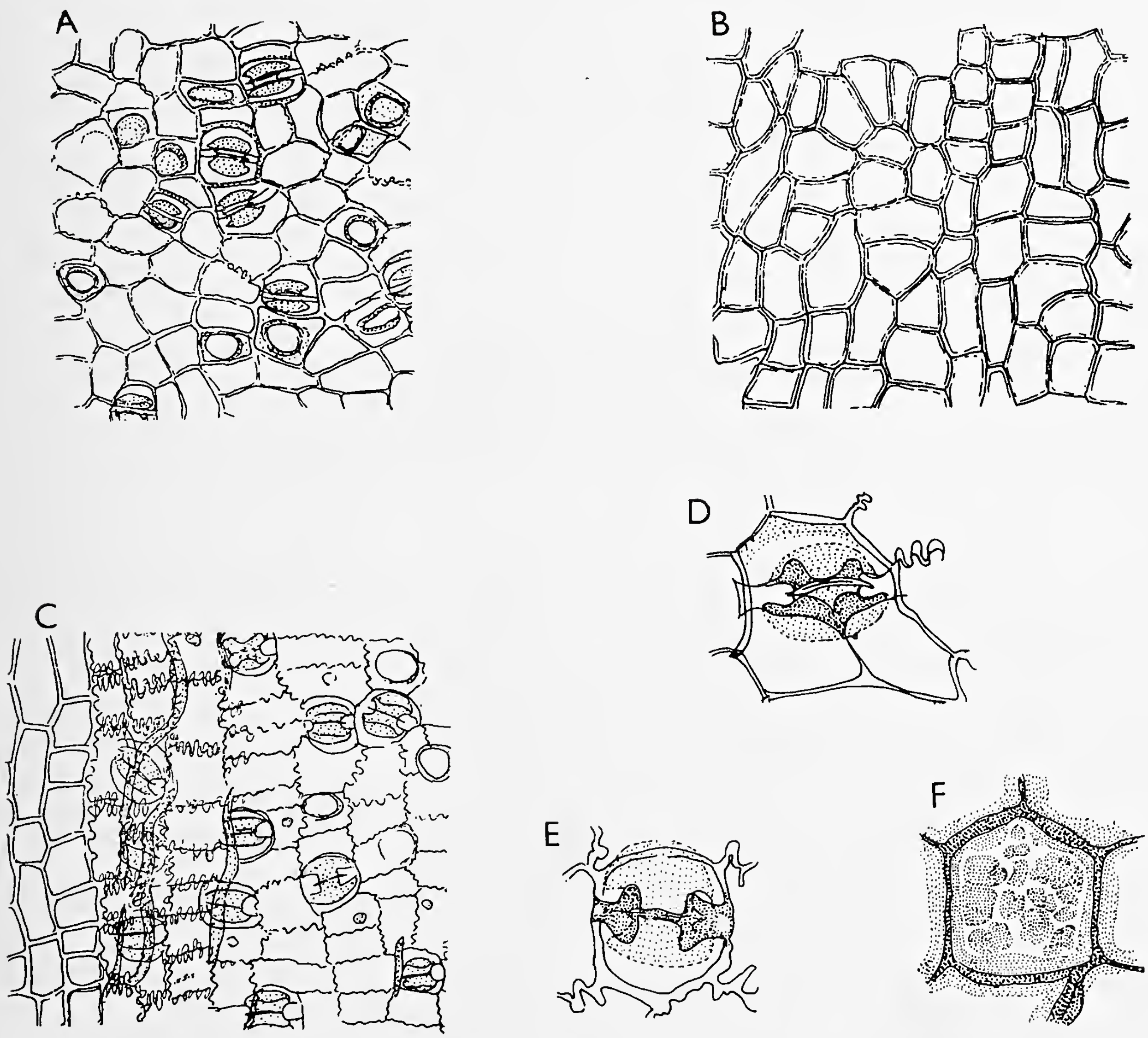

Fig. 46. **Pterophyllum fossum** Harris

A, lower cuticle, form with nearly straight walls and irregularly placed stomata, V.29483, ×200. B, upper epidermis, V.29484, ×200. C, lower epidermis showing folds at edge of stomatal groove (normal form), V.29484, ×200. D, abnormal stoma with divided subsidiary cell, V.29483, ×500. E, stoma with well protected guard cells, V.29484, ×500. F, cell of upper epidermis, V.29483, ×500.

The specimens in A, D, F are from Hartoft Coal Pits, those in B, C, E from Saltwick. All the figures are from Harris (1952).

COMPARISON. *P. fossum* is exceptional in the shape of its leaf as well as in its channelled pinnae, but it must be remembered very few hand specimens have been seen. It shows some resemblance in cuticle to *P. cycadites* and to *P. thomasi*, though it is distinguished by details. The most similar fossil known to me is *Cycadites manchurensis* Oishi (1935) from the Upper Jurassic of Manchuria. *P. fossum* differs in having longer and less crowded pinnae (and probably is a differently shaped leaf). The blunt apices and margins of the pinnae and the cuticles seem similar.

In 1952 I distinguished only two Yorkshire species of *Pterophyllum* (based on hand specimens) and assigned a considerable number of cuticle fragments isolated by maceration of rock in bulk to these two species which I supposed showed rather varied structure. Since then a third species has been found and also many more cuticle fragments. It now appears more likely that the cuticle of each species may be fairly constant and that these scattered cuticle fragments represent a number of further species. Accordingly I now identify only those fragments which agree perfectly with the hand specimens and leave open the determination of most of the cuticle fragments. In this genus as in others the evidence is clear that many more species grew in the area than have been described.

OCCURRENCE. *P. fossum* is rare. The two hand specimens are unlocalised and I am not prepared to guess their origin. Excellent fragments of cuticle agreeing with it fully are known as follows:

Middle Deltaic Gristhorpe Series . .	2 localities
Lower Deltaic	6 localities

This is considerably fewer localities than was given earlier as a number of the cuticle fragments then accepted are now considered doubtfully determined. In particular that figured by Harris (1952, text-fig. 6 D) from Birkbrow is rather unlikely to belong to *P. fossum.*

Pterophyllum cycadites Harris & Rest
Text-fig. 47

1966 *Pterophyllum cycadites* Harris & Rest, p. 105, text-figs. 1, 2. (Figures repeated here.)

DIAGNOSIS (taken from Harris & Rest 1966). Leaf (form and size unknown). Rachis up to 3 mm. broad; central region marked with transversely broad lumps, forming vague longitudinal rows. Pinnae attached slightly above lateral margins, at edge of lumpy region of rachis the smooth marginal region overlapped by the pinnae is 0·5 mm. wide. Pinnae attached at 80°–90° to rachis. Width typically 1 mm. (but Brora fragments up to 3 mm.). Pinna base slightly expanded, width then uniform (contracted to a point at apex of Brora specimens). Pinna lamina flat, margins not thickened. Veins faintly visible or obscure.

Upper cuticle about 5μ thick (in folds) showing rows of uniform rectangular cells, length 2–3 times width. Longitudinal walls strongly marked, nearly straight, transverse walls slightly sinuous.

Cell surface nearly flat but with obscure local thickenings, occasionally (in certain Brora specimens) showing a small hollow papilla 10–15μ wide. Veins not indicated, stomata and trichomes absent. Lower cuticle thinner, divided into a marginal region about 50μ wide resembling upper cuticle and an inner region with scattered stomata, there is no crushed zone occurring between the two regions. Veins sometimes unrecognisable but usually recognisable by tracts of elongated cells 3 cells wide and uninterrupted by stomata. Epidermal cells rectangular, length about twice width. Longitudinal walls strongly marked, nearly straight but slightly more sinuous than on upper epidermis (occasionally distinctly sinuous). Cell surface flat, not papillate but occasionally showing a small thin area. Cell surface sometimes irregularly mottled or longitudinally striated. Stomata mostly transversely orientated, scattered but often forming short files most commonly of 2–3, occasionally of 4. Guard cells sunken and overhung by subsidiary cells; subsidiary cells exposed, smaller than ordinary cells, surface not papillate. Trichome bases frequent, usually adjacent to a subsidiary cell, consisting of a round cell with a thicker surface than rest of epidermis, occasionally showing an obscure imprint on the surface. (Hair always absent.)

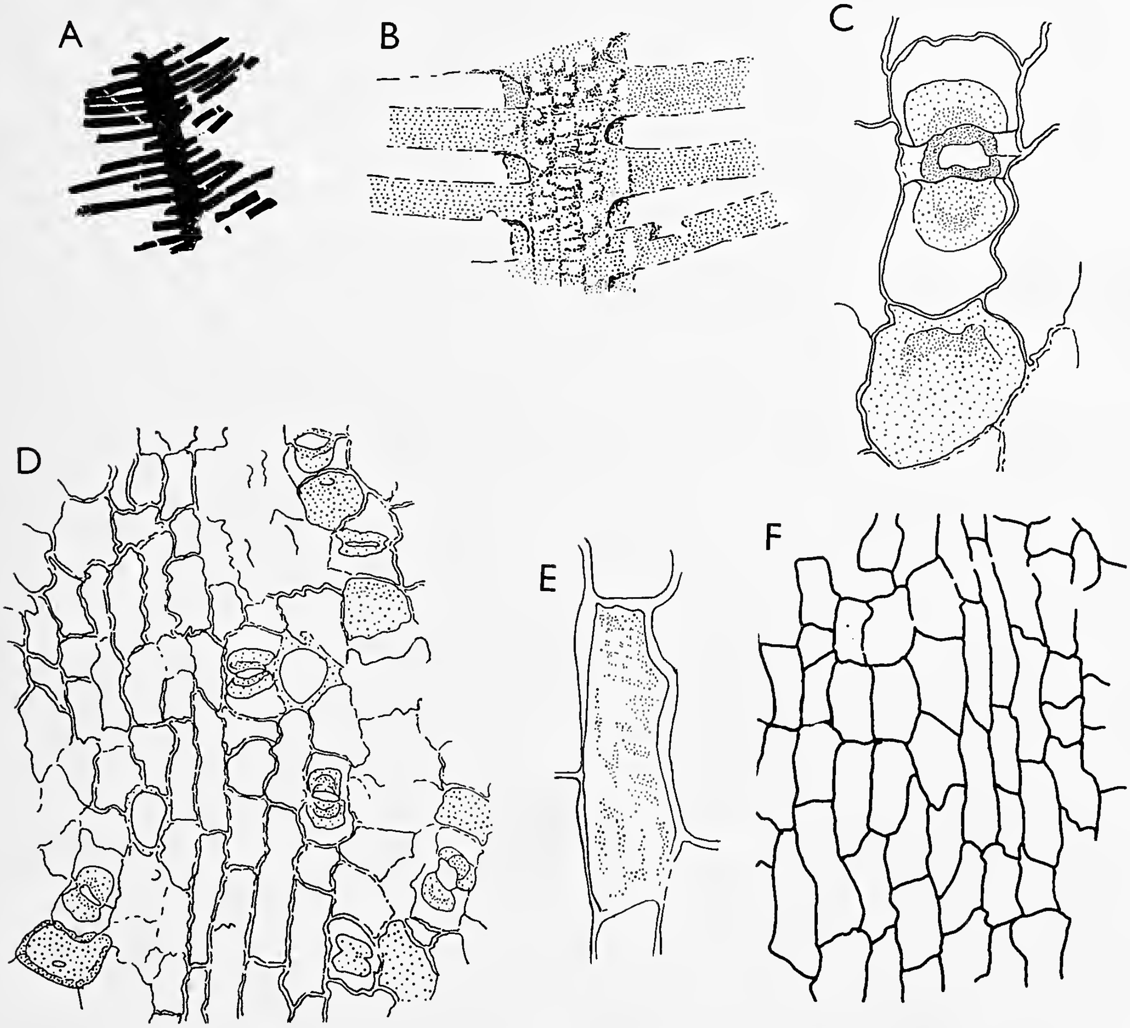

Fig. 47. **Pterophyllum cycadites** Harris & Rest

A, leaf fragment, the top was broken in collecting but the other imperfections were caused in preservation, $\times 1$. B, details from A, $\times 5$. C, stoma and trichome base, $\times 500$. D, lower cuticle, $\times 200$. E, one cell of upper cuticle under phase contrast lighting, $\times 500$. F, upper cuticle, $\times 200$.

The drawings all represent the holotype, V.52121, from the Gristhorpe Bed. The drawings are by J. A. Rest and the figures are reproduced from Harris & Rest (1966) by permission of the Geological Magazine, London.

Holotype. V. 52121. Text-fig. 47.

Description. *P. cycadites* is rare in Yorkshire where it is only represented by the holotype, a water worn fragment from the Gristhorpe Bed, and a single small cuticle fragment from an Upper Deltaic locality. Cuticle fragments agreeing with it are, however, frequent in the Bathonian Coal, equivalent to Upper Deltaic, of Brora in N.E. Scotland (see Harris & Rest 1966). There are a number of cuticle fragments from other Yorkshire localities which agree moderately well with the holotype and may indeed belong to this species, but only if its range of cuticle structure is rather greater than has yet been established. The fragment figured by Harris (1952, text-fig. 6 D) as *Pterophyllum fossum* is an example of one of these imperfectly similar cuticles.

Comparison. *P. cycadites* is distinguished from nearly all species of *Pterophyllum* by its very narrow pinnae. It looks like specimens that have been called *Cycadites rectangularis* but it differs fundamentally in that the pinnae have several veins instead of just one and its well developed cuticle is of Bennettitalean character. The most striking feature of its cuticle is the strong association of trichome bases with stomata, but while nearly all trichomes are next to a stoma they are not as numerous and some stomata lack a trichome.

Occurrence. Its Yorkshire localities are as follows:

Upper Deltaic	. .	1 locality (Roxby, Keld Hole)
Middle Deltaic	. .	1 locality (Gristhorpe Bed)

It also occurs in the Brora Coal of Upper Deltaic age.

Genus CYCADOLEPIS Saporta 1874, p. 201

Diagnosis (as emended by Harris 1953). Scale leaves of rather large size, shape varying from lanceolate to circular. Margin entire. Surface concave on one side, convex on the other. Cuticle where known different on the two sides. Stomata with syndetocheilic subsidiary cells opposite each guard cell.

Type Species. *Cycadolepis villosa* Saporta (1874, p. 201, pl. 114, fig. 4).

Discussion. Saporta's original definition was written for *C. villosa* and *C. hirta* which is possibly the same as *C. villosa.* Later authors, particularly Seward, have widened it to include scales which are glabrous and which range from linear lanceolate to rounded. This widened usage is accommodated in the emended diagnosis given above, but I have restricted the genus to scales showing Bennettitalean stomata. We do not know the cuticles of Saporta's specimens, but we know that very similar scales do have Bennettitalean stomata. The diagnosis thus excludes *Deltolepis* (of Cycadean affinity) and also the Bennettitalean scale *Cycadospadix dactylota* Harris 1932 (which has pinnate branching). This was renamed *Bennettitolepis dactylota* by Florin (1933) on the grounds that the type species of *Cycadospadix* is probably a Cycadean organ (a matter on which we still need evidence, see also Carpentier 1938).

A striking feature of many kinds of *Cycadolepis* is their strong transverse wrinkles. These seem to be formed post-mortem by the contraction of tissue beneath the epidermis into little blocks. We know no reason for this contraction but it is shared to some extent by the petioles of Bennettitalean leaves, but is scarcely seen in Mesozoic Cycadean scales and leaves.

Several species of *Cycadolepis* bear hairs all over the outer side or along the margins, but these are perhaps only borne on the outer scales, the inner scales of the same flower being glabrous (cf. Harris (1944) for *Williamsoniella*).

Cycadolepis often forms the caducous involucre of a Bennettitalean female flower and the Yorkshire species may all be of this nature.

Saporta (1875) compared the original specimens with the bud scales of *Cycas*. Seward (1917) suggested that the narrow scales are likely to be floral but that the broad Wealden ones (*Eury-Cycadolepis*) were borne on stems. We do not yet know the cuticles of any of these Wealden scales. No Bennettitalean stem has yet been proved to bear scale leaves.

In a female *Williamsonia*, the scales may form a series, the outer robust and with plenty of stomata and no doubt with assimilatory tissue, the inner membranous and with few stomata or none. In this it resembles the flower head of *Cynara* (with which it was compared from the first by Young & Bird 1822). In some species of *Williamsonia* the scales are retained, in others they fall off. The outer scales do have some specific character but the inner ones very little.

As a rule a *Cycadolepis* is strongly associated with a Bennettitalean leaf and where associated repeatedly with a particular leaf may be linked with it with some confidence. Their cuticles scarcely show specific but merely family agreement, but sometimes an intermediate organ is found, a *Cycadolepis* bearing a small lamina with the normal leaf cuticle and this identifies it securely.

The stratigraphic value of a *Cycadolepis* determination is small. Nearly always the corresponding leaf will already have been determined, and even when we have good cuticles the differences between *Cycadolepis* species are rather slight. Without a cuticle a *Cycadolepis* species is nearly worthless.

The main interest in *Cycadolepis* perhaps comes from the help it may give in linking a female *Williamsonia* flower with a particular species of leaf, but I admit very little progress in this direction has yet been made.

Two genera which may be merged in *Cycadolepis* are *Cloughtonia* Halle 1911 and *Hildesheimia* Florin 1936. Both are broad, entire scales with Bennettitalean stomata.

Key to the Yorkshire species of Bennettitalean scale leaves

This key only applies to the robust (outer) scales with numerous stomata. There are certainly other species of *Cycadolepis* in Yorkshire which are left undescribed because they are too ill-known. No mention of these is made in the key.

1	Scale leaf noticeably hairy	7
	Scale leaf apparently without hairs	2
2	Length over 4 cm.	3
	Length under 4 cm.	4
3	Shape linear lanceolate	*C. spheniscus*
	Shape broadly ovate	*C. hallei*
4	Apex pointed	5
	Apex truncate	*C. pelecus*
5	Scales over 1 cm. long	6
	Scales under 1 cm. long	*C. stenopus*
6	Apex gradually narrowed	*C. hypene*
	Apex often abruptly narrowed and mucronate	*C. nitens*
7	Scale broadly ovate	*C. eriphous*
	Scale narrow lanceolate	*C. thysanota*

Cycadolepis spheniscus Harris
Text-fig. 48

1953 *Cycadolepis spheniscus* Harris, p. 37; text-fig. 2 A–C, F–I. (Figures repeated here.)

DIAGNOSIS (slightly emended). Scale-leaf; shape linear-lanceolate, upper third tapering to an acute apex, middle third evenly wide, lower third narrowing slightly towards the base, base itself truncate. Length of holotype 6 cm., width 8 mm.; widest specimen 11 mm. (length unknown). Surface slightly concavo-convex below but nearly flat over most of the scale, neither side keeled. Surface markings similar on the two sides, consisting of irregular but mostly short transverse wrinkles and shallow longitudinal ridges or furrows. Substance very thick; veins not seen, fibres not apparent. Scar of attachment on adaxial surface, extending from the base nearly 2 mm. high and almost as broad as the base of the scale, showing a transverse row of about six obscure prints. Interior of scale containing many slender longitudinal fibres.

Cuticle thick on both sides. Adaxial (concave) side slightly thinner, showing fairly regular rows of nearly square or slightly elongated rectangular cells. Cell walls straight without lateral thickenings, very broad, but by no means prominent; quite straight. Cell surface evenly thick or with an ill-defined thicker central area. Hypodermal cells occasionally visible as rectangles 300μ long, 60μ broad. Stomata rare; the few present as on abaxial side.

Abaxial (convex) side rather more thickly cutinised. Cells forming ill-marked rows; cells square, irregular, often rectangular and shorter than broad. Cell walls very prominent (often showing the cell outline in a confused manner), straight, but sometimes with a few jagged thickenings extending over the surface. Cell surface often showing a large solid papilla. Stomata numerous, evenly scattered, transversely orientated. Whole-apparatus occasionally superficial, but usually slightly sunken in a shallow pit formed by surrounding epidermal cells, sides of pit rarely overhanging. Subsidiary cells rather small, unspecialised and not papillate, surface often rather thin. Guard cell thickenings well developed. Trichomes absent. Hypodermal cells (if visible) roughly isodiametric.

HOLOTYPE. V. 30767. Figured Harris (1953, text-fig. 2 C, F–I).

DISCUSSION. Additional specimens which agreed fully with those already described gave some information which was previously lacking. The scale in Text-fig. 48 D originally showed its convex surface and when transferred it showed the concave surface with the broad attachment scar. At one point the epidermis had separated from the inner tissues, and this gave a cuticle preparation which confirmed that the cuticle previously thought to be of the concave side is in fact from that side. No doubt the concave side which lacks stomata and also shows the attachment scar is adaxial.

Other specimens add to the range of form. That in Text-fig. 48 A is 11 mm. broad and though incomplete, better than the previous fragment of this width. That in Text-fig. 48 B shows a diminutive lamina at the apex and the cuticle of the small pinnae agrees with *Otozamites gramineus*. The specimen in Text-fig. 48 C becomes thinner in substance above and the wrinkles become smaller and finally there are none and the apex is transversely truncate. Near the top, the scale consists of little more than the two cuticles which, however, remain thick. The two cuticles were similar in a small preparation made from the margin and showed uniform square cells and no stomata.

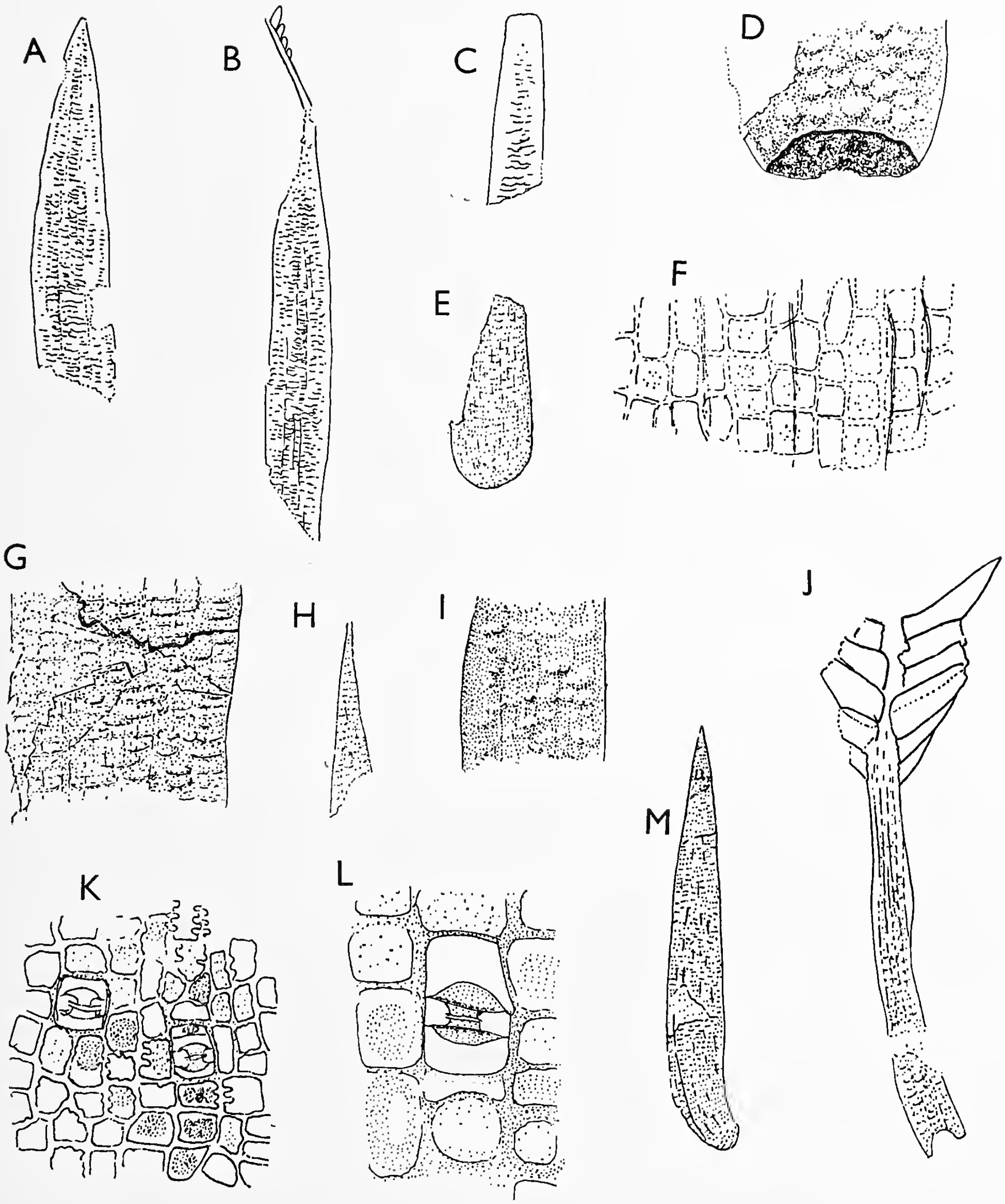

Fig. 48. A–H, K–M, **Cycadolepis spheniscus** Harris; I, J, **Otozamites gramineus** (Phillips)

A, broad specimen, V.52836, ×1. B, unusual specimen with diminutive lamina, V.52835, ×1. C, unusual specimen with truncated apex, V.52834, ×1. D, adaxial side of base (transfer), V.53478, ×4. E, abaxial side of base, V.30766, ×1. F, adaxial cuticle of holotype, V.30767*a*, ×200. G, surface of holotype, ×4. H, narrow specimen, V.30765, ×1. I, surface of J, ×4. J, petiole and lamina base, V.30771, ×1. K, abaxial cuticle of holotype, V.30767*b*, ×200. L, stoma of holotype, V.30767*b*, ×400. M, holotype specimen, V.30767, ×1.

Figs. A–D are new, the rest from Harris (1953). The specimens in C and E are from Saltwick, the rest from Beast Cliff *Otozamites* Bed.

Perhaps this scale is an inner perianth scale, but since this specimen is unique while we have perhaps twenty of the ordinary ones it seems that scales like this were relatively few. Another possibility is that the inner scales were normally retained on the flower (which is not yet available).

It is very probable that *C. spheniscus* belongs to the same plant as *Otozamites gramineus*. The two fossils are associated in four localities but *C. spheniscus* is always less common. One of these localities, represented by K194 in the Sedgwick Museum, which shows fragments of both organs, is labelled Haiburn Wyke, but I do not know the exact bed and it might be the same as my 'Beast Cliff *Otozamites* Bed'. Then in the Whitby Plant Bed (represented both in the Sedgwick Museum and in the Hamshaw Thomas Collection) *O. gramineus* is second only in abundance to *Ptilophyllum pectinoides*. There are good specimens from the Saltwick Waterfall where *O. gramineus* is again abundant. However it must be mentioned in all these three localities other Bennettitales occur also. In the final locality, Beast Cliff *Otozamites* Bed, this species is the only Bennettitalean, in the part which gave *C. spheniscus*. Then there is resemblance in texture between the rachis of *O. gramineus* and the thick lower part of *C. spheniscus* and more important there is an intermediate specimen, a normal looking *C. spheniscus* bearing a diminutive pinnate leaf, the lamina of which shows the cuticle of *O. gramineus*.

COMPARISON. The most similar *Cycadolepis* of those whose cuticles are known is perhaps the scale of *Wielandiella angustifolia* (see Harris 1926, p. 82). It differs in being rather larger and in its smaller wrinkles, its transverse instead of longitudinal stomata and its lack of trichome bases. Scales of moderately similar appearance but unknown structure have been figured under the name *Cycadolepis corrugata* Zeiller from various localities.

OCCURRENCE. *C. spheniscus* has four localities, all belonging to the Lower Deltaic series.

Cycadolepis hallei nom. nov.
Text-figs. 49, 50

1880 *Anthrophyopsis* sp. Nathorst, pp. 35, 62, 63. (Brief comments.)
1911 *Cloughtonia rugosa* Halle, p. 2, pls. 1, 2. (Form and cuticle.)
1953 *Cycadolepis rugosa* (Halle) Harris, p. 39, text-fig. 3 C, D, F. (Form and stomata, figures repeated here.) (Not *Cycadolepis rugosa* Johannson 1922.)

EMENDED DIAGNOSIS. Scale typically spatulate, apex rounded or obtusely pointed, base usually extended and narrowed, then transversely truncate. Margins entire but often somewhat waved and folded. Length typically 5–10 cm., width 4–5 cm. above, tapering to 1–2 cm. below. Middle region much thickened (or thick region nearer one side) showing about twenty longitudinal strands crossed by transverse wrinkles, lateral strands (veins) forking frequently and bending outwards to meet the margin at a wide angle; concentration of veins about 10 per cm. Veins often scarcely seen. Substance becoming thinner near margins. Hairs absent on both sides.

Cuticles thick all over both sides, appearing to be 6μ in folds. One side (described as adaxial) with fewer stomata. Epidermal cells typically twice as long as broad, not forming files, veins not marked. Walls broad and ill-defined, surface flat. Hypodermal cells present, length two or three times as long as broad, walls nearly straight, marked by a fine but distinct ridge. Stomata as on other side.

Abaxial cuticle showing isodiametric cells with prominently marked outlines, walls prominent, thick, usually straight but sometimes with slight jagged thickenings, surface wall flat but with mottled sculpture. Cells occasionally in longitudinal files but usually not. Veins scarcely marked. Hypodermis present under most of epidermis, as on adaxial side.

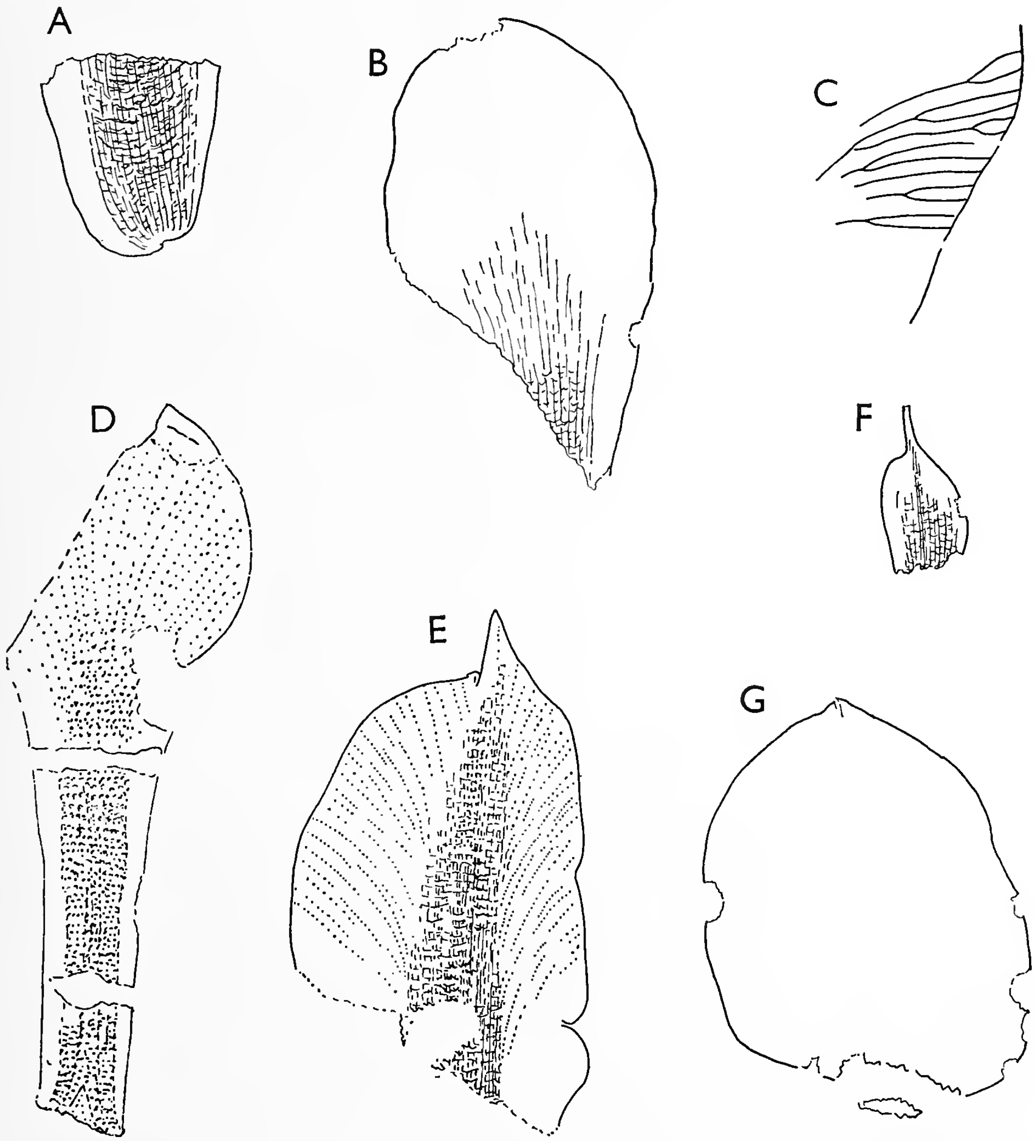

Fig. 49. **Cycadolepis hallei** nom. nov.

In the figures at natural size the ridges and transverse wrinkles are indicated in a general way but individual ones are not shown accurately. Where none are shown this may be because the interior substance has vanished through decay.

A, base, V.52828, ×1. B, upper part, V.52827, ×1. C, margin showing veins, V.52825, ×4. D, nearly complete specimen, K.447, Sedgwick Museum, Cambridge, ×1. E, upper part with a mucro, V.52830, ×1. F, abnormally small scale with a long extension (broken off), V.52826, ×1. G, upper part, V.52829, ×1.

D is from Harris (1953).

Stomata often about 10 per sq. mm., but occasionally much fewer particularly in marginal regions, evenly scattered and not forming rows, orientation longitudinal or oblique, rarely transverse. Stomatal apparatus sunken, often at the bottom of a shallow oval pit, or with subsidiary cells partly exposed, subsidiary cells very narrow. Trichomes absent from both sides.

This species which was described as *Cloughtonia rugosa* by Halle was renamed by me (1953) as *Cycadolepis rugosa* (Halle). However the binomial *Cycadolepis rugosa* was pre-occupied by Johannson (1922) for a different species. I therefore give the new specific name *hallei* to Halle's species.

Holotype. Stockholm Museum. Figured Halle (1911, pl. 2).

Description. None of the present specimens is complete, but this is mainly because the rock is somewhat fragile and difficult to extract from the cliff. Some were almost certainly complete when preserved. The figures show the range of form. The specimen in Text-fig. 49 F is exceptional in its mucronate top; the mucro was broken off but since it tapers it is likely that it never bore any lamina.

Most of the specimens have undergone some natural maceration (as have many fossils in this bed) and rather little remains in the distal parts but the two cuticles, and often a layer of mud has penetrated between these. The fossil, or at least its lateral parts, may then appear as a very delicate brown membrane, but I am sure this is due to decay.

The thick central region is more robust and some of its internal substance usually remains. Where it has vanished the surface has no wrinkles. Transfers of the scale on celloidin may or may not show veins; they never show any well marked fibres such as are seen in various other fossils when similarly decayed. The only internal cells clearly recognised were the hypodermal ones (seen also in the cuticles).

The cuticles vary somewhat in different specimens and in different parts of the same specimen. Towards the margins the two sides become more alike and the stomata become less frequent than in the thicker middle region. They also are very few in the basal region. As Halle (1911) found, preparations from certain scales show no stomata. I cannot say if there are scales with none at all because a good deal of the substance had been lost during collecting, but certainly some have extremely few.

Discussion. The present material is like Halle's except that the preparations Halle examined showed no stomata, unfortunately. Later preparations made from other specimens at Stockholm did show stomata. All the present specimens show some stomata, at least in the thicker parts, but the number varies and there may be none in the distal regions.

Halle placed this species in the non-committal new genus *Cloughtonia* because he felt unsure about its nature. He considered it possible that it might be a *Cycadolepis* (in the broad sense in which *Cycadolepis* had been used by Seward) but having no stomata he was not sure it belonged to the Bennettitales. It was the finding of typical stomata that led me to include it in *Cycadolepis*.

Halle's original material is from Cloughton Wyke as I believe is the unlocalised Leckenby Collection specimen K447. I feel sure they all come from the main Cloughton Wyke Bed (the *Solenites* Bed). One of my specimens was from the part of this bed exposed in the beach but all the others were from a point further north (54° 20′ 50″ N) where the bed is exposed in the cliff a few metres above the beach. Here in the cliff, *C. rugosa* is locally common throughout the bed and not merely on certain bedding planes, but the bed is awkward to collect. It is strikingly associated with *Pterophyllum thomasi*. The Leckenby specimen as noted earlier shows the association of six fragments with *P. thomasi*. This bed often shows a marked local abundance of a species with different parts of the same species lying near one another. This localisation may be nearly as marked as in the Gristhorpe Bed. I agree with Thomas that such

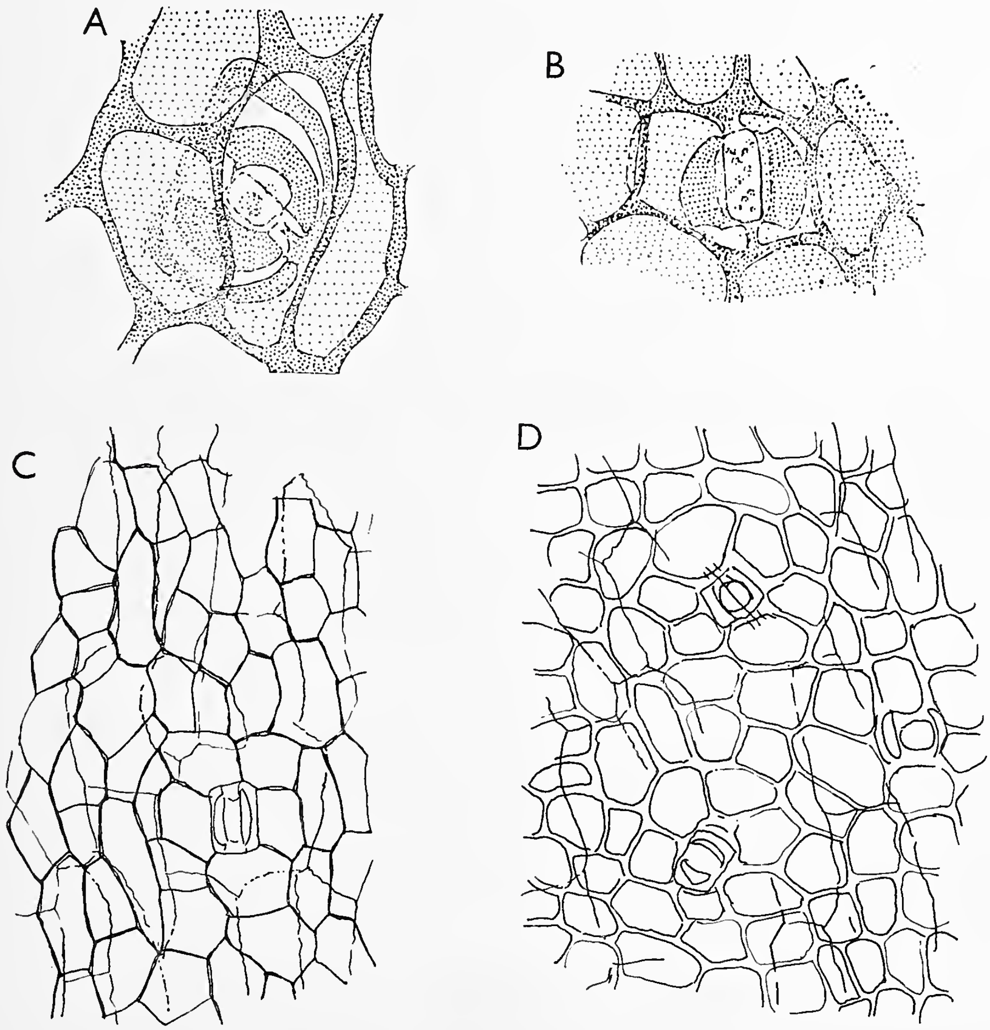

Fig. 50. **Cycadolepis hallei** nom. nov.

A, B, two stomata of a specimen in the Stockholm Palaeobotany Museum, ×500. C, adaxial cuticle, V.52830*a*, ×200. D, abaxial cuticle, V.52830*a*, ×200.
A and B are from Harris (1953).

localisation probably represents material from a particular stand of a species, probably near at hand. With such localisation association of organs of different kinds strongly suggest that they may come from the same species. Thomas called this occurrence in the Gristhorpe Bed 'autocthonous', but that word should be restricted to plants like *Equisetum columnare* still attached to their roots in a fossil soil.

The cuticles show only family agreement, as usual between Bennettitalean leaves and scales. The only other Bennettitales known at this point in the cliff are the widespread *Nilssoniopteris vittata*, *Ptilophyllum pecten* and *Anomozamites nilssoni* in all of which the scale leaves are already known.

I support Halle's suggestion that this fossil was an investing scale of a large *Williamsonia* and would go further and suggest that specimens with few stomata may be inner and more scarious scales, those with numerous stomata the outer, green ones. There is nothing to suggest the colour of the inner scales, but I would compare them with the inner scales of *Cynara* or a Proteaceous inflorescence rather than, say, *Magnolia* petals because they have thick cuticles.

There is some resemblance between *C. hallei* and the fossil described by Lignier (1895, 1907) as *Propalmophyllum liasinum* from the French Lias. Though *C. hallei* shows none of the striking folds of *Propalmophyllum*, its vascular strands run in similar directions, and I suggest the possibility that Lignier's fossil is a similar Bennettitalean scale leaf and has nothing to do with any palm or other Angiosperm. Depape (1960) gives a useful review of *Propalmophyllum*.

Occurrence. *C. hallei* is known only from the Cloughton Wyke *Solenites* Bed (Middle Deltaic, Gristhorpe Series).

Cycadolepis stenopus Harris
Text-fig. 51

1943 *Cycadolepis stenopus* Harris, p. 513, text-fig. 3.

Diagnosis. Typically small, about 8 mm. long, 4 mm. broad. Shape typically lanceolate, apex acute, base constricted. Surface showing small wrinkles in middle regions, but marginal parts smooth. Substance rather thick in middle region. Cuticle typically thick (up to 10μ) on convex or lower side, much thinner (about 1μ) on concave side but becoming thicker towards margins and apex. Cells of both sides short, straight-walled, forming longitudinal rows; surface of cells finely mottled, but without any median papilla. Stomata typically very rare, but a few occurring near the apex on the convex side; subsidiary cells small. Margin bearing numerous minute hairs, making it appear microscopically serrate, similar short hairs often borne on both surfaces near margin; each hair consisting of a basal cell resembling an ordinary epidermal cell and a short hair with thin cuticle, but thick underlying wall layers; extremity of hair often slightly enlarged.

Holotype. V. 26860. Figured Harris (1943, text-fig. 3 a, e).

Discussion. This small scale leaf was found as a result of search for an appropriate associated scale leaf in a local part of the Gristhorpe Bed full of *Anomozamites nilssoni*. It proved very common. Since then *A. nilssoni* has been found widely, but in small numbers and mixed with other species. However a local pocket of shale just above the main plant bed at Cloughton Wyke was noted which had more of *A. nilssoni* than anything else, and this shale when searched yielded *C. stenopus*. One of the Cloughton specimens differed from those previously figured in having rather numerous oblique or longitudinally orientated stomata on the convex side and also in having the cuticle of the concave side nearly as thick as on the convex. I presume this is a scale leaf produced on the outside of whatever bud or flower was enclosed and that it had more photosynthetic tissue than those previously described. This specimen showed few of the sac-like trichomes on its surface (represented in Text-fig. 51) but its margins are minutely hairy (as in Text-fig. 51). Apart from this the figures cover the range of form observed.

C. stenopus is attributed to the same plant as *Anomozamites nilssoni* on the evidence of association (now in two localities) and on the occurrence of intermediate specimens (Text-

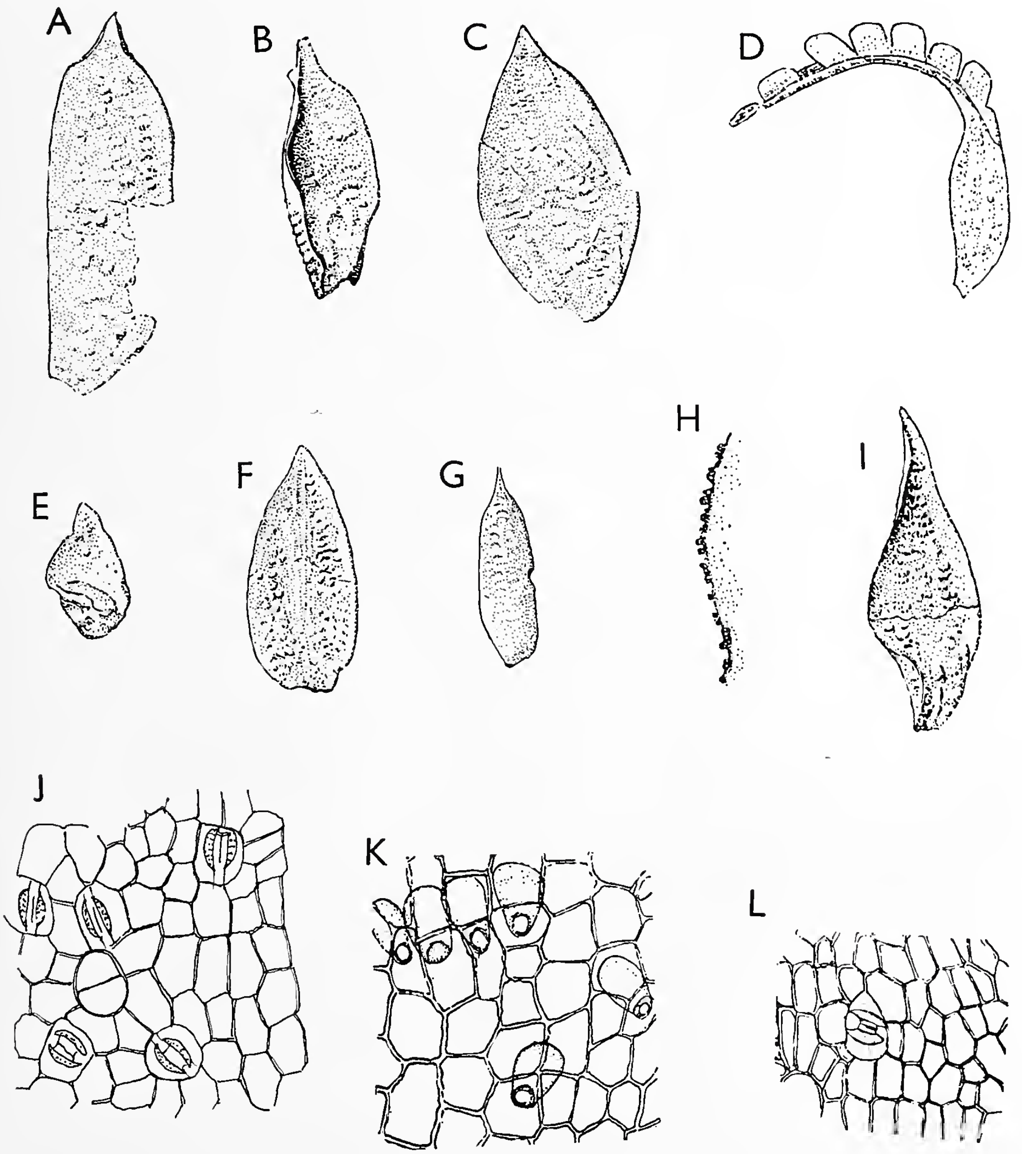

Fig. 51. **Cycadolepis stenopus** Harris

A, largest specimen, V.26867, ×4. B, adaxial side of a scale with a minute outgrowth, V.26865, ×4. C, holotype specimen, V.26860, ×4. D, adaxial side of scale bearing a small *Anomozamites nilssoni* leaf, V.21394*a*, ×2. E, V.26866, ×4. F, V.26861, ×4. G, V.52842, ×4. H, margin of holotype showing dark hair bases, ×40. I, V.26864, ×4. J, abaxial side of a scale with numerous stomata, V.53477, ×200. K, abaxial cuticle near edge of scale, V.26862, ×200. L, stoma from near apex, V.26863, ×200.

G and J represent new specimens from Cloughton Wyke, *A. nilssoni* Bed. The rest are from the Gristhorpe Bed and the figures are from Harris (1943).

fig. 51 D). It is very possibly the floral bract of *Bennetticarpus diodon* (see p. 153). It is true that the bracts of *B. diodon* though similar in several respects differ in being two or three times longer than what is here described as typical *C. stenopus*, but it is possible that the method of isolating *C. stenopus* by maceration has resulted in none but small specimens being seen. After realising this I did succeed in macerating out one that was 17 mm. long, see p. 154.

The discovery of the flower *Bennetticarpus diodon* raises the possibility that knowledge of *C. stenopus* may be very incomplete, for the scale leaves round *B. diodon* have much in common with *C. stenopus* but are longer, probably about 2 cm. long. It must be remembered that *C. stenopus* was recovered by macerating rock and sieving off plant residue, a process which favours plant organs which are small, coherent and recognisable, while larger organs get broken and then are not perceived as things of interest but regarded as meaningless rubbish. Thus if there had been a few long scales in my macerations I would very probably have missed them. This calls for further study now we know what to look for.

COMPARISON. The original specimens of *C. stenopus* were remarkable not only for their very small size, contracted base and longitudinal stomata but also for their much thicker cuticles on the outer side and the fewness of their stomata. They were more like protective (and non-photosynthetic) bud scales than the usual floral bracts. However, the later found specimen is more like an ordinary *Cycadolepis* in cuticle and if the flower *B. diodon* does belong to the same plant, then the diagnosis would need to be enlarged to include a range of scales from the small ones already dealt with to long and narrow ones. If the range does extend to long scales, then the main specific characters may include the blunt apex, sac-like trichomes and longitudinally orientated stomata.

OCCURRENCE. The two localities of *C. stenopus*, the Gristhorpe Bed and a shale just above the main (*Solenites*) plant bed at Cloughton Wyke, both belong to the Gristhorpe Series of the Middle Deltaic. As *A. nilssoni* is widespread and ranges the whole series (though seldom locally abundant) *C. stenopus* is likely to occur more widely also.

Cycadolepis nitens Harris
Text-fig. 52

1944 *Cycadolepis nitens* Harris, p. 428, text-figs. 4, 5. (Figures and description repeated here.)

DIAGNOSIS. Shape of scale leaf lanceolate, apex mucronate, length typically 12 mm., width typically 5 mm. (extreme lengths 21 and 6 mm., widths 7 and 3 mm.). Surface concavo-convex, substance very thick, back projecting as a keel. Interior containing longitudinal fibres which project on both surfaces as fine longitudinal ridges. Surface wrinkles and tubercles absent. Outer, convex, side glabrous, glossy, inner side dull, usually covered densely with short fine hairs. Scar of attachment broadly rhomboidal, situated above the base of the concave side; showing prominences due to ends of fibres.

Cuticle very thick, typically 10μ on convex and 5μ on concave side. Cells on both sides isodiametric or slightly elongated, tending to form longitudinal rows. On concave side stomata absent, cell outlines broad, often obscurely marked, straight and entire or with very feeble jagged thickenings. Trichomes typically borne on nearly every cell; hair base often indistinct, sometimes covering the whole surface, sometimes distinctly smaller, forming a ring on the surface. Hairs about 1 mm. long, simple, tapering to a fine point, walls fairly thick but with

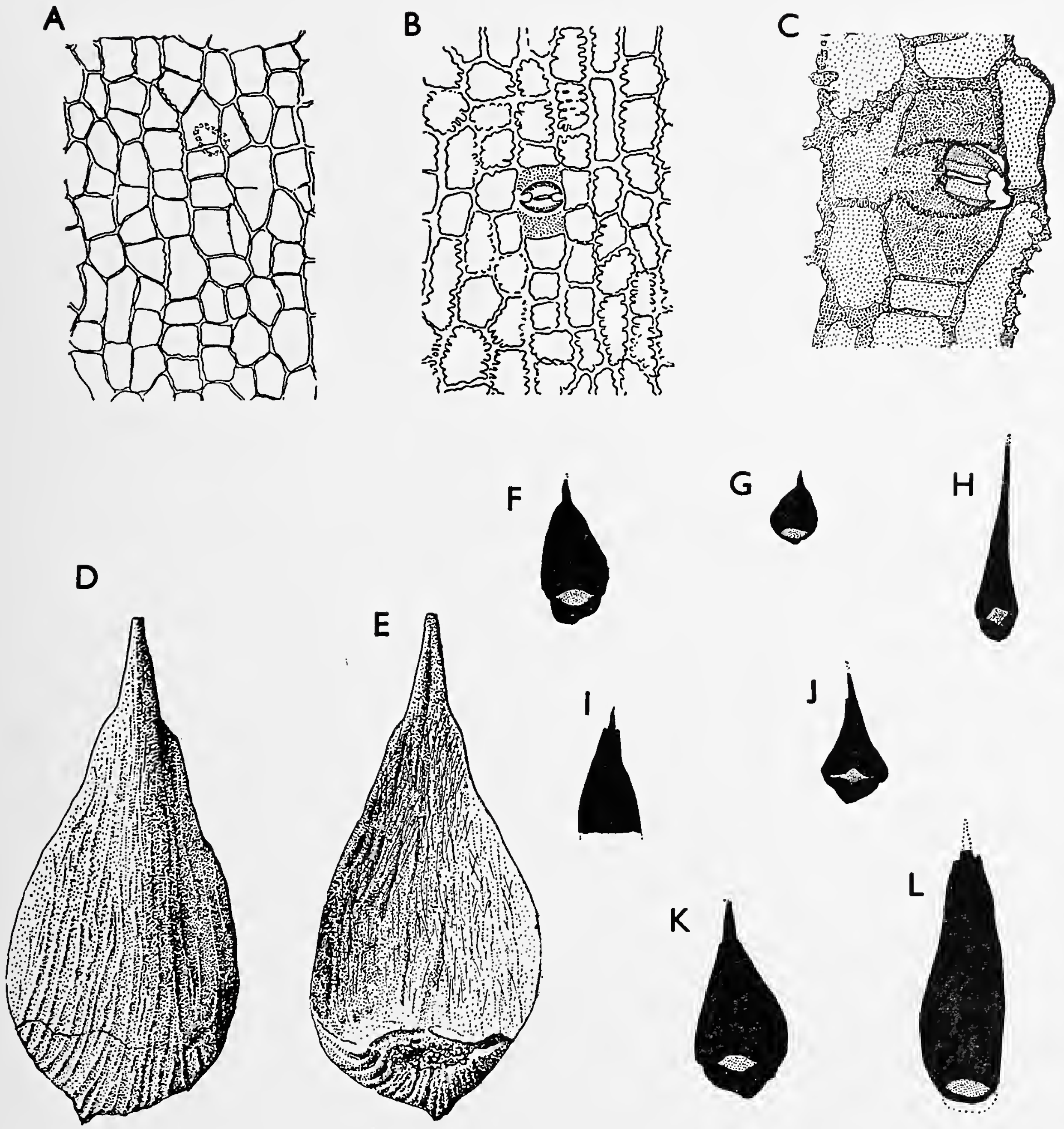

Fig. 52. **Cycadolepis nitens** Harris

A, upper cuticle. B, lower (convex side), V.24695, ×200. Although only one hair base is obvious in A, the hairs were so numerous that nearly every cell must have borne one. C, a stoma compressed rather obliquely showing the pit, V.24695, ×600. D, E, back and front of holotype specimen, V.24722, ×6. F–J, series of scales showing range of form, all ×1. F is V.24724, G is V.24725, H is V.24721, I is V.23944, J is V.24724. K, L specimens at ×2, K is V.24720, L is V.24723.

All the figures represent specimens from Gristhorpe Bed and are from Harris (1944).

only a thin cuticle on the outside. In occasional specimens concave side almost glabrous.

Convex (lower) side showing a few, scattered stomata, about 3 per sq. mm., trichome bases normally absent but a few sometimes present near margins. Cell outlines very broad, prominent, straight and entire in the lower part of the scale, straight but with more-or-less developed jagged thickenings in the upper part of the scale; cell surface flat, coarsely mottled. Stomata usually transversely orientated, subsidiary cells the same size as other epidermal cells, but surface thicker, and margins entire. Cutinised thickenings of guard cells well developed, aperture sunken in a moderately deep oval pit formed by the subsidiary cells.

Both sides often showing outlines of elongated hypodermal cells.

Holotype. V.24722. Figured Harris (1944, text-fig. 4 A, B).

Description. *C. nitens* is abundant in the part of the Gristhorpe Bed where *Ptilophyllum pecten* is abundant and also occurs generally in the Cloughton Wyke *Solenites* Bed (where *P. pecten* is widespread also). *C. nitens* is unknown elsewhere and *P. pecten* is only represented as a few small cuticle fragments in other localities.

I have made some further observations on the Cloughton specimens.

A good many scales prove to have rather few hairs and some are glabrous and do not even show the scars of trichome bases. Also the hairs that do occur may be short. Certain very thickly cutinised scales show faint imprints of rectangular hypodermal cells $70\mu \times 30\mu$ on the convex side. Naturally macerated scales show the internal fibres very plainly; they are 2–3 m. $\times$ 30μ and appear to be solid. Laterally compressed scales show the original thickness which is as much as 2 mm. in the middle but the margins are thin.

I previously suggested that *C. nitens* might belong to the same plant as *Ptilophyllum pecten* (which I called *P. gracile*). This was based on their association. The fact that this association is repeated in a second locality greatly strengthens this suggestion. There is no other Bennettitalean plant likely to possess this scale for the only other frequent associate in the two localities is *Nilssoniopteris vittata*, the scale of which is believed to be distinct. I admit that there is no striking structural agreement between the scale and the leaf.

I previously thought it might be a vegetative scale because I found no flower fragments with it, but at Cloughton it is noticeably associated with *Williamsonia leckenbyi* and I now suggest that it is the sepal-like scale originally surrounding that flower. *C. nitens* has rather few stomata (0–6 per sq. mm.) so it is unlikely to have had much photosynthetic function. None of the specimens is noticeably more delicate and I conclude that all were thick and sepalloid, none petalloid.

Comparison. *C. nitens* is very like *C. hypene* (which I link with *Ptilophyllum pectinoides*) and is compared with it on p. 115. It is not particularly like any other kind known to me.

Occurrence. The Gristhorpe Bed and the Cloughton Wyke *Solenites* Bed, both Middle Deltaic Gristhorpe Series.

Cycadolepis hypene Harris

Text-fig. 53

1953 *Cycadolepis hypene* Harris, p. 34, text-fig. 1 A–J. (Figures and description repeated here.)

Diagnosis. Shape lanceolate or narrow lanceolate with a filiform apex, length typically about 2·5 cm., width just above the base about 6 mm. (Extremes noted, 36 and 20 mm. long, 9 and 3 mm. wide.) Surface concavo-convex, back rounded below, grooved and keeled in the apical region. Substance thick, containing longitudinal fibres which may project on the surfaces as ridges, but surfaces otherwise smooth, without wrinkles or tubercles. Both sides moderately glossy; margins either smooth or covered with short fine hairs 1 mm. long. Scar of attachment large, broadly rhomboidal, situated well above the base. Apex attenuated and often filiform, not abruptly marked off from the body of the scale.

Cuticle of convex side thick (3μ in folds). Cells of both sides roughly isodiametric, forming longitudinal rows. Concave side slightly thinner (1–2μ) lacking stomata and usually lacking trichomes. Cell outlines straight, well marked, fairly broad. Cell surfaces smooth or with obscure longitudinal striations. Convex (lower) side with evenly scattered stomata. Cell outlines strongly marked, broad, straight; cell surface often considerably thickened, but not forming a definite papilla. Stomata orientated transversely, as a rule sunken together with the subsidiary cells in a shallow depression. Subsidiary cells small, unthickened.

Trichome bases rare except towards the margins of some specimens; consisting of a single thickened cell bearing a ring-shaped print. Free part of trichome consisting of a simple hair 1 mm. long, 30μ wide, but tapering towards the apex and, so far as is known, not septate.

The name *hypene*, moustache, refers to its resemblance in shape to one-half of a (waxed) moustache.

HOLOTYPE. V. 30751. Figured Harris (1953, text-fig. 1 C).

DESCRIPTION AND DISCUSSION. *C. hypene* is common in at least eight Lower Deltaic localities where *Ptilophyllum pectinoides* is abundant. Five were known originally and three additional localities have been noted since the previous account was written. These include Marske Quarry (Hamshaw Thomas Collection).

The cuticle of *C. hypene* is rather thinner than that of *C. nitens* and the convex side of the scale is much less glossy. There are often numerous hairs on the concave side of *C. nitens* (but there may be only a few or none) but in *C. hypene* while some show a few, most show none. Jagged cell walls are often seen in *C. nitens* but not in *C. hypene.*

The specimens from Marske (Text-fig. 53 L–P) are of intermediate form, some look typical specimens of the one, others of the other species. They are notably broad. Two show a mucro, but their cuticles are more like *C. hypene*. It was noted that the associated Marske *Ptilophyllum* leaves include ones with rather bulging epidermal cells (though none that could be identified as *P. pecten*). It seems possible that the two species of *Ptilophyllum* may not be rigidly distinct everywhere but that in certain localities, like Marske, forms occur with characters that are partly intermediate.

In all its localities *P. pectinoides* occurs on the same blocks as *C. hypene*. In some no other Bennettitalean leaf is known to occur in the locality but in others (e.g. Marske) there are a good many, but certainly none of these others is noticeably associated with *C. hypene*. A specimen has been previously noted which is somewhat intermediate between *C. hypene* and a *Ptilophyllum* leaf (Text-fig. 53 K)—an exceptionally attenuated specimen of *C. hypene* showing a series of minute bulges along a groove in the upper part (Text-fig. 53 J). Leaves of *Ptilophyllum* show their lowest pinnae beginning in just this way.

I believe that *C. hypene* surrounded the flower *Williamsonia hildae*. Most of the flowers it is true show no scales at all, but merely scars suitable for scale bases, but one from Hasty Bank which seems very young is still surrounded by numerous *C. hypene* scales.

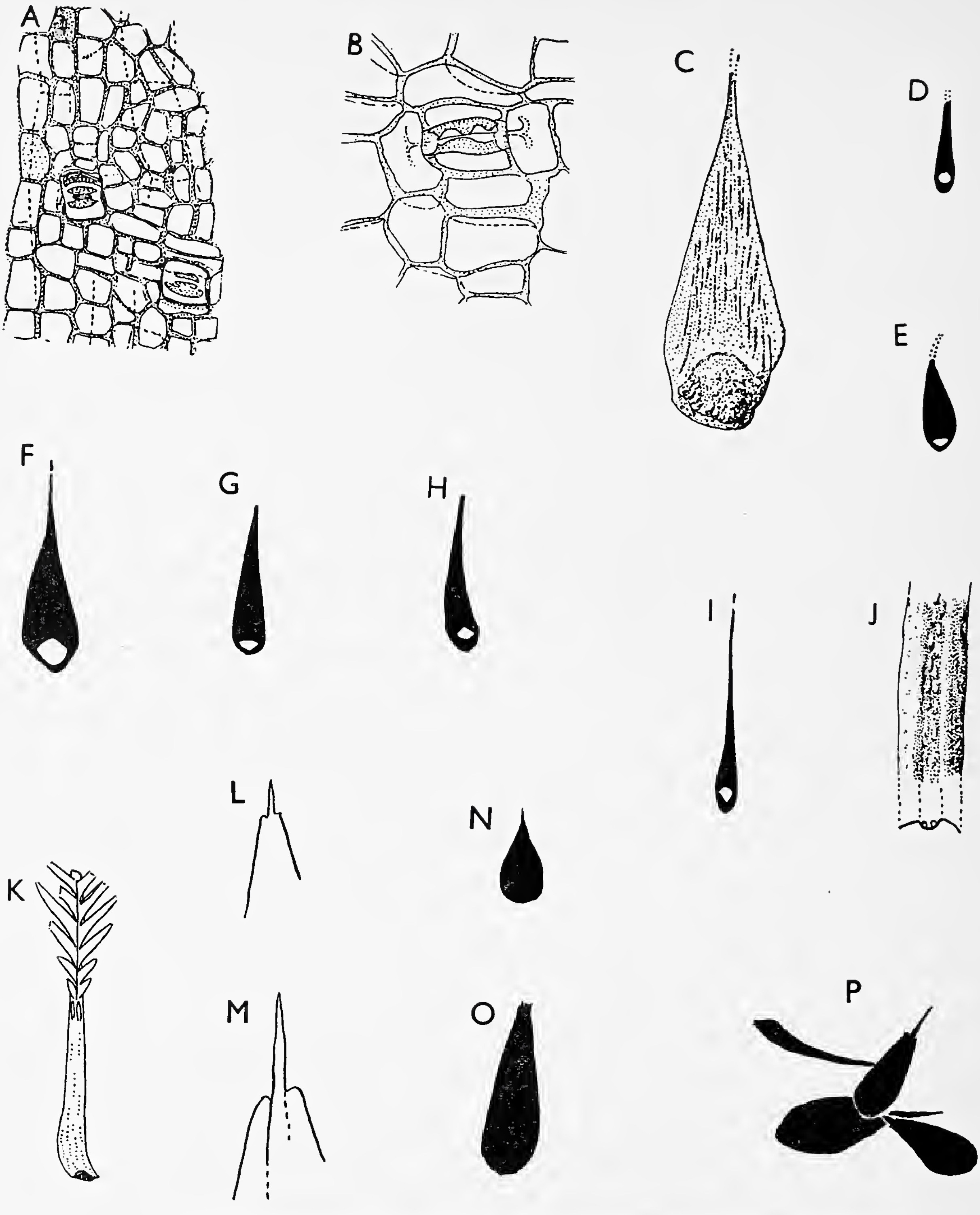

Fig. 53. **Cycadolepis hypene** Harris and **Ptilophyllum pectinoides** (Phillips)

A, lower cuticle showing hypodermal cells, V.30750, ×200. B, stoma, V.30750, ×400. C, holotype showing scar of attachment and ridges due to fibres, V.30751, ×3. D, V.30755, ×1. E, V.30756, ×1. F, unusually broad specimen V.30757, ×1. G, V.30758, ×1. H, V.30755, ×1. I, abnormal specimen, V.30752, ×1. J, upper part of I showing suppressed pinnae. Below is a reconstructed section through the fossil, ×12·5. K, lower part of a leaf of *P. pectinoides* with no petiole, and a broad base resembling *Cycadolepis*, V.30764, ×1. L, M, apices of two of the scales in P, ×2. N, O, P, scales on a single block, the narrow one being compressed laterally, V.53447, ×1.

A–F, H–K are from the Whitby Plant Bed, G from Hasty Bank, L–P from Marske Quarry. A–K are from Harris (1953).

COMPARISON. *C. hypene* is very like *C. nitens* and at each locality where specimens are numerous there are a few which look like forms of the other species. However the populations as a whole seem satisfactorily distinguishable. In *C. hypene* the apex is usually attenuated but in *C. nitens* abruptly narrowed and then has a short mucro. *C. hypene* is commonly rather longer and typically about 25 mm. as against 12 mm., and as they are both typically 5 mm. wide *C. hypene* is relatively narrower. But scales of very different shape occur in both.

OCCURRENCE *C. hypene* has eight localities, all in the Lower Deltaic, except one (Lockton Hagg Beck E. which is just above the Eller Beck Bed).

Cycadolepis pelecus sp. nov.

Text-fig. 54 A–D

DIAGNOSIS (based on holotype alone). Scale wedge-shaped, 10 mm. × 7 mm. at the base, 4 mm. at the truncate apex. Surface flat (not keeled) but both sides showing strong transverse wrinkles; substance thick showing a few longitudinal thick strands, becoming thin towards lateral and apical margins but margins not scarious. Scar of attachment occupying whole of base of scale. Apical margin transversely truncate but slightly irregular. Neither surface nor margins bearing any hairs or ramenta. Cuticles thick and robust on both sides. One side (described as adaxial) with few stomata (up to 3 per sq. mm.), cells rectangular forming well marked longitudinal files, shape often broader than long. Anticlinal walls, especially longitudinal walls often very broad but not prominent, straight with or without small jagged thickenings. Cell surface coarsely mottled but not papillate. Hypodermal cells well developed, occurring over nearly the whole surface, shape elongated, walls straight but more or less interrupted by pits. Stomata as on abaxial side.

Abaxial surface showing isodiametric cells arranged irregularly or in longitudinal files. Anticlinal walls rather narrower and more distinct than on adaxial surface. Cell surface most often thickened in middle region to form a large solid papilla, or surface irregularly mottled. Stomata frequent (about 30 per sq. mm.), irregularly spaced but all transverse. Stomatal apparatus superficial, guard cells with well-developed crescent-shaped plates, but region around aperture very thin. Subsidiary cells small, surface unthickened. Hypodermal cells occasional, absent near a stoma, less conspicuous than on adaxial side.

The name is from πέλεκυς (an axe) and refers to the resemblance of the whole scale to an axe head.

HOLOTYPE. V.52882. (Text-fig. 54 A–D.)

COMPARISON. *C. pelecus* is a typical species of *Cycadolepis* in all its details, it is distinguished by its truncate apex from others whose cuticles are known. Its cuticle is similar to that of *C. spheniscus* but the anticlinal cell walls are less prominent and the stomatal apparatus is superficial instead of slightly sunken. The hypodermal cells of *C. pelecus* are elongated instead of isodiametric.

DISCUSSION. *C. pelecus* possibly belongs to the same plant as *Otozamites falsus*. It occurs in the *O. falsus* bed at High Whitby with no other Bennettitalean fossils and indeed with little other determinable plant material. It must, however, be remembered that this bed is only known from blocks fallen from high in the cliff.

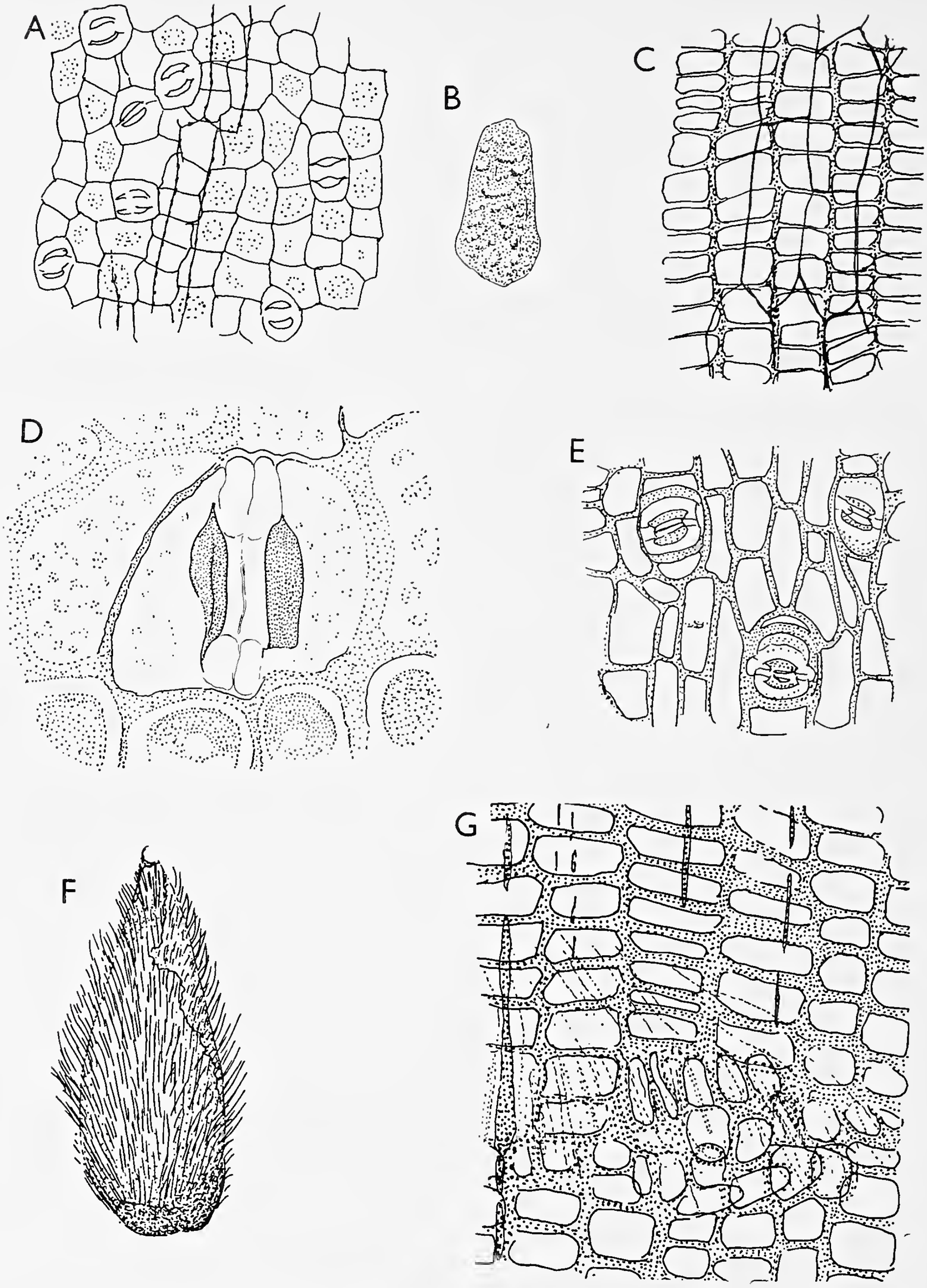

Fig. 54. **Cycadolepis pelecus** sp. nov. and **C. eriphous** Harris

A–D, *C. pelecus*. A, stomatal side, V.52882*a*, ×200. B, holotype specimen, V.52882, ×2. C, non-stomatal side, V.52882*a*, ×200. D, stoma, V.52882*a*, ×800. D is turned through 90°. E–G, *C. eriphous*. Holotype, V.30772. E, stomatal surface, ×200. F, specimen, ×1 (the ramenta are not all represented individually). G, non-stomatal surface showing half a ramentum base and traces of hypodermal cells, ×200.

Figs. E–G are from Harris (1953).

Though there are some points of agreement in cuticle these are in no way conclusive. If *O. falsus* were found with *C. pelecus* in a second locality the circumstantial evidence would become impressive.

The cuticles show disturbed areas which were considered as possible ramentum bases but instead they were regarded as produced in preservation, perhaps at the sides of the wrinkles. A few cells show a thin area in the middle of the papilla-like thickening and this was thought to be a cavity produced by a pyrites crystal and not original.

Cycadolepis eriphous Harris
Text-fig. 54 E–G

1953 *Cycadolepis eriphous* Harris, p. 41, text-fig. 3 A, B, E. (Figures and description repeated here.)

DIAGNOSIS. Scale leaf 6 cm. long by 2 cm. broad, shape lanceolate, broadest slightly below middle, base truncate, apex blunt, probably hooded, surface of scale strongly concave above, convex below. Substance very thick, not at all wrinkled; veins not shown. Both surfaces thickly covered with ramenta about 1 cm. long.

Cuticles very thick. One side, presumed to be from lower or convex side, especially thick; lacking stomata. Cells arranged in longitudinal rows; cells shorter than broad near the top of the scale. Cell walls straight, very thick, prominent (probably extending inwards to the base of the cell). Cell surface not papillose but sometimes showing a central thick area or else two or three thick areas connected to the side walls.

Upper cuticle showing cells in rows, but rows much broken by stomata; cells square or slightly elongated; cell walls straight, thick, well marked but less prominent than on the lower side. Cell surface not papillose. Stomata very numerous, evenly scattered, not forming rows. Stomatal apparatus superficial or only slightly sunken, never forming a distinct pit. Subsidiary cells small, outer wall usually very thick; surface not papillate. Guard cells rather small, orientated transversely.

Ramenta evenly scattered on the two surfaces of the scale. Base placed transversely, 100μ–400μ broad but only one (or two?) cells thick; free part 10 mm. long, gradually tapering, clothed in fine unicellular curled hairs.

The name refers to its resemblance to a kid's ear in its size, shape and hairs.

HOLOTYPE. V. 30772. Figured Harris (1953, text-fig. 3 A, B).

COMPARISON. *Cycadolepis* scales are often covered with hairs, but none of these hairy kinds happens to be broadly lanceolate like the present scale. The other hairy scales are mentioned under *C. thysanota*.

DISCUSSION. *C. eriphous* is associated with two species of *Otozamites* to which it might belong—*O. graphicus* abundant and *O. beani* occasional. I had suggested that it might belong to *O. graphicus*, but the finding of another scale (*C. thysanota*) with *O. graphicus* elsewhere now suggests that *O. beani* might however be the plant. There is no specific agreement in structure with either.

The two scales *C. eriphous* and *C. thysanota* have rather similar cuticles, and I am not at present willing to use the evidence of the association of hairy *Cycadolepis* cuticles with *O. beani* or *O. graphicus* in macerated coals.

In the hope of getting further evidence, residues of macerated shales in which *O. beani* or *O. graphicus* occur frequently were searched for associated *Cycadolepis* scales. Small *Cycadolepis* fragments were indeed found, but I did not feel sure enough of their identity to use them as evidence. It happens that *C. eriphous* and *C. thysanota* though of very different shape do have somewhat similar cuticles, and we know too little of the variation in either to be able to discriminate reliably.

Occurrence. The only specimen is from the Sycarham Series at Cloughton and was obtained from a fresh cliff fall that since has been unavailable.

Cycadolepis thysanota sp. nov.

Pl. 1, figs. 2, 3; Text-fig. 55

Diagnosis. Scale leaf narrow, wedge-shaped, length at least 3 cm. (base unknown), width 5 mm., tapering evenly to filiform apex. Substance thick, marked on both sides with transverse wrinkles and showing a few longitudinal ridges (? fibres). Both surfaces bearing ramenta but ramenta more strongly developed on one side (described as lower side). Ramenta up to 13 mm. long, spreading at sides at an angle of 45°, flexible, about 300μ wide at base but only about 70μ thick, tapering towards the point and becoming more delicate, smooth, not bearing any smaller hairs.

Cuticles of scale fairly thick on both sides but ramenta scarcely cutinised.

Cuticle of surface described as upper (adaxial) with few stomata. Epidermal cells broad, rather short, forming longitudinal fibres or packets. Anticlinal walls fairly prominent, broad, straight or with an occasional thickening extending towards centre of cell. Surface wall not papillate but showing a coarse or fine mottled sculpture. Ramentum bases occasional. Hypodermal cells present and their outlines shown in the cuticle, long and narrow.

Lower cuticle unevenly thick, showing numerous stomata. Epidermal cells as on upper side but cell outlines more prominent. Hypodermis not seen. Stomata orientated transversely, scattered (not forming files) but avoiding region of hair bases. Subsidiary cells exposed, as large as an ordinary epidermal cell, surface not thickened, not papillate, guard cells partly exposed, not papillate. Ramentum bases typically 400μ broad, 100μ high (about 20 cells broad, 3–5 cells high), but cells very obscure. Cells of ramentum base rounded, very heavily cutinised and their outlines hard to distinguish.

The specific name *thysanota* refers to the fringe of ramenta or hairs along the margins.

Holotype. V.53449.

Discussion. *C. thysanota* is represented by two very similar specimens, both incomplete below. One was in a fallen block of shaley sandstone at Whitby representing an unknown Lower Deltaic plant bed above the main plant bed and contained numerous leaves of *Otozamites graphicus* but no other determinable plants. The other specimen is in the main Whitby plant bed where many Bennettitalean leaves occur and a good many of these are of species to which no scale leaf is assigned. One of the commonest of these is *Otozamites graphicus*.

Finally there is a coaly shale which on maceration gave many cuticles agreeing with *Otozamites graphicus* and others agreeing with *C. thysanota*, but others had smaller ramentum bases and fewer stomata than the Whitby specimens. As already noted the cuticle of *C. thysanota* is rather like that of *C. eriphous*.

A few other Bennettitales occur in small numbers, in particular *Nilssoniopteris vittata* and a few fragments I could not identify. This shale is from Snilesworth, Stony Moor Sike, loc. 2 at 54° 22′ 8″ N, 1° 12′ 57″ W and probably belongs to the Middle Deltaic Gristhorpe Series.

This repeated association suggests, at least as a possibility, that *O. graphicus* and *C. thysanota* are organs of one plant, and that it would be worth looking out for further association. There is no structural agreement to support this idea.

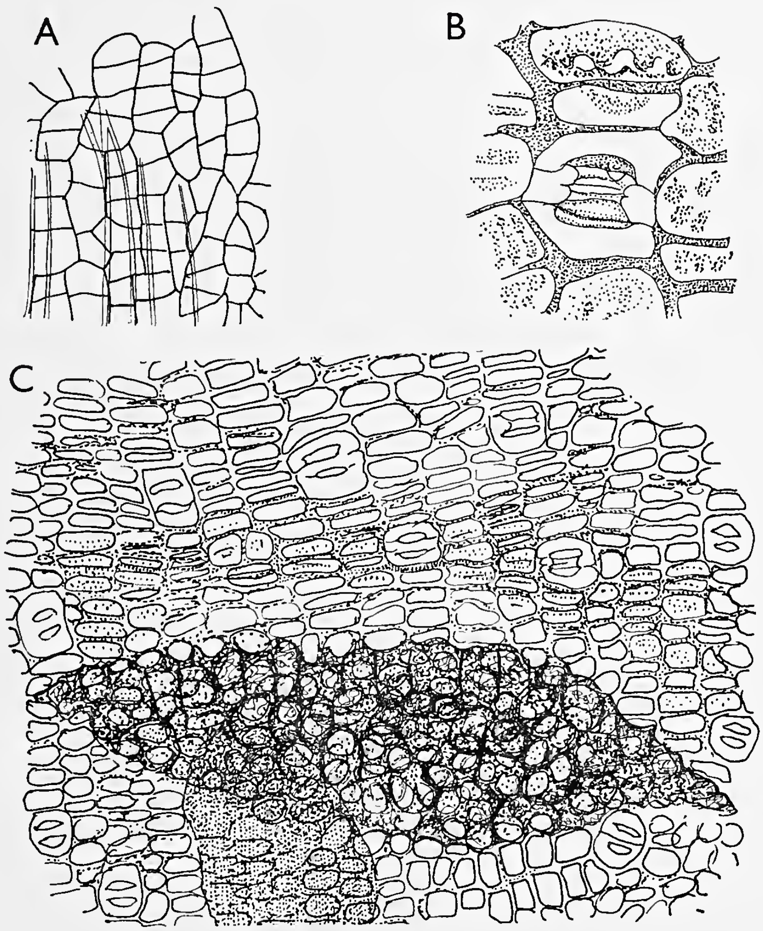

Fig. 55. **Cycadolepis thysanota** sp. nov.

A, cuticle and hypodermis of presumed adaxial side, ×200. B, stoma, ×500. C, cuticle of presumed abaxial side showing a ramentum scar. The dark body at the bottom is a mineral particle, ×200.
The figures are from the holotype specimen, V.53449*a*.

Comparison. The only other hairy scale leaves with Bennettitalean stomata described from Yorkshire are *C. eriphous* which is very much broader and the scale of *Williamsonia gigas* which is normally retained on the flower. The *Z. gigas* scale differs in being (probably) much larger, in shedding all its hairs at maturity and in details of cuticle. The scales round the flower of *Williamsoniella coronata* are smaller and their hairs finer and much less conspicuous.

Numerous hairy scale leaves have been described which are of about the same size and shape as *C. thysanota*. Of these, the following differ however in having a smooth (not wrinkled) surface: *C. villosa* and *C. hirta* Saporta 1875, *C. cf. villosa* Zeiller 1903, *C. pilosa* Feistmantel 1876, scale of *Williamsonia virginiensis* Fontaine 1889, *C. mexicana* Wieland 1914, *C. hoerensis* Johansson 1922 (=*problematicum* 1 & 2 Antevs 1919). I have little confidence in wrinkles as a specific character. We are ignorant of the cuticles of all these forms.

C. rugosus Johansson 1922 (wrongly renamed *C. johanssoni* by Harris 1932) agrees in shape and surface wrinkles as well. The Greenland specimens at least differ in cuticles for their stomata are longitudinally orientated. The hairs (ramenta) of the Greenland specimens appear to be thinner—one cell thick as against three or more in large ramenta of *C. thysanota*.

C. lanceolata Menéndez and *C. oblonga* Menéndez from the (?)Upper Jurassic or Lower Cretaceous of Argentina (Menéndez 1966) look rather similar, but their trichomes appear—from the scars on the cuticle—mainly to arise from single-celled bases although their length is considerable.

Bennettitalean Flowers

Genus WILLIAMSONIA Carruthers

1870 *Williamsonia* Carruthers, pp. 680, 691, in part.

Carruthers used the name *W. gigas* for all the organs he believed to belong to one plant species. Though his belief is here accepted, the name *Williamsonia* is now restricted to female flowers.

Emended Diagnosis. Bennettitalean female flower. Floral receptacle bearing scale leaves below, scale leaves numerous, free, undivided, crowded, overlapping. Upper part of receptacle elongated, bearing very numerous interseminal scales and small seeds, micropyles of seeds projecting slightly and surrounded by unspecialised interseminal scales.

Type Species. *Williamsonia gigas* Carruthers in part (female flower only).

Carruthers gave the name *Williamsonia* to the whole plant while Saporta (1891) restricted it to flowers, this was because he believed that the *Zamites* leaves belonged to a plant with a different flower. It was Nathorst (1909) who, while accepting the whole plant with *Zamites* leaves, used the name *Williamsonia* in its modern sense for flowers alone, and I here restrict it still further to the female flower for reasons given below.

Although the flowers we call *Williamsonia gigas* were recognised and described earlier than any other Bennettitalean flower, the name is rather late and there are earlier names for what may well be similar flowers.

'*Podocarya*' Buckland 1836 (made into a binomial *P. bucklandi* by Unger 1850—see Saporta 1886, p. 127, pl. 238, figs. 1–3; pl. 239, fig. 1) is an isolated Bennettitalean gynoecium. I reject it because there is no proof that the whole flower is organised as in *Williamsonia*. (The specimen is said to be lost.)

Blastolepis otozamitis Zigno 1867 is attached to the base of an *Otozamites* leaf and though probably a female flower was described as a bud. We have no details, but two other 'species' look like opened female flowers. Seward (1917) renamed them *Williamsonia otozamitis* (Zigno). We again have no certain information about its nature. Neither of these genera has been used for a long time.

Weltrichia mirabilis Braun 1849 (for figures and description see Saporta 1886, p. 191, Nathorst 1909, Schuster (in part) 1911). I regard this as the earliest name of what we have for long called male *Williamsonia* flowers. I consider that the name *Weltrichia* has clear priority and should be used for these flowers. Thus the name *Williamsonia* is in danger and the right way to save it is to restrict it to the female flower. This restriction to a single kind of organ is in accordance with usual modern practice. As it happens the female flowers were far more familiar than the male from the early days until the work of Nathorst (1909) and the name *Williamsonia* was thus more often used for them than for the male flowers.

Williamsonia gigas Carruthers (in part)
(Female flower and peduncle only)
Pl. 1, figs. 1, 6, 7; Text-fig. 56

1822 'Head of a plant', Young & Bird, p. 183, pl. 11, fig. 6. (Flower base, from Saltwick.)
1828 'Head of a plant', Young & Bird, pl. 1, figs. 1 (?), 7, 8. (Not fig. 2 which was refigured by Williamson (1870) as the 'carpellary disc' and by Nathorst (1911) as probably *W. whitbiensis*.)
1840 '*Zamia gigas* fruit', Williamson, pp. 223, 230.
1844 'Fruit of *Zamites lanceolata*', Mantell, p. 161, lign. 39.
1855 *Zamia gigas*, Yates, p. 37, text-figs. 1, 2. (Good restorations of plant and receptacle.)
1855 *Zamia gigas* L. & H.; Williamson, p. 46, text-figs. 3, 4. (Restorations showing terminal funnel.)
1870 *Zamia gigas* L. & H.; Williamson, in part, p. 663, pl. 52, figs. 3–6; pl. 53, figs. 3–13, ? 14, 15. (Not pl. 52, figs. 1, 2; pl. 53, fig. 1 the 'Carpellary disc'—see p. 126 in present work.)
1870 *Williamsonia gigas* (L. & H.) Carruthers, in part, p. 693. (Name.) *Williamsonia gigas* here refers to the whole plant (stem peduncle, leaf, both kinds of flower) and was intended to replace the name *Zamia gigas* L. & H.
1875 *Williamsonia gigas* (L. & H.); Phillips, in part, p. 224, pl. 24, figs. 1, 2, 4, 5. (Flower base and perianth.) (Not fig. 3 which is the 'carpellary disc'; not lign. 53—leaf and stem.)
1875 *Zamites gigas* (L. & H.) Saporta, p. 87, pl. 81, fig. 1. (The stem, leaf and peduncle figured later and better by Seward 1900 and by Wieland 1908.)
1877 'Cycadean fructification', Williamson letters dated 1832, 1833, *in* Lebour, pp. 129, 130.
1881 *Williamsonia gigas* (L. & H.); Nathorst, p. 37, pl. 7.
1883 *Williamsonia gigas* (L. & H.); Williamson, p. 3, text-figs. 1–4. (Redrawn restorations of plant and flower.)
1886 (1891) *Williamsonia gigas* (L. & H.); Saporta, in part, p. 132, pl. 239, fig. 2; pl. 240, figs. 1–3; pl. 241, fig. 1; pl. 242, figs. 1–3; pl. 243, figs. 1–4; pl. 244, figs. 1–4; pl. 235, figs. 1–3; pl. 236, figs. 1, 2, ? 4, 5, 6 (not fig. 3 which is the 'carpellary disc'). Not pl. 237, figs. 1, 2 (male flowers); not pl. 241, figs. 1, 2 (male flower ?). Fine series of female flowers and peduncles, long description.
1895 *Williamsonia gigas* (L. & H.); Seward, p. 146. (History and comparison with Wealden species.)
1897 *Williamsonia gigas* (L. & H.); Seward, p. 275. (Notes on specimens in Yates Collection, connection of flowers and leaves reaffirmed.)
1900 *Williamsonia gigas* (L. & H.); Seward, in part, p. 178. (Description of female flowers, but also figures of leaves, peduncles and male flower.)
1903 *Williamsonia gigas* (L. & H.); Lignier, pp. 19–56, text-figs. 1, 3, 4, 6–8. (Details of female flowers, restoration.)
1906 *Williamsonia gigas* (L. & H.); Wieland, p. 152, text-fig. 76. (Interpretation of female flower.)
1907 *Williamsonia gigas* (L. & H.); Lignier, pp. 3–13. (Re-interpretation of flower.)
1908 *Williamsonia gigas* (L. & H.); Wieland, p. 98, text-figure. (Outlined photo of Yates specimen in Paris.)
1909 *Williamsonia gigas* (L. & H.); Nathorst, p. 19, pl. 7, figs. 2–5 only (not fig. 1 which is *W. setosa*). (Details of gynoecium.)
1911 *Williamsonia gigas* (L. & H.); Wieland, p. 436, text-figs. 2, 3, 6–13. (Peduncles and aspects of flowers.)
1911 *Williamsonia pseudogigas* Schuster, p. 23, pl. 5, figs. 9, 10; text-fig. 9. Not pl. 4, fig. 12, which is one of Wieland's figures of *Cycadeoidea*.
1914 *Williamsonia gigas* (L. & H.); Wieland, p. 83, text-fig. 4. (Flowers from outside.)
1916 *Williamsonia gigas* (L. & H.); Wieland, pp. 175–204. (Reaffirms absence of terminal funnel but accepts some of Lignier's ideas.)

1917 *Williamsonia gigas* (L. & H.); Seward, pp. 419–434, text-figs. 541–548. (Good figures of corona.)
1933*b* *Williamsonia gigas* (L. & H.); Florin, p. 6, text-figs. 1*b*, 5*b*. (Stomata from bracts.)

References to the male flowers excluded from this list will be found on p. 163 under *Weltrichia sol.*

EMENDED DIAGNOSIS. Female flower or fruit persistent on its peduncle. Receptacle typically 5–6 cm. long, 2–3 cm. wide below reduced to 1 cm. above, then expanding slightly and continuing as the 'corona', a cone up to 1·5 cm. wide below and 1·5 cm. long, contracting to a point, just below the point forming a small flange. Surface of cone longitudinally striated. Interseminal scales and seeds normally shed at maturity except just below the corona. Perianth scales persistent, robust and thick, numerous, crowded, overlapping, all of similar length and texture, shape typically elongated, about 10 cm. × 1·3 cm., margins parallel over most of the length but tapering near apex; surfaces smooth, margins smooth in fruit but bearing marginal hairs 7 mm. long in flowering stage. Perianth scales growing at first outwards and forwards but then bending inwards to enclose whole gynoecium and receptacle, width of whole group 10–12 cm.

Micropyles in mature fruit projecting slightly about 180μ wide, interseminal scales about 500μ wide, well cutinised. At flowering stage interseminal scales with only central region exposed and cutinised.

LECTOTYPE. Specimen figured by Williamson (1870, pl. 5, fig. 4).

History of the female flower

The long history is often difficult to follow. Though specimens were numerous and impressive they were mostly imperfect and their organisation was so strange that many were unwilling to express their views in unambiguous words. The idea that the plant was a Cycad greatly confused the interpretation of the flower.

From the first the Yorkshire naturalists recognised that the flower and leaves belonged to the same plant, I suppose because they were strikingly associated and perhaps also because *Z. gigas* pinnae look rather like the scales on the flower and peduncle. Almost certainly they had no knowledge of Recent Cycad morphology to confuse them. Unfortunately they never stated their evidence in any clear way and most European authors (except Brongniart) were either unconvinced or else sure that the restoration of a plant bearing *Z. gigas* leaves and these flowers was wrong.

Young & Bird (1822) figured *W. gigas* leaves and *W. gigas* flowers (without names) as organs of one plant. They remarked that the flower was like an artichoke. In 1828 they added a male flower (now recognised as *Weltrichia whitbiensis*) and this was to be a source of great confusion.

In 1822 Williamson (who must then have been six years old) was taken by his father to Saltwick to collect the flowers. In 1832 and 1833 he wrote letters to Hutton about these flowers (printed in Lebour 1877), but he is hard to follow as he refers to drawings which are lost. He published accounts in 1837 and in 1855 giving restorations showing a funnel-shaped organ (that of Young & Bird 1828) surmounting the gynoecium, but Yates (1855) who collected by far the best material restored it without any funnel. I do not know how this idea of the terminal funnel originated. Williamson at first held that here *was* a terminal funnel, but in

1870 he abandoned the idea and stated clearly that no specimen had ever been seen that showed the presence of one and he restored it with none. He still, however, got the sexes of the two flowers wrong and called what we now know as the male flower the 'carpellary disc'. Certain later authors (Lignier, Seward) still held firmly to the ideal of the funnel even though they had the sexes right. Up till 1870 the whole plant had been called *Zamia gigas*, but in that year Carruthers gave it the new name *Williamsonia gigas*. This did not refer specially to the flowers (which he treated casually), but was a renaming of a whole plant that he realised was very different from *Zamia*. He gave the name in honour of the Williamsons, father and son.

Fig. 56. **Williamsonia gigas** (L. & H.)

Diagrammatic restoration of nearly mature fruit in L.S. The seeds are imaginary and both seeds and scales are too large, $\times 1$. (By permission of Phytomorphology.)

Saporta (1891) was the first to use the name *Williamsonia* for the flowers alone and he did this because he believed that they were borne on very different plants from the leaf *Z. gigas*. He made an advance by getting the sex of the female flower right and he saw the interseminal scales and seeds. Seward (1897) having studied the same specimens as Saporta (the Yates collection in Paris) convinced himself, however, that the leaves and flowers really did belong to the same plant because one specimen of a stem still bearing leaves also bore a scaly peduncle, while other slabs showed flowers attached to similar scaly peduncles. Since then no one has disputed this connection. Seward followed Carruthers in calling the whole plant including the separate leaves *Williamsonia gigas*, but Nathorst (1909, 1913) protested against this and was the first to restrict the generic names *Zamites* and *Williamsonia* to different organs of what he believed to be one plant and this practice is now usual, though still not always followed.

In 1900 Seward described additional female flowers and for the first time, I believe, figured a true male flower of *Z. gigas*. (I believe that the funnel-shaped organ which for a period was supposed to be a male *W. gigas* is an unusual specimen of *Weltrichia whitbiensis*—see Nathorst 1911). Seward was not however clear about the nature of the male flower. Despite its huge size (20 cm. in diameter) he still thought that it was borne on the top of the gynoecium. Lignier (1903, 1907) made progress with the structure of the gynoecium but gave a restoration of a funnel (male flower) on top of it. Nathorst (1909) prepared cuticles of *W. gigas* interseminal scales and a micropyle. He also studied the original specimen of the 'Carpellary disc' and recognised it as a male flower. He first called it *W. bituberculata* (Nathorst 1909) but later (1911) *W. whitbiensis*.

In 1917 Seward still held that the male flower surmounted the gynoecium, but he too recognised that no specimen shows an attached male flower. He explained away its absence by supposing that it was protandrous and fell off early. (Williamson and others had also pointed out no gynoecium shows an attached male flower.)

Thus what might seem the most difficult step—the recognition that the female flower belonged to the same plant as the *Z. gigas* leaf was made by the Yorkshire amateur naturalists very early, but progress in morphological understanding was slow, and what seems a gratuitous error—the addition of the funnel-shaped appendage was long persistent.

As we now have it (see restoration in Text-fig. 56) *W. gigas* is a simply organised flower and is similar to other flowers which we call female Williamsonias. This is fortunate for otherwise we might have to change still more names.

Description. Many collections of Yorkshire Jurassic plants made during last century include female flowers of *W. gigas* and in the British Museum (Natural History) there are about twenty. These are preserved as more or less hollow casts in ironstone or ironbound sandstone and though they give the size and shape they provide no details beyond what earlier authors published. None of these British Museum specimens is very well preserved and all are the remains of an old fruit from which the seeds and scales have been lost. Saporta however describes an intact gynoecium and one of Nathorst's specimens still has fragments of the seeds and scales preserved with cuticles.

There are no specimens of *W. gigas* in the Hamshaw Thomas Collection and I have only three compressions in shales and these would have been neglected by the early collectors. Two show the bases of female flowers end-on, that is scales radiating from a coaly mass. They are remains of ripe fruits without any seeds or interseminal scales and the scale-leaves are hairless. The other is immature, the only specimen of its kind. The gynoecium is of about half its normal size and though both interseminal scales and micropyles are seen (Pl. 1, fig. 1) they are very small. Their cuticles are extremely thin and the scales show merely what will later be the central boss. I found no pollen in my micropyle preparations. The perianth scales are of full length, and still very hairy and they already have fairly thick cuticles.

This specimen settles the suggestion of Seward (1917) that the young female flower might have borne a male flower terminally. This flower is young—the gynoecium only half grown, but it has no terminal male flower or scar suggesting one.

The scale-leaves of *W. gigas* surrounding the flower and on the peduncle look like leaflets of *Z. gigas* as earlier authors noted, but I think they have little in common beyond size and shape. They are of much thicker substance. The surfaces show longitudinal ridges or short longitudinal wrinkles but I think these are caused by fibres and not veins as none continues for more than a few mm. The true veins have not been observed. There are no transverse wrinkles on the *W. gigas* perianth scale. These scales are persistent and I have not recognised any detached ones.

The mature, hairless scale-leaf has rather thick cuticles but in the specimens studied they were not very satisfactorily preserved. One side (described as adaxial or upper) is also the thicker. It shows uniform, rather elongated cells in longitudinal rows. The anticlinal walls, especially the longitudinal ones, are very thick and tend to obscure details. No stomata or hair bases were seen. Robust sub-epidermal fibres are frequent. They occur singly and are about 100μ broad and of considerable length and are probably the cause of most of the surface ridges. A few broad parenchyma-like cells are also preserved.

The cuticle described as lower has numerous stomata. They nearly all have transversely orientated apertures and form short longitudinal files. Between files, or pairs of files there are strips without stomata and under the epidermis are traces of longitudinal fibres. The epidermal cells are short with thick straight walls giving a confused pattern. No clearly recognised papillae were seen. The stomata have small subsidiary cells. In some the whole apparatus is slightly sunken but as a rule it is superficial. A few stomata also show a round thickening which may represent subsidiary cell papillae but this is not certain. Hair (ramentum) scars are occasional. They are seen as a round or oval patch of thicker and even more confused cells than the normal ones.

OCCURRENCE. The female flowers I have collected are from three points in the Lower Deltaic; Saltwick Alum quarry near the Waterfall, Haiburn Wyke *Zamites* Bed and a fallen block in Jump Down Bight, Whitby. The classic localities of the ironstone casts are given as Runswick Bay, Saltwick and Hawsker (also all Lower Deltaic), but there is nothing more precise and the beds from which they were obtained are no longer known. So far as I can tell all the old Museum specimens may have been collected a century ago.

Williamsonia leckenbyi Nathorst

Pl. 2, figs. 3–9; Pl. 3, figs. 1, 6, 8; Text-figs. 57, 58 A–C

1870 *Williamsonia pecten* Carruthers, in part, p. 694. Reference to female flower only in Leckenby Collection (but called male); Leckenby's 'Reticulate structure with *Palaeozamia pecten*'.
1881 *Williamsonia Leckenbyi* Nathorst, p. 39, pl. 8, fig. 5 right.
1891 *Williamsonia Leckenbyi* Nathorst; Saporta, p. 161, pl. 248, fig. 1, 1a. (Female flower only; interseminal scales drawn too large.)
1900 *Williamsonia pecten* Carruthers; Seward, in part, p. 202, text-fig. 35 only.
1909 '*Williamsonia pecten* female flower (fruit)', Nathorst, p. 14, pl. 2, figs. 16–19; pl. 3, figs. 1–3 right, 10; text-fig. 3 (from Seward). Specimens in Sedgwick Museum, Cambridge.
1911 *Williamsonia leckenbyi* Nathorst, p. 21, pl. 6, figs. 1–10; text-fig. 5 (from Seward 1900); text-fig. 6 (restoration).
?1912 *Williamsonia leckenbyi* Nathorst; Krasser, p. 946, pl. 1, figs. 1–6. (Sardinia.)
1917 *Williamsonia leckenbyi* Nathorst; Seward, p. 439; text-fig. 553 only (from Nathorst).

A specimen from Whitby described by Nathorst (1909, pl. 3, figs. 4–9) as *W. leckenbyi* is excluded from this synonymy. It is considered to be *W. hildae*.

Emended Diagnosis. Gynoecium most commonly becoming detached from its peduncle and any surrounding bracts. Peduncle 6–7 mm. broad and about 7 mm. long. Gynoecium with basal scar 7–10 mm. wide in a depression. Lower part of gynoecium formed by coherent interseminal scales with somewhat elongated heads; after fall of seeds coherent scales curving back strongly to form 'palisade ring', upper surface (originally inner) of palisade ring coarsely striate, lower (outer) surface showing numerous scale heads but no micropyles. Gynoecium 40–50 mm. wide, probably somewhat elongated, pointed and with a small protrusion, the 'corona'. Just below top of gynoecium no ovules present and interseminal scales concrescent and persistent but short and position remaining unchanged after fall of seeds. Corona a truncated cone 2 mm. long × 2·4 mm. broad basally, sides showing about nine facets, apex hollowed out and funnel-shaped. Top surrounded by ring of minute points, interior of funnel with a few pointed projections. Denuded gynoecial axis (receptacle) usually under 10 mm. broad (possibly through shrivelling), surface rough with crowded scars; tissue spongy, mainly soft but including short thick-walled fibres. Interseminal scales of palisade ring with stalks about 10 mm. long, gradually enlarging to the head, stalks accompanied by filamentous hairs.

Cuticles of interseminal scale heads thick, strongly adherent with next scales along their inturned margins but cuticle quickly thinning below and absent from stalk. Scale heads polygonal, elongated towards a micropyle, diameter in full-sized gynoecium 0·5–0·6 mm., increasing to 0·75 mm. between two micropyles. Surface divided into an inner boss 250μ wide surrounded by a border 250μ wide. Boss hemispherical or with a flat apex, margins of boss with occasional stomata. Cells of boss isodiametric with thick, smooth lateral walls, and unornamented but bulging surface; cells of margin somewhat elongated, particularly in direction of a micropyle. In young gynoecium interseminal scale heads smaller, mainly composed of boss, margins concealed in inwardly directed flanges. Micropyles projecting up to 0·3 mm., about 0·15 mm. wide below but tapering slightly, surface cells of micropyle each with a hollow dome-shaped papilla.

Description. This account is based on a large number of specimens from Cloughton Wyke which form a series. This series includes forms just like those described by Nathorst, but also some which are outside the range of his. Almost all, however, yielded interseminal scale cuticles which agreed closely with one another and formed the main basis for determining all as a single species. Many match specimens which Nathorst first determined as *W. leckenbyi* but later as *W. pyramidalis*, but *W. pyramidalis* is here regarded as merely a form of preservation of *W. leckenbyi*. Nathorst indeed suggested that *W. pyramidalis* was bisexual, but I feel sure that the superposition of a gynoecium on a male flower was chance, for in parts of the *Solenites* Bed, flower fragments of both sexes are common and I have even seen two gynoecial fragments overlapping a male flower. The flowers are distributed at random.

No specimen shows the shape of the whole gynoecium perfectly. There are almost complete specimens in nearly vertical compression which merely show it as a round disc 40–50 mm. wide (Pl. 3, fig. 1) and there are a few more or less lateral compressions, but these have suffered distortion and pieces of armour with seeds have broken away from the main mass. The information suggests that the gynoecium is longer than broad, with a flattened base and a pointed apex (Pl. 3, fig. 8). Perhaps Nathorst realised its pointed shape when he distinguished *W. pyramidalis*. The base had been seen as for example a specimen figured by Seward, but the corona of the apex had been missed though it is shown in some of the early specimens.

Though most of the specimens are fragments, they are fragments of substantial size, none less than 1 sq. cm. A few gynoecia seem immature since their interseminal scales are very small, but even these are isolated and broken, like the mature ones. In whole gynoecia one face may show the basal scar, the other (if necessary exposed by picking away the coal) shows the corona. A few specimens show the axial core or receptacle of the gynoecium. A frequent form is an isolated sheet of gynoecial armour, just the brown coherent cuticles of interseminal scale heads, sometimes with micropyles still in position, sometimes with open holes where they have fallen out. Transfers show there is nothing behind this sheet of cuticle.

Many specimens show a compact mass of interseminal scales belonging to one or other end of the gynoecium, that at the bottom being the more conspicuous. This forms the 'palisade ring' and consists of firmly coherent scales but no seeds at all. One side of the palisade ring shows the laterally compressed interseminal scale stalks while the opposite face shows the heads of the interseminal scales (and yields their cuticles). In the old fruits which have shed their seeds the palisade ring is bent back, close to the peduncle. At the top of the gynoecium, the scales though similarly coherent remain in position and do not diverge in the old fruit.

Many transfer preparations were made but these showed very little, merely demonstrating that the other side of a structure under study was as had been supposed. It was possible to see some filamentous hairs among the interseminal scale stalks. Gynoecial fragments showed some rather unsatisfactory seeds but no isolated ones were found on the rock, nor in residue of the solution of rock in HF.

Macerations gave always the same result, excellent cuticles of interseminal scale heads and usually excellent though thinner cuticles of projecting micropyles but very little more.

Corona. The corona is interpreted as the sterile top of the gynoecium, consisting of an axial core and concrescent appendages which are more or less modified interseminal scales.

The corona of the specimen in Pl. 3, fig. 8 was macerated. Its cuticle was resistent, hard and at least 10μ thick. The cells are small and isodiametric with a strongly bulging surface and very broad lateral walls. A few small stomata occur, the whole apparatus is somewhat sunken. At the top of the corona where the cuticle is even thicker the cells are so convex that their height exceeds their width and they may form little prickles. In its less strongly thickened parts the cuticle a good deal resembles the central boss of an interseminal scale.

The gynoecium has normal structure with micropyles and interseminal scales up to 3 mm. below the corona, but then there are no more micropyles but there are a few normal-looking scales, though some of these are rather elongated. Then the facets of the corona begin and on the lower parts of the facets are a few low ridges which possibly represent ill-formed scales. The facets with their projecting points may be a further form of scale. Finally the little finger-like organs inside the apical hollow may well be the uppermost scales, they are much more convex than ordinary scales and their width is about half normal.

The cuticle structure of these finger-like organs and indeed other parts of the corona is consistent with the idea that its surface is formed of modified interseminal scales but is scarcely proof that that is their nature. Perhaps in some other species of *Williamsonia* a corona will be found which gives further guidance through its comparative morphology.

No biological function can be suggested for the corona. It might be that the perianth scales pressed against it in bud, at least at some stage, but what we know of the flower bud of *W. hildae* is against this idea. In any case such contact would seem to give no better protection than contact of the scales with one another. It recalls the apex of some Bromeliad inflorescences or the varied apical proliferations seen on the female cones of occasional conifers, particularly cultivated varieties of *Larix*, *Cryptomeria* where it is a genetically caused abnormality. In *W. leckenbyi* however it is constant and no doubt normal.

Whatever its morphological nature and its function, the corona is taxonomically useful for it provides specific characters, the best we know for separating *W. hildae* from *W. leckenbyi*.

Its presence is not a generic character for it is shared by *Williamsoniella*. Its existence was first recognised though with much confusion in *W. gigas* and first clearly recognised in *Williamsoniella* by Hamshaw Thomas. It has not been reported in other *Williamsonia* flowers, but as it had been missed in the long known and well studied *W. leckenbyi* I cannot be confident that it is absent in other species. It is not astonishing that it had been missed for it is small and all the specimens were rather imperfect fragments and therefore difficult to interpret.

Peduncle. The specimen in Pl. 2, fig. 4, shows a peduncle about 7 mm. long. No details are visible in the figure because cleavage has passed through the coaly substance, but when some of the coal was picked off the imprint of its under surface was exposed. This shows rhomboidal scars at about 1 mm. apart, just as in *W. hildae*. Since the base of this peduncle is nearly transverse (again as in the specimens of *W. hildae*) we may suppose that it is complete and was shed by abscission.

We have no specimen of *W. leckenbyi* to match the one of *W. hildae* still showing *Cycadolepis* scales on a peduncle, but we may assume they were attached in the same way to form a rather loose perianth. This perianth certainly did not enclose the ripe gynoecium, for the *C. nitens* scales are much too short (seldom exceeding 25 mm. and often much less than this). They could have enclosed it fully while it was still young and small, but when it expanded they could at best only overlap the base: very possibly they fell off early. The specimen is not good enough to provide an estimate of the number of scale scars.

Seed. No isolated seed has been seen. Certain fragments of gynoecia however have split to expose a longitudinal section through the seeds and scales, extending from the outer surface to the base where they were attached to the receptacle (now missing) – see Pl. 3, fig. 6. On this surface there are imprints which look like seeds. They are fusiform bodies 13 mm. long and about 0·5–0·7 mm. wide at 2–3 mm. from the outer end and then tapering to half or a third of this width at the base. Unfortunately there is no proof that these imprints really are seeds (for the micropyle was not seen), but if seeds they are then their shape is almost needle-like. We know from cuticle preparations that rather less than 1 mm. from its outer end the seed is round in section and its outer cuticle is 250μ wide.

When macerated most gynoecia gave excellent though delicate cuticles of the micropyles and a certain amount below the gynoecial armour. The seed cuticles become progressively more delicate when traced inwards and even the most favourable broke in preparation after a few tenths of one mm. We know nothing of the cuticles of the middle and basal parts of the seed.

The following cuticles were distinguished in the apical part.

1. Outer cuticle of integument forming the outside of the micropyle and sometimes

traceable for 250μ below the surface of the gynoecium. On the micropyle it is fairly robust and shows files of straight-walled cells each with a single bulge on its surface. At the top of the micropyle the cuticle changes; it becomes very thin and there is no longer any bulge on the cell surface. This thin cuticle then turns inwards as the cuticle of the micropylar canal and at the same time becomes rather more robust. Very commonly there is a break at the delicate region at the top of the micropyle, but in favourable specimens continuity is visible and the cells continue in the same longitudinal files.

Inside the fruit the integument cuticle continues but becomes more delicate and has always been broken and lost after a short distance. On the inner face of this cuticle there is a second set of cell outlines, of narrower cells. They are sometimes seen in the exposed part of the micropyle but more clearly in the part below the armour. They are never conspicuous and in the seeds of one fruit very inconspicuous indeed. They are described as hypodermal. Where there is a bulge on an integument cell, the hypodermal cells clearly pass beneath it and thus establishes that they are within and not outside the integument.

2. The cuticle lining the micropylar canal and continuing below as the inner cuticle of the integument. This membrane contracts strongly just below the mouth of the micropyle and while some of this contraction is no doubt original, there is also shrivelling resulting in folds; presumably this happened after pollination-time; and even in vertically compressed micropyles the canal is almost obliterated.

This cuticle shows longitudinal files of long, straight walled cells. At a level just beneath the interseminal scale armour the cuticle continues as the inner cuticle of the integument and expands somewhat but the cells do not change, in fact the same cell files continue. The inner (lining) cuticle of the integument only gradually becomes more delicate when traced inwards and in the longest specimens has been followed for about 0·4 mm. from the surface. In the inner parts the cells are broader and also shorter than above. As would be expected, the cell outlines project outwardly; in seeds from one fruit only slightly, but in another for 10μ.

3. Immediately below the micropyle there is another cuticle, regarded as the nucellus, which adheres inseparably to the integument lining; presumably as a result of compression, this being usual where there is no insulating material between two cuticles. The nucellar cells are rather broader, shorter and also tend to be more rounded than those lining the integument. Also while the outlines of the integument cells are firm and entire, those of the nucellus are often less definite and show minute ridges or points running on to the cell surface. The drawing (Text-fig. 57 A) is simplified. The specimen shows four cuticles, each with its own set of cells. At the top is the lining of the integument and immediately inside and adherent to it the cuticle of the nucellus. Then there is a minute gap representing dissolved matter and below there is the nucellus and finally the integument adherent to it. Only the two cuticles above the gap are drawn.

The seed cuticles are so delicate and minute that the number of fairly satisfactory specimens studied was rather small. A preparation from one fruit gave about eight good inner seed cuticles (micropylar canal and inner integument cuticle + nucellus); and another from a different fruit gave five and both gave many less satisfactory seed cuticles. Of the first eight, two possess several pollen grains at the top of the nucellus; the rest almost certainly have none. Of the five seeds of the other one has pollen, four none. The pollen grains are oval and about 15–20μ long but details are obscured by the seed cuticles.

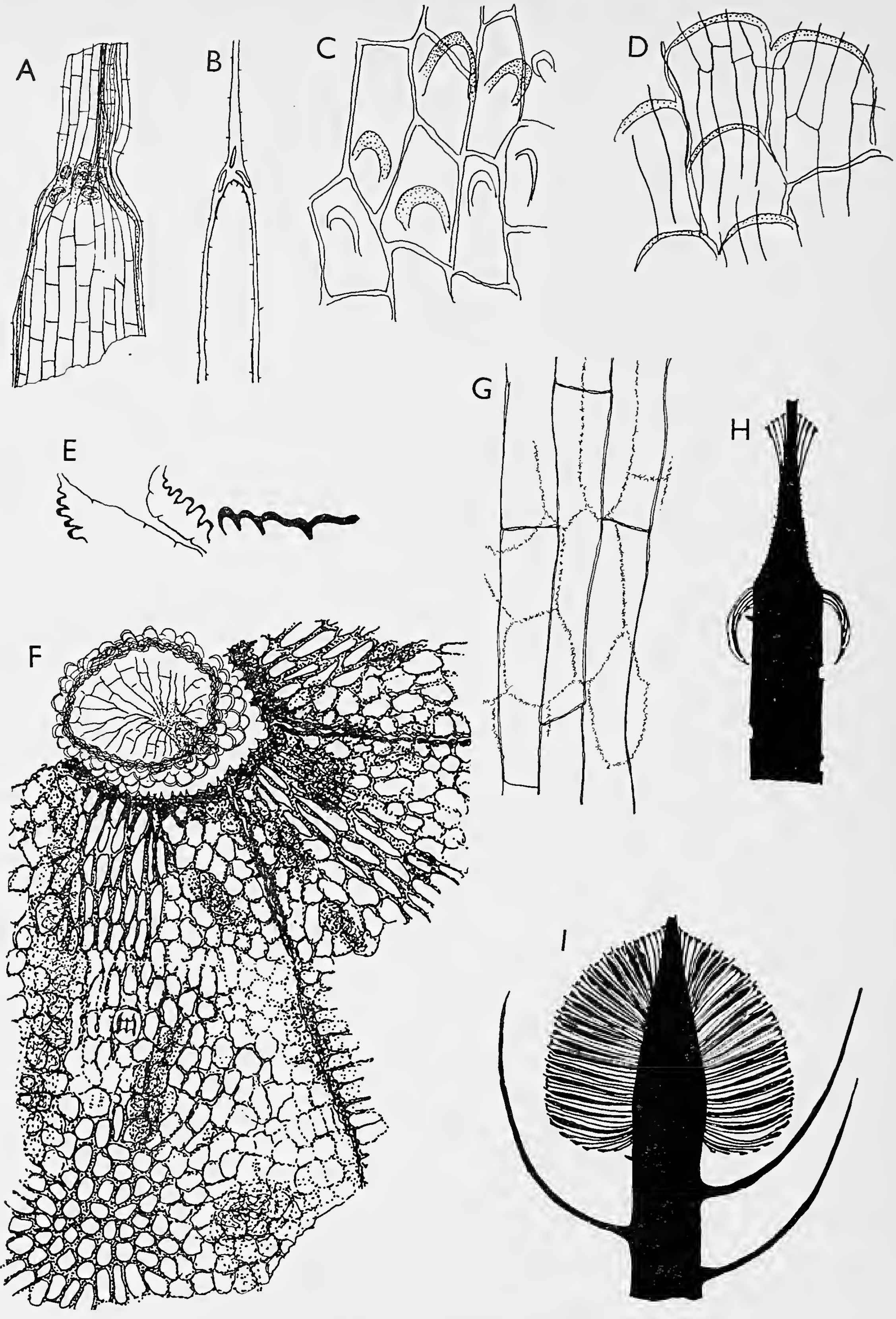

Fig. 57. **Williamsonia leckenbyi** Nathorst

A, micropylar canal and inner cuticle (lining) of integument. Uppermost cuticle (and pollen) alone drawn, V.52996*a*, ×200. B, imaginary L.S. of A showing all the cuticles. C, cells of outside of micropyle, V.52996*b*, ×800. D, cells of outer cuticle of integument and narrow hypodermal cells, V.52996*b*, ×800. E, imaginary section through micropyle and adjacent scales in F. F, three scale heads adjacent to a micropyle, V.52996*c*, ×200. G, inner cuticle of integument (firm cell outlines) and nucellus (broken outlines), V.52996*b*, ×800. H, diagrammatic restoration of old fruiting axis, palisade ring bent back, ×1. I, diagrammatic restoration of fruit just before the loss of the seeds. Both seeds and scales are too large, ×1.

It is noteworthy that there is no cuticle at all inside the nucellus. True, we have only the top of the nucellus and it is conceivable that a cutinised megaspore existed lower down, but my preparations which were made with care, should have revealed a cutinised megaspore membrane. I prefer to believe that the embryo sac (megaspore wall) was uncutinised.

It was astonishing that no ripe isolated seeds were found either lying on rock surfaces or in the products of maceration of the rock in bulk. To be sure, they must be small, but they should not be impossible to find for every gynoecium has hundreds of ovules and I must have seen a hundred gynoecia at Cloughton. Nathorst (1909, p. 15) suggested that the gynoecium was succulent, I concur and go further and imagine that the flesh with seeds was edible and that nearly all our specimens are fragments of the useless parts, rind or core left by some animal after its meal.

Though incompletely known, the seeds are interesting. We now know something about the cuticles of about ten Bennettitalean seeds in compressions (see Harris 1932, 1953) in addition to what we know of seed anatomy from petrifactions, but unfortunately knowledge from the two sources has not been related.

The various Bennettitalean seed compressions agree closely in their inner cutinised membranes. In none is there anything like the spongy, pitted, megaspore membrane of most gymnosperms, but the innermost cuticle is a compound membrane of the cuticle of the nucellus + the lining cuticle of the integument. In some species we do not know the seed base but in others this cuticle continues to the base leaving a minute chalazal gap. Round this is the cuticle of the outside of the integument continuing as the outside of the micropyle. The micropylar canal is lined by cuticle and in those suitably studied pollen is found at the base, immediately above the nucellus.

In many seeds this is apparently all, for the integument forms the outside of the seed, as far as we know. This group includes *Williamsonia leckenbyi*, *W. hildae* and *Williamsoniella* in the present work and the following from the Greenland Liasso-Rhaetic (Harris 1932) – *Wielandiella angustifolia*, *Bennetticarpus tylotus*, *B. oxylepidus* and *B. exiguus* (perhaps an immature form of the last). These *Bennetticarpus* species may prove to belong to *Williamsonia*.

The other group which so far has but three species all in the Greenland Rhaetic, has two species of *Vardekloeftia* and *Bennetticarpus crossospermus*. Here the integument is surrounded by a fairly thick tissue which has an external cuticle. We do not know how to regard this outer layer.

I have suggested (Harris 1954) that a good many seeds fall into two groups in respect of their cuticles. The one group includes Cycads, Conifers, Ginkgos and a number of fossils of these groups and also Mesozoic Pteridosperms. Here there is usually a robust cuticle round the outside of the integument, but inside the seed the integument is lined by a very delicate cuticle which ceases where it fuses with the nucellus. The nucellus may be well cutinised at its apex but its cuticle also becomes very delicate below. Then there is a robust cuticle of peculiar appearance, being densely pitted and this, the megaspore membrane, forms a complete sac.

The other group includes Caytoniales, Bennettitales and a considerable number of Angiosperms. Here the outside of the integument may be well cutinised or not, and its inside even though free from the nucellus is scarcely cutinised at all. The nucellus however often has a well developed cuticle extending from its apex to a minute chalazal gap, thus forming an almost complete sac round the endosperm. In some angiosperms the robust cuticle belongs not to the nucellus but to an inner integument, but the difference is not obvious in the mature seed. Thus in many seeds there is an almost complete inner cuticle almost enclosing the endosperm; it may be megaspore membrane, or nucellus or an inner integument. There is

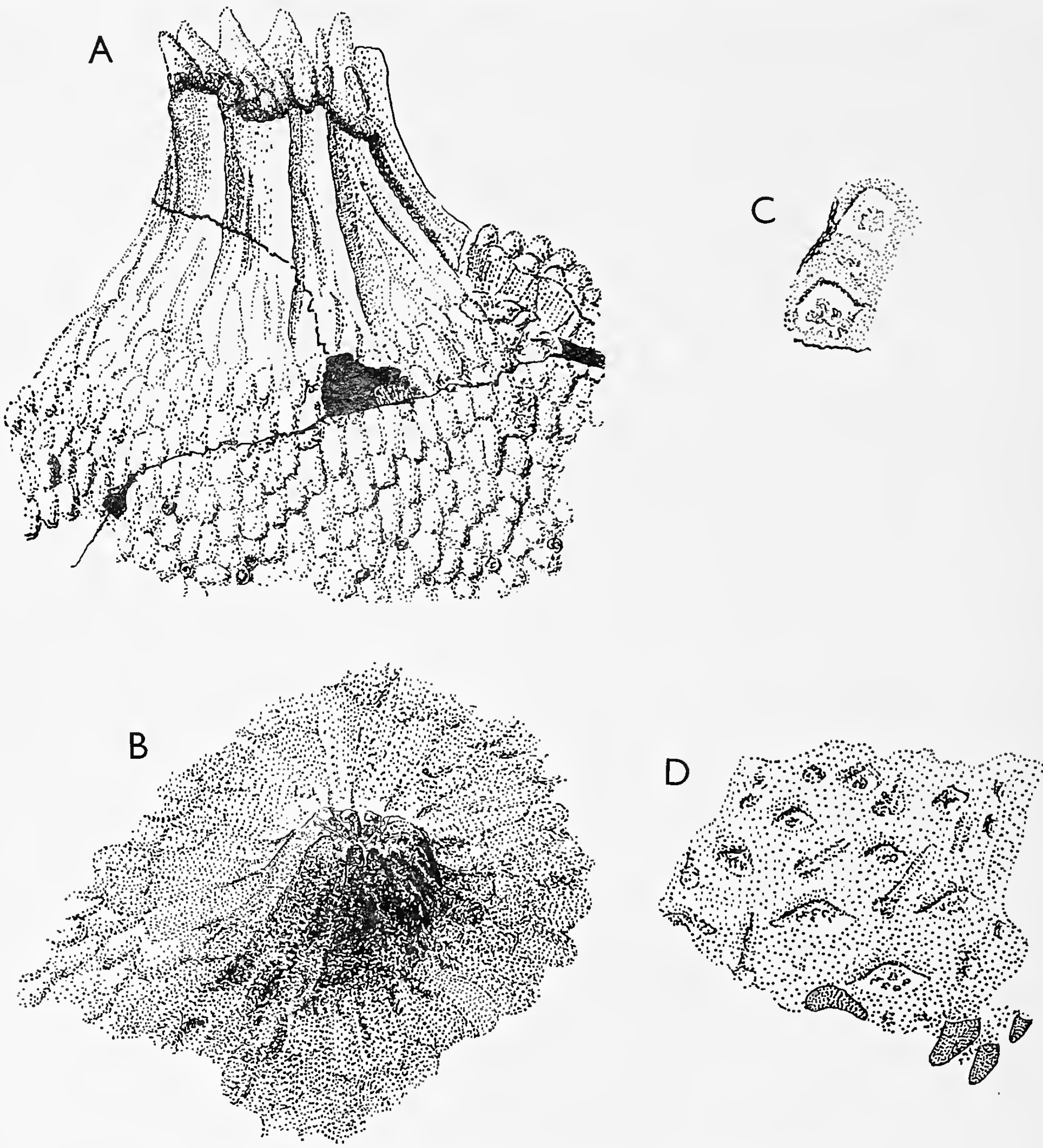

Fig. 58. **Williamsonia leckenbyi** Nathorst, **W. hildae** sp. nov.

A, corona of laterally compressed *W. leckenbyi* after further cleaning, from specimen in Pl. 2, fig. 9, V.52985, ×10. B, corona of nearly vertically compressed specimen, from specimen in Pl. 2, fig. 8, V.52979, ×10. C, *W. leckenbyi* perianth scale scars on peduncle of specimen in Pl. 2, fig. 4, exposed by picking away some of the coal, V.52992, ×4. D, *W. hildae*, drawing of specimen in Pl. 3, figs. 3, 4, showing scale scars and ramental imprints. The four small leaves at the base belong to a conifer shoot beneath this specimen, V.52977, ×4.

one membrane but in no seed I examined more than one and I suggested that this membrane might be physiologically important. The weakness of this generalisation is evident; it is based on far too few seeds studied, and an insufficiently intense study of even these few.

RESTORATION. The restoration represents nearly sessile female flowers attached to the smaller twigs but the male flowers are not shown at all. The terminal scars on these twigs might indeed have borne a male flower for they are large enough but if they were attached in this way, I imagine they fell off a good deal earlier than the female flowers.

Stem. As we have no specimen of an attached flower or leaf, the stem that bore *Williamsonia leckenbyi*, *Weltrichia pecten* and *Ptilophyllum pecten* is unknown. Nevertheless the remarkable stem (p. 173) described as *Bucklandia pustulosa* is here attributed to the same plant, and since the corresponding stem of *W. hildae*, *Weltrichia whitbiensis* and *P. pectinoides* is indistinguishable from *B. pustulosa* what amounts to the same stem is attributed to that series of organs also.

On the assumption that *B. pustulosa* does belong to our plant, the consequence is startling, for *B. pustulosa* must be a large tree with fairly slender leafy and fruiting twigs. It is true that similar twigs were known for the Bennettitales, those of *Wielandiella* (Nathorst 1888, 1909) and *Williamsoniella* (Thomas 1915) have been long accepted though un-Cycadean. There was (and is) nothing to suggest that either was a great tree but rather they were considered as shrubs, I suppose on the assumption that what was known fairly represented the plant. However, the great slabs of bark of *B. pustulosa* clearly come from large logs. This is used for the restoration in Text-fig. 59. Here I have assumed that the tree produces branches of gradually reduced size as is usual, but I admit other forms remain possible.

We know from Indian work (see Bose 1953) that certain species of *Ptilophyllum* were borne on *Bucklandia* stems. One of these, *B. indica*, differs considerably from the shoots of *B. pustulosa* for it is two or three times thicker and has more crowded leaves and it does approach a Cycad form. Other Indian Bucklandias are more slender and thus like *B. pustulosa* though we have no suggestion of massive main branches or trunks, nor of course any evidence against them. Even if it had a massive trunk, *B. indica* could not have looked like an ordinary tree for its leafy shoots were too thick. If then I am right in attributing the series of stems called *B. pustulosa* to our Yorkshire plants it follows that leaves of the genus *Ptilophyllum* were borne on plants of a rather wide range of form.

Such a tree as the one imagined for *B. pustulosa*, *P. pecten* and the flowers could have been an ordinary forest dominant. If indeed most Yorkshire Bennettitales were trees then our picture of the landscape would look very different from the restorations that have become conventional. Indeed these restorations seem to me inherently unlikely for along with much water we have on the low-lying land the strange mixture of forest trees (Conifers and Ginkgos) and open Savannah with separate-standing Cycads. The ferns give no trouble for they could be placed under the trees and the Equisetales in shallow water as reeds, but the Cycad-like Bennettitales looked out of place. However if the Bennettitales were tall trees and part of a mixed forest they could fit in. Then the only vegetation which would be partly open would be on river banks.

Williamsonia hildae sp. nov.

Pl. 2, figs. 1, 2; Pl. 3, figs. 2–5, 7, 9–11; Pl. 4, fig. 1; Text-fig. 58 D

1909 *Williamsonia pecten* 'female flower (fruit)' Nathorst, in part, pl. 3, figs. 4–9 only (specimen from Whitby) and discussion of this specimen on p. 14 *et seq.*

?1912 *Williamsonia leckenbyi*, Krasser, p. 946, pl. 1, figs. 1–6. Middle Jurassic; Sardinia, see p. 139.

1917 *Williamsonia leckenbyi*, Seward, in part, fig. 554 (from Nathorst, pl. 3, fig. 6).

DIAGNOSIS. Bennettitalean female flower; details as in *W. leckenbyi* except for points noted below.

Top of peduncle 10–12 mm. thick, 10 mm. long, showing rhomboidal scars of bracts in alternating whorls. Axis (core) of gynoecium slightly over 10 mm. thick; apical corona a truncated cone about 4 mm. wide below, and 3 mm. wide above, top flat. Sides formed by about 15 flat facets, angles between facets projecting upwards as small points around the flat top.

HOLOTYPE. V.52976.

DESCRIPTION. The specimens are very similar to those of *W. leckenbyi* but a few fall outside the range. In particular there are two from Hasty Bank which include the moderately well preserved top of the peduncle. These are particularly valuable in showing the scars of the perianth scales, which are easier to see on the imprint on the matrix than on the fossil itself. In addition to the perianth scale scars there are small persistent organs which are described as ramenta, and one ramentum occurs just above each scale scar. The scale scars are largest near the base and grow steadily smaller toward the gynoecium.

The scale scars are arranged in alternating whorls or, to put it in other words, in vertical ranks: oblique parastichies are also obvious. Each whorl shows about three members across the face making perhaps six or eight on the whole peduncle and I estimate the total number at about 18–24. Each vertical rank shows two or three, but perhaps those with two are incomplete. The scars are raised (in the fossil) and of broadly rhomboidal shape. The middle part shows about five or six small tubercles – presumably vascular bundles.

The ramenta are perhaps all strictly in the vertical perianth scale ranks and half way between one scale and the next, but there are a few irregularities in the fossil which must be discounted to make this rule hold. Each consists of a prominent base about 1 mm. wide and a free part pointing more or less upward and 2 mm. long and 0·6 mm. wide. There is a groove along the middle and the rather thick substance as far as it can be seen is a crumbly coal with no sign of cuticle.

The two kinds of organ leave most of the peduncle surface, about three-quarters, smooth and unoccupied. This is strikingly different from the base of the floral receptacle of, say, a *Magnolia* flower or fruit where the perianth scale scars are as close as can be without being continuous. In fact the scales on the peduncle, considered as a perianth, are remarkably loosely placed and perhaps more like a scale covered peduncle of some angiosperm (e.g. species of *Protea*) than any normal perianth.

It seems unlikely that the scales could have covered the ripe gynoecium which appears to have been rather larger than in *W. leckenbyi* where its length was at least 4 cm. The scale *C. hypene* is typically 25 mm. long and the longest is only 36 mm. In any case I think it likely that the scales fell off early, well before the gynoecium was full grown.

Buds. At a late stage in the investigation, in fact when unpromising specimens were being broken up and thrown away, two remarkable immature flowers came to light. They were inconspicuous objects until excavated.

The first specimen is from Hasty Bank where mature flowers and fragments of flowers are frequent. The isolated bud shown in Pl. 3, figs. 10, 11 consists of an axis nearly 7 mm. wide bearing numerous, overlapping *Cycadolepis hypene* scales. Their length, about 25 mm., is normal, but their substance is less thick than usual but this may be merely due to poor preservation. Their cuticles are normal. The axis shows small rhomboidal scars which are close together, both their size and the distance between them is less than on the mature peduncle.

At first nothing was seen of the structure enclosed but when some of the scales were picked away a crumbly mass of coal was exposed, and when this too was picked away to expose the imprint of its lower surface it was seen to be a minute rounded gynoecium about 7 mm. wide. Its coaly substance is thick below but rather thinner above and its general shape is convex with a convex dome of matrix pressing into it. I assume that this shape was caused by collapse in compression, the fossil being originally the other way up.

The gynoecium is covered with little bulges about 100–150μ wide which look like interseminal scales and among them are tiny cups which look like micropyles. Unfortunately crumbs of the gynoecium substance when macerated (with considerable care) gave no recognisable cuticles. The corona was not recognised but a small mass of smooth coal at the top of the gynoecium may be this. If so it has no special relation with the bracts which extend far beyond it.

The second specimen which appears to be rather younger, was found in a sandstone at the foot of Beast Cliff, at Rocky point, which yielded plenty of *Ptilophyllum pectinoides* but nothing else determinable. The bud is composed of closely overlapping *Cycadolepis hypene* scales. The lower scales are distinctly smaller and shorter than the upper ones. Unfortunately the top of the specimen was lost when collected. No attempt to macerate out interseminal scales was made as it was thought unlikely that they would be adequately cutinised.

The bud is at the top of a stem nearly 1 cm. wide at its base but only 7 mm. just below the bud. On the right is seen a slender appendage which is a *Ptilophyllum pectinoides* petiole and rachis. It has lost nearly all its pinnae but near the top there are some poorly preserved pinnae which however show their character under the microscope. On the left are two similar appendages which are broken short and are also regarded as leaf petioles. It is interesting that the top one arises just below the flower bud.

There is a scar on the stem surface where another petiole may have been borne but leaves are certainly not numerous. There are no crowded rhomboidal scars below the flower such as are seen on the peduncles of old flowers, and I feel sure that this is because the involucral bracts are still all attached and the rhomboidal scars of denuded peduncles belong to *Cycadolepis* scales exclusively.

The stem itself shows a number of coarse but ill defined longitudinal ribs and probably small and isodiametric surface cells, though these are poorly preserved in the rather coarse matrix. Still the stem does agree as far as its characters go with the more slender forms of *Bucklandia pustulosa*. It seems to be partly impregnated with some mineral and where broken shows a densely fibrous rind and a compact inner tissue, presumably xylem.

These specimens are of value in several ways. They prove that *Ptilophyllum pectinoides* and *Cycadolepis hypene* are borne on one plant and that *C. hypene* envelopes the female flower, this being doubtless *Williamsonia hildae* though this is not yet proved. We also know that the young stem is like the slender forms of *Bucklandia pustulosa*. The second specimen shows a good deal about the general organisation of the shoot and gives weight to the restoration (Text-fig. 59C).

The present bud is of value in proving that *C. hypene* really is borne on the peduncle of

W. hildae (previously this was a hypothesis). Its interest might be greatly enhanced had a series of rather older buds been available for the little gynoecium in this is too small and ill preserved for detailed study.

There is a remarkable block from Marske bearing R. Kidston's name which shows two

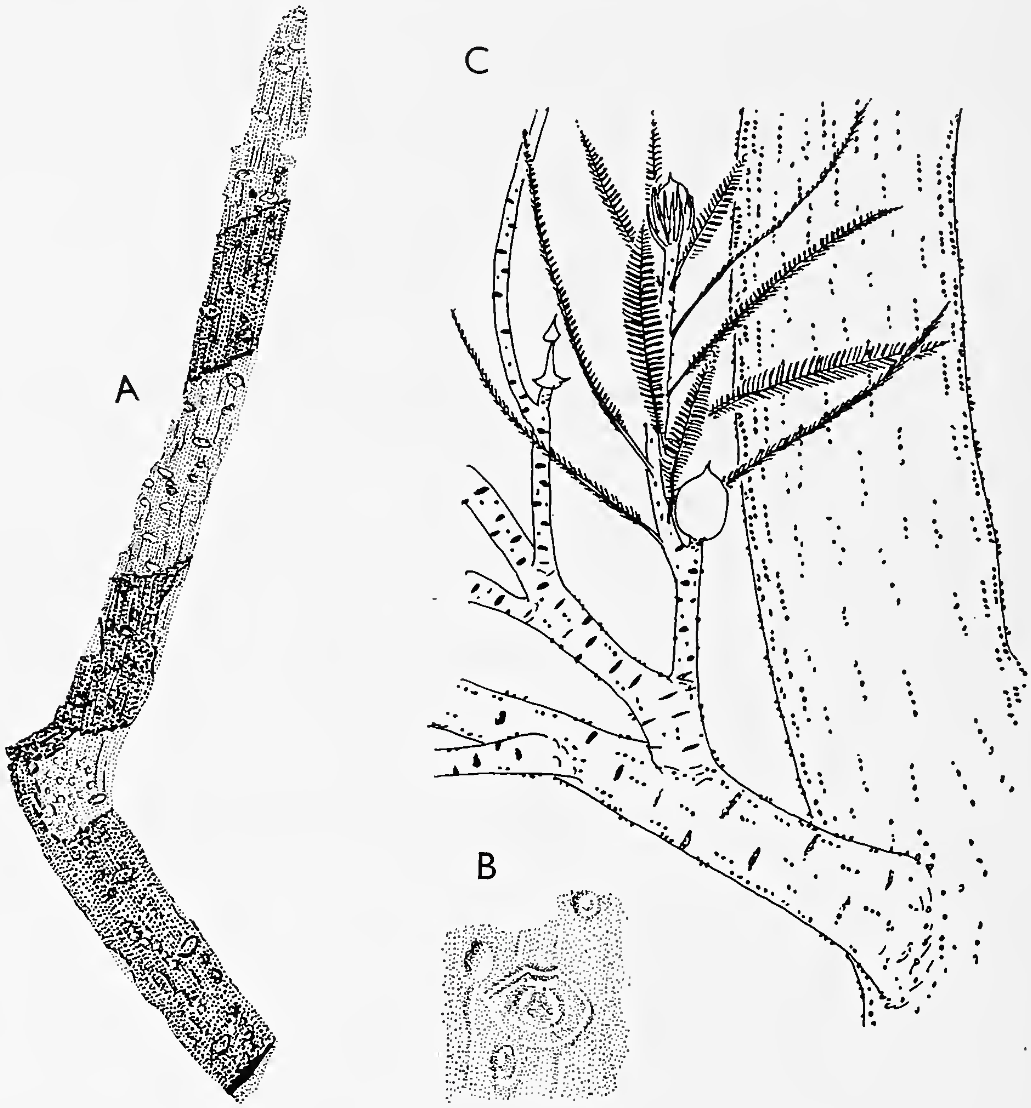

Fig. 59

A, *Bucklandia pustulosa* sp. nov. Holotype. The stem shows leaf scars, a flower ? scar, lenticels and ridges, V.53464, ×1. B, the clearest of the leaf scars and three lenticels, ×4. C, restoration of the plant composed of various sized *Bucklandia pustulosa* axes, *Williamsonia leckenbyi* and *Ptilophyllum pecten*. Reduced to one-quarter natural size.

flowers side by side as casts, one inverted in relation to the other. Thus, with part and counterpart, each shows its base and apex. I do not explain their strange position. The substance of these flowers has vanished. The interseminal scales of every specimen (except Kidston's) were prepared. They looked alike, and like those of *W. leckenbyi*.

The name *hildae* refers to St. Hilda of Whitby Abbey, to whom is attributed the origin of Ammonites (snake stones) by casting vipers over the Abbey cliff. *W. hildae* also occurs below Whitby Abbey.

DISCUSSION. Most of the specimens of *W. hildae* are Lower Deltaic fragments which show nothing that distinguishes them from similar Middle Deltaic fragments of *W. leckenbyi*. They are identified merely because of their locality, and among these fragments is Nathorst's original Whitby specimen. There are, however, a few good specimens from the same Lower Deltaic localities (Whitby, Marske, Roseberry Topping, Hasty Bank) which do show the distinctive corona and other characters. *W. hildae* and *W. leckenbyi* have not been found together and this is not surprising as the associated leaves of *P. pectinoides* and *P. pecten* are not normally found together.

In every locality where *W. hildae* is found, *P. pectinoides* is abundant and is usually seen on the very specimen with a flower. In some of the localities several other leaf species do occur but none that shows marked or repeated association. While this repeated association powerfully suggests that these two organs belong to one plant, there is no supporting anatomical evidence, nor is it obvious how it might be obtained.

For comparison and morphological discussion see *W. leckenbyi*.

The specimens from Sardinia described by Krasser (1912) as *Williamsonia leckenbyi* are equally like the present species, but as the associated leaf though called *Ptilophyllum pecten* is like *P. pectinoides* it is more likely the flowers are *W. hildae*. None of Krasser's figures shows the corona.

OCCURRENCE.

Whitby plant bed, at the foot of Abbey cliff (and in fallen blocks probably from the upper part of this bed).

Marske Quarry; in sandstone (R. Kidston) and in clay (Hamshaw Thomas).

Roseberry Topping (Hamshaw Thomas).

Hasty Bank – frequent, but in a fragile shale.

All the above localities are near the base of the Lower Deltaic.

Williamsonia himas Harris
Text-fig. 60

1953 *Williamsonia himas* Harris, p. 43, text-figs. 4, 5 A–C. (Figures and description repeated here.)

DIAGNOSIS. Female flower. Perianth scales about 12, persistent, 5–6 cm. long, 6–8 mm. wide, strap-shaped but somewhat narrowed near the base, apex obtuse, inner surface only slightly concave; substance thick, both sides showing 10–12 parallel veins; surface without wrinkles except near the base, ramenta occasional but inconspicuous, surfaces appearing polished.

Cuticles fairly thick, tough and easily prepared. One side (presumed to be upper) with very few stomata; showing longitudinal rows of nearly uniform roughly square cells. Walls straight, not very broad, very sharply marked by fine longitudinal ridges. Trichome bases occasional, some unicellular, others up to 5 cells broad, consisting of rings situated on the surface of ordinary or slightly thickened cells. Base of free part cutinised, upper part in larger

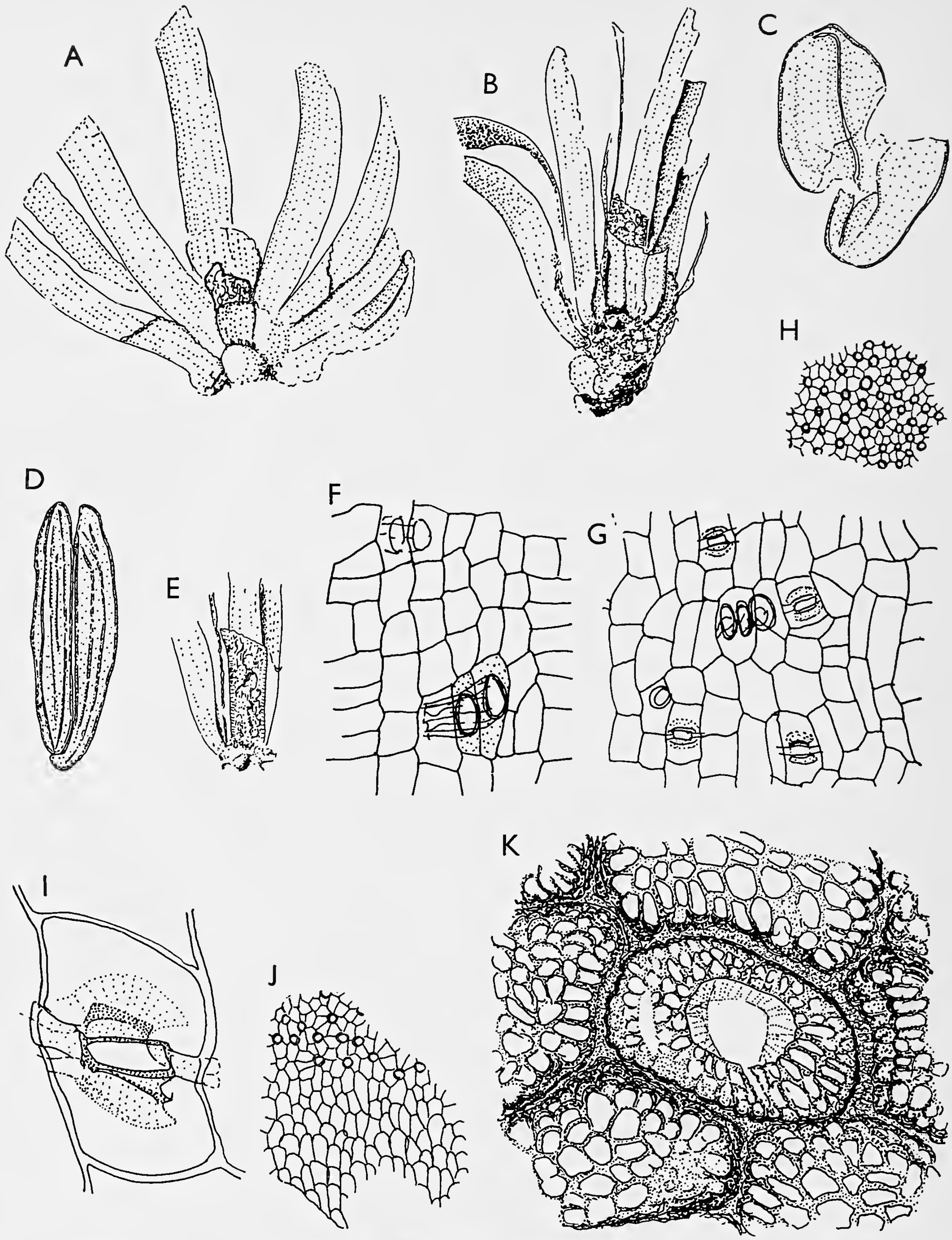

Fig. 60. **Williamsonia himas** Harris

A, Whitby Museum specimen showing bracts and impression of gynoecium, ×1. B–K, holotype, Leeds City Museum. B, showing axis, bracts and some of gynoecium, ×1. C, D, pollen grains adhering to holotype, ×800. E, gynoecium after overlying bracts have been removed, ×1. F, non-stomatal side of bract. G, stomatal side of bract, ×200. H, fragment of gynoecial armour, ×10. I, stoma of bract, ×800. J, fragment of gynoecial armour (near base), ×10. K, micropyle surrounded by interseminal scales, ×200.

All the figures are from Harris (1953).

ones forming a flat ramentum about 5 mm. long and 0·3 mm. broad, smaller ones hair-like. Stomata absent in some parts, present in numbers of about 1 per sq. mm. in others, details as on lower side. Other side (presumed to be lower) showing numerous or very numerous stomata. Epidermal cells of rather irregular shape, cell rows not obvious. Stomata scattered, not forming rows but all transversely orientated. Epidermal cell outlines very strongly marked, sides straight, surface-wall flat, not papillate. Subsidiary cells fairly large, forming an oval group, not at all sunken. Inner cutinised wall of guard cells (not the aperture) well cutinised, outer wall (shared with subsidiary cell) very feebly cutinised, forming a striated, faintly visible crescent. Trichome bases occasional, usually 2-celled.

Gynoecium forming a cylinder 6 mm. wide, at least 2 cm. long (apex not seen). Surface formed by minute interseminal scales about 0·3 mm. broad and numerous seed micropyles. Surface of interseminal scales almost flat, surface of micropyle scarcely projecting at all. Interseminal scales well cutinised, cuticle extending a short distance inwards along margins, cells of head thick-walled, surface bulging as a dome but not papillose, cuticle often growing thinner towards the middle of the cell. Stomata rare, where present occurring at about the middle of the head. Micropyles of seeds round, well cutinised, lining of micropylar canal 70μ wide. (Inner parts of interseminal scales and seeds not observed.)

Associated pollen grains oval, averaging $50\mu \times 30\mu$, monosulcate, often split longitudinally, wall fairly thick, almost smooth.

Holotype. Leeds City Museum Collection, No. 9. Figured Harris (1953, text-figs. 4 B–H, 5 A–C).

Discussion. The holotype is fairly well preserved in fine grained clay ironstone. The other specimen in the Whitby Museum is in a grey shale and must have been well preserved but has deteriorated. The substance of the gynoecium has been lost and the whole surface has been obscured with varnish. Still the bracts gave satisfactory cuticles. Neither is localised. The holotype is in matrix of a kind frequent in the Lower Deltaic but not above; the Whitby specimen matrix is widespread.

The Whitby specimen has no associates but the holotype has a large number of adherent pollen grains, almost all looking alike. These are like grains which have been figured (e.g. by Nathorst) from Bennettitalean male flowers and many are characteristically split with each half curled up (Text-fig 60 D). In addition there is a single leaf of *Otozamites beani*. This association is worth bearing in mind but of course we do not know whether other Bennettitalean leaves occurred with it also.

Comparison. The very narrow gynoecium of *W. himas* is remarkable, but we must remember the possibility that the specimens may be incompletely grown and abortive. The bracts are persistent, as in *W. gigas* but not as in some other species. Their cuticles are sufficiently characteristic to be distinguished from all other Yorkshire species.

Genus WILLIAMSONIELLA Thomas 1915, p. 115

Diagnosis. Flower pedunculate, hermaphrodite. Floral axis elongated, at base bearing involucral bracts, then microsporophylls, then seeds and interseminal scales, and at its summit projecting as a corona. Involucral bracts lanceolate, simple, overlapping, crowded. Androecium a whorl of about 12 free microsporophylls, microsporophylls wedge-shaped, laterally compressed, bearing on adaxial face usually two or three pairs of short fertile branches, each branch bearing a two-valved pollen capsule; all parts compacted to give a simple outline to microsporophyll. Pollen grains oval, sulcate. Gynoecium pyriform, axis bearing very numerous minute interseminal scales and ovules. Ovules fusiform, sessile, micropyle prominent; integument thinly cutinised, enclosing a delicate cutinised sac (? largely free nucellus). Corona truncate, with lateral facets.

TYPE SPECIES. *Williamsoniella coronata* Thomas.

DISCUSSION. *Williamsoniella* is one of the more completely known Bennettitalean flowers. I accept Thomas' restoration of the fruiting branch bearing *Nilssoniopteris* leaves; but there is nothing to suggest whether it belongs to a shrub or a tree.

The microsporophylls are less peculiar than was once thought, for they can be interpreted as pinnately branched in the ordinary way, though the branching is condensed.

Thomas described *Williamsoniella coronata* carefully but gave no diagnosis. Subsequent work has only altered the description slightly and has added a few details. Thomas included two further species in the genus, *W. roseberriensis* and *W. lignieri* (Nathorst) Thomas. These are certainly Bennettitalean flowers and I suspect one or both may be a state of preservation of *W. coronata*, but neither is adequately characterised as a species or indeed proved to be organised in the same way as *W. coronata*.

Williamsoniella ferganensis Brick (refigured by Vachrameev & others 1963) is much larger than either *W. coronata* or *W. papillosa*. The figure available does not make it possible for me to compare it more closely. Several other species described by Brick (1963) merely agree in being small round flowers but have not been proved to possess the characters of *Williamsoniella* as defined here. However, she was merely following Thomas who included two species not proved to agree with *W. coronata*. I consider that the name should be restricted to fossils where we have positive evidence of agreement in essential characters, and not merely in general aspect.

The fossil called *Itieria Brongniarti* Saporta 1873 from the Kimmeridgian of France and described as an alga raises a different problem, for its figure looks remarkably like Thomas' restoration of *Williamsoniella coronata*. It may indeed be the earlier name of the same species. However until more is learnt about *Itieria* I leave *Williamsoniella* undisturbed.

Authors have from time to time used the name *Williamsoniella* for the isolated leaf *N. vittata*, but the objections to this practice were made clearly by Nathorst in 1913.

Williamsoniella coronata Thomas

Pl. 4, figs. 3, 4, 7–9, 12, 13; Text-figs. 61, 62

All of the following except Saporta (1873) refer to Yorkshire specimens:

?1873 *Itieria Brongniartii* Saporta, p. 122, pl. 4.
?1909 *Williamsonia lignieri* Nathorst, p. 20, pl. 4. See p. 144.
1915 *Williamsoniella coronata* Thomas, p. 115, text-figs. 1–5; pl. 12, figs. 1–3, 5–10; pl. 13; pl. 14, figs. 22–28, **29**. (Other figures are leaves and stems of the same plant.)
?1915 *Williamsoniella roseberriensis* Thomas, pl. 12, fig. 4; pl. 14, fig. 21. (Involucral bracts, possibly of this species.) See p. 144.
?1915 *Williamsoniella lignieri* (Nathorst) Thomas, p. 134. See p. 144.
1933 *Williamsoniella coronata* Thomas; Zimmermann, p. 322, text-figs. 1–3h, i. (Leafy shoot and flowers.) See p. 146.

1944 *Williamsoniella coronata* Thomas; Harris, p. 313, text-figs. 1–6; pl. 25, 26. (Revision and additional details.)
1958 *Williamsoniella coronata* Thomas; Couper, p. 127, pl. 26, fig. 2. (Pollen grains.)

DIAGNOSIS. Mature flower about 2 cm. long, gynoecium 1 cm. wide in lower part, corona typically 2–3 mm. long, 3 mm. wide, cylindrical. Microsporophylls 1·0–1·5 cm. long, substance thick, narrow base rather short. Surface of cells of micropyle nearly flat.

HOLOTYPE. V.19151. Figured Thomas (1915, pl. 12, figs. 1, 5).

DESCRIPTION. This account is condensed from Thomas (1915) and Harris (1944). Nearly all the material is from the Gristhorpe Bed which has yielded perhaps twenty gynoecia still with some of the bracts or microsporophylls and a larger number of isolated gynoecia and detached microsporophylls and bracts. There are a few isolated microsporophylls from Roseberry Topping and from Marske Quarry.

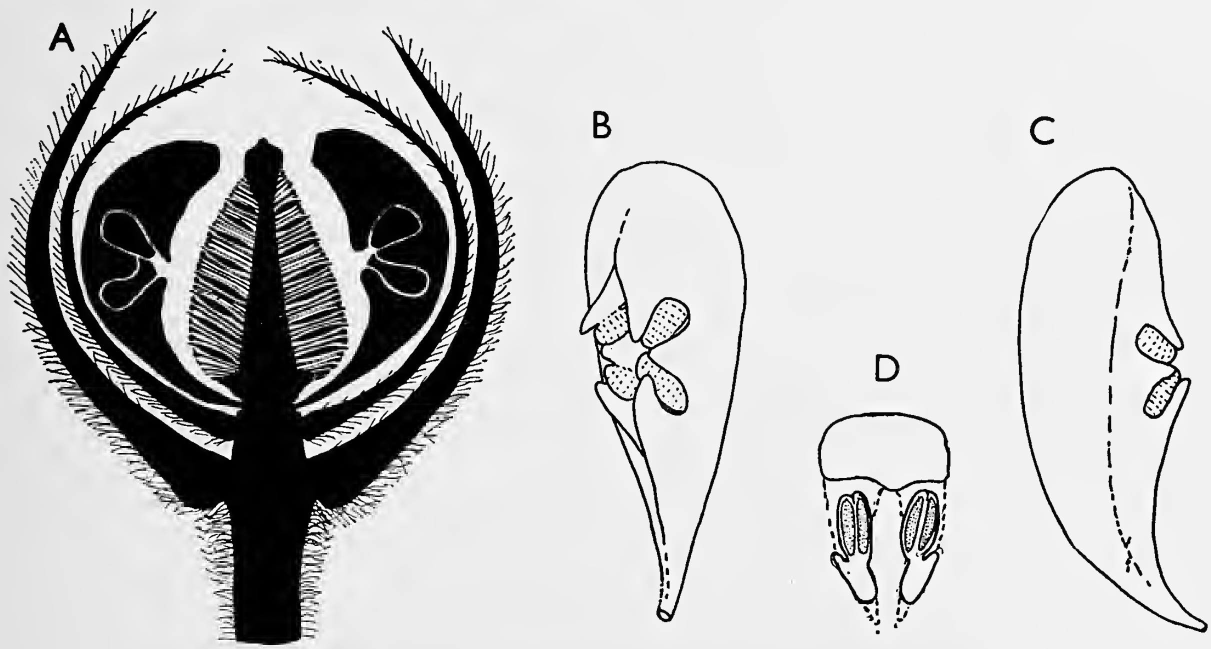

Fig. 61. Restorations of **Williamsoniella coronata** Thomas (flower)

A, whole flower, ×3. B, C, two views of microsporophyll, ×5. D, transverse section of microsporophyll, ×5.

All figures from Harris (1944), by permission of the Royal Society.

The peduncle is 2–4 cm. long and covered with simple hairs about 1 mm. long. At its top it bore probably 20–30 bracts, the outer ones being stouter and probably hairier than the inner. The bracts readily fell off and none of Thomas's specimens showed any. The bracts are lanceolate and up to 25 mm. × 4 mm. but often smaller. The surface shows little swellings. The upper (adaxial) cuticle has no stomata but some hair bases; the lower has numerous stomata and hair bases. The stomata are scattered and longitudinally orientated and the hair bases consist of 1, 2 or 3 cells.

The microsporophyll had the laterally compressed shape of an orange segment but with the lower end prolonged and the upper end rounded. The thick, outer part is covered with pimples.

The surface was probably smooth in life and the pimples were caused in compression by collapse on to nests of sclerotic cells. The epidermis is glabrous and the cuticle thin and shows cells with nearly straight walls. Usually there are two pairs of fertile branches and one pair of sterile ones at the base, but there may be three or even four pairs of fertile branches. Each fertile branch bears a pollen sac (synangium) about 2 mm. × 1 mm.

The pollen sacs have two smooth valves and in each valve are a number of elongated sporangia. I recognised five but Thomas gave the figure of twenty (which almost certainly included the sporangia of both valves). These pollen sacs are of the purse-like kind widespread in the Bennettitales, *Cycadeoida* and *Weltrichia* (male *Williamsonia*), but they were first regarded as simple wedges and their further elucidation is due to balsam transfers.

The pollen grains are 30μ × 20μ and have fairly thin, smooth walls.

Gynoecia are known at many stages. The mature but complete gynoecium is pear-shaped and at the narrow top is the conspicuous corona which forms a short, broad cylinder, the top being truncate or more often raised. The sides show about twelve flat facets. The interseminal scale has a stalk 5 mm. long ending in a bulbous head with a thick cuticle. The central part of the head forms a raised boss. The cells have thick lateral walls and the middles of the cells project as large papillae. The ripe seed is sessile and about 5 mm. × 0.9 mm. The micropyle projects about 250μ. Its cells are well cutinised and have nearly straight walls and nearly flat surface. This cuticle can be traced inwards as the integument but becomes very delicate. It shows broad epidermal cells often with jagged extensions on the walls and narrow hypodermal cells. The micropylar canal is continued as the inner cuticle of the seed, a delicate membrane showing elongated cells (perhaps lining of the integument) and broader cells believed to be of the nucellus.

The series of small specimens described by Harris (1944) is held to represent flowers which had stopped growing at early stages and then had fallen (abortive flowers). These may well represent the normal stages of flower development and growth but we cannot assume that the growth of different parts is proportionate, for example that the microsporophylls fell off when the gynoecium was of the size when they fall in the normal flower. In fact there is very little relation between the sizes of parts in these abortions. The proportion of small abortive flowers is high and this accounts for the smaller dimensions given by Thomas.

DISCUSSION. Apart from some added details the main differences between Thomas's account and mine are that none of his specimens still retained any involucral bracts while a few of mine do retain some. Though he thought none existed round the flower, he did recognise the right bracts as organs of *W. coronata* and supposed they were borne elsewhere on the plant. Had he known that they surrounded the flower, he might have interpreted '*W. roseberriensis*' and *W. lignieri* differently. I suggest *W. roseberriensis* consists merely of the converging tops of the involucral bracts above the top of a vertically compressed gynoecium. I suggest that *W. lignieri* is the base of a complete, young flower, mainly showing the involucre but on maceration yielding interseminal scales and micropyles (Nathorst 1909, pl. 4, fig. 7) as well as pollen from microsporophylls. I have not studied the original specimens of either flower.

Stem. Thomas believed that some associated forking axes which seem to show flower scars in the fork bore these flowers, and also on their lateral scars the leaf *Nilssoniopteris vittata.* He had no proof of this but merely noted their association and the suitable sizes of the scars.

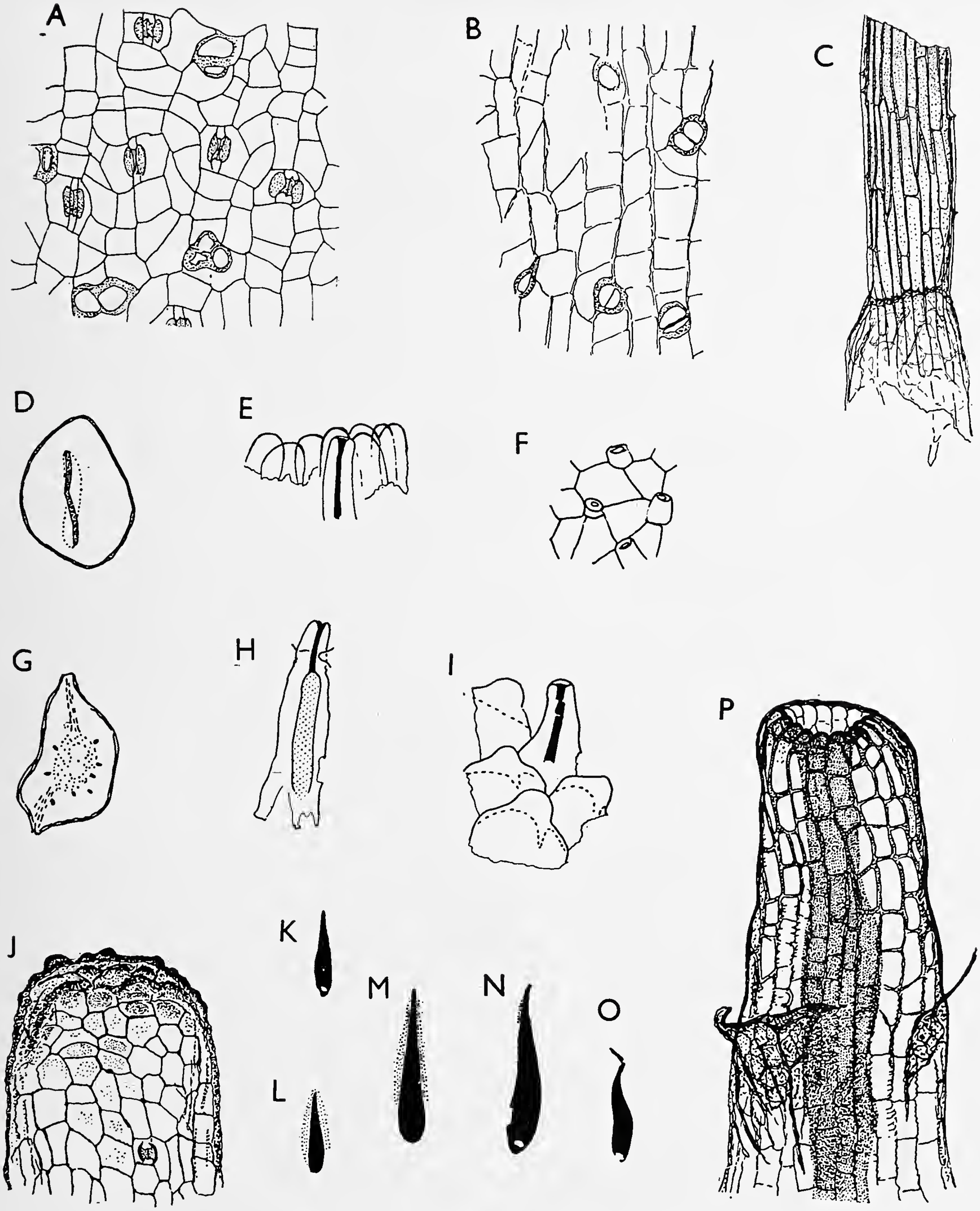

Fig. 62. **Williamsoniella coronata** Thomas

A, lower and B, upper (adaxial) cuticle of perianth bract, V.25838, ×200. C, micropylar canal and top of nucellus, V.26858*f*, ×200. D, pollen grain, V.23947, ×800. E, F, two views of armour of immature gynoecium, V.21387*a*, *b*, ×25. G, interseminal scale of mature gynoecium, V.25833*c*, ×25. H, immature seed, V.26858*e*, ×25. I, interseminal scales and micropyle of mature gynoecium, V.25833*d*, ×25. J, immature scale, V.26858*d*, ×200. K–O, isolated perianth bracts (hairs where visible stippled), all ×1. K, is V.21399. L, M, are V.25831. N, is V.23948. O, is V.21890. P, micropyle with adherent fragments of scales. The shrunken canal is stippled, V.26858*c*, ×200.

All figures from Harris (1944), by permission of the Royal Society.

I figure a similar forked stem which is associated with leaves and flower fragments. Zimmermann found and figured a stem which certainly bears *N. vittata* leaves and probably also flowers but these flowers (if really attached as they seem to be) are axillary. I make no judgment between these two styles of branching but they are so different that I doubt if both occur in the one plant.

If Zimmermann's specimen really shows continuity, then it does of course prove that *N. vittata* and *W. coronata* are organs of one plant.

Apart from this we have only circumstantial evidence but this is very strong. There is more evidence that *N. vittata* is the leaf of *W. coronata* than was available to Thomas. Thomas thought that certain bracts belonged to the *W. coronata* plant, but now specimens are known which prove they belong and surround the flower. Both Thomas and I have noticed such bracts (isolated ones) which bear a diminutive *N. vittata* lamina. There is thus a transition between the bracts and the leaves. Since Thomas's paper *W. coronata* has also been found at Marske and at Roseberry Topping and each locality has *N. vittata*, but I know no details of the association.

OCCURRENCE.

Middle Deltaic	. . .	Gristhorpe Bed
Lower Deltaic	. . .	Marske Quarry
		Roseberry Topping

Williamsoniella papillosa Cridland
Text-figs. 63, 64

1957 *Williamsoniella papillosa* Cridland, p. 383, text-figs. 1–3. (Figures repeated here.)

DIAGNOSIS (slightly modified from Cridland 1957). Mature flower about 40 mm. long, free part of corona 4–5 mm. long, 4–5 mm. wide below, tapering. Microsporophylls about 2·0–2·5 cm. long, narrow base extended. Cells of micropyle with a strongly bulging surface.

(Peduncle unknown, involucral bracts not known with certainty.)

HOLOTYPE. V.34250. Figured Cridland (1957, text-figs 1 C, F).

DESCRIPTION. The original material consists of three gynoecia and a few detached microsporophylls. They were found closely associated with one another in part of the classic Whitby Plant Bed.

The gynoecial axis consists of four parts. From the base upwards there are: (1) the basal flange about 4–5 mm. long × 14 mm. wide; (2) the seed-bearing part a cone 20 mm. long and tapering from 12 mm. below to 4 mm. above; (3) the concealed part of the corona an inverted cone 10 mm. long, 4 mm. wide below enlarging to 6 mm.; (4) the exposed corona a truncated cone 6 mm. wide below tapering to 1–2 mm.

The basal flange is divided longitudinally by ridges separating shallow basins which suggest the attachment of lateral organs (microsporophylls and bracts), up to four of these basins being visible on one face so the whole number of basins may be about twelve.

The denuded seed-bearing part of the gynoecial axis showed nothing beyond what is figured. It may have shrunk after maturity and losing its seeds as it is considerably broader in the holotype which still retains seeds. The upper part of this axis termed the concealed part

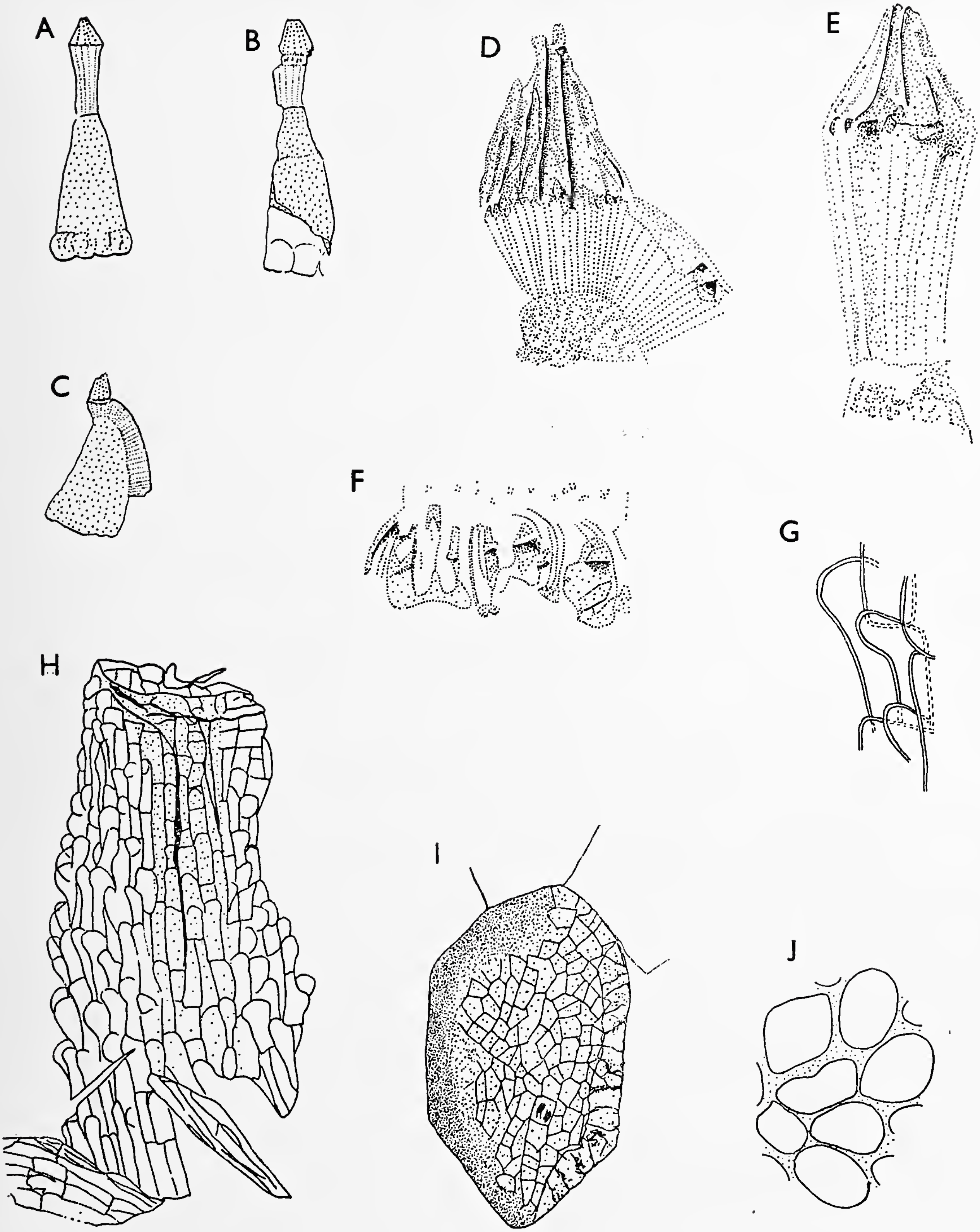

Fig. 63. **Williamsoniella papillosa** Cridland

A, gynoecial axis showing basal flange, seed-bearing receptacle, striated column and corona, V.34251, ×1. B, similar axis, part of the coaly substance has been lost, V.34252, ×1. C, holotype, axis still with some seeds and interseminal scales, V.34250, ×1. D, apex of C, ×4. E, apex of A, ×4. F, details of basal flange of B, ×4. G, details of cells from H, ×500. H, micropyle, the shrunken canal is stippled, V. 34256, ×200. I, head of interseminal scale, V.34250, ×200. J, details of cells from I, ×600.

All figures from Cridland (1957).

of the corona is of varied length. It is strongly striated and appears to consist of some apical interseminal scales adherent or adnate to the gynoecial axis. The exposed corona is strongly cutinised and its surface shows about twelve ridges separating flat or sunken facets. At the truncated top the ridges project upwards.

The seeds and interseminal scales are only known from preparations of their cuticles taken from the edge of the holotype specimen. The scale heads are rather small, typically 300μ wide. Their cells have unevenly thickened walls. The projecting micropyles 400μ × 100μ are the only part of the seeds known. Their surface cells project as hollow papillae.

The microsporophylls are oval in outline with an attenuated stalk. The substance is rather thick and the surface is dull (not glistening) and marked with little lumps. On the adaxial side the upper appendages at least nearly always project. The pollen capsules are oval and about 3 mm. long, and while most were empty, one yielded a good deal of pollen which is taken as belonging to it. The grains are oval, with thin smooth walls and typically 27μ long.

The involucral bracts of *W. papillosa* are unknown, but in *W. coronata* such bracts are known still attached to the flower and also there are similar isolated ones lying near the flowers. No bracts remain attached to *W. papillosa* but a few associated bracts were noted which may belong to it. One is a lanceolate scale 5 mm. wide just above the base and tapering steadily upwards, but the top is missing. The margins bear numerous simple hairs about 1·5 mm. long. The surfaces are dull and irregularly lumpy. Its cuticle could not be prepared.

A few more microsporophylls have been found at Whitby since Cridland's account. They agree fully with the earlier ones. There is also one large microsporophyll from the Gristhorpe Bed which agrees with *W. papillosa.*

Discussion. Cridland attributed the different specimens to a single species mainly because they are analogous to corresponding organs of *Williamsoniella coronata* and because they were closely associated. He also tentatively attributed *W. papillosa* to the same plant as *Nilssoniopteris major* and this idea is strengthened.

The evidence of association is as follows. In the Whitby Plant Bed I have only found *N. major* as an abundant fossil very locally and in certain bedding planes and here alone *W. papillosa* occurs and is common. I give the flora of one slab (not examined by Cridland).

Nilssoniopteris major	15 good or fragmentary leaves
Williamsoniella papillosa	4 microsporophylls, 1 good, 3 badly preserved
Cycadolepis sp. (hairy) possibly belonging to *W. papillosa*	1 fragment
Cycadolepis cf. indet.	1 fragment
Cycadolepis hypene	1 scale
Ptilophyllum pectinoides	4 leaves
Bucklandia cf. *pustulosa*	1 fragment
Taxus jurassica	1 shoot and several detached leaves

In addition there is some ill preserved and undetermined plant matter.

I would formerly have determined some of the narrower specimens of *N. major* as *N vittata* but I now realise that *N. major* can be narrow, but even the narrow specimens have distinguishing characters. I have not seen true *N. vittata* in this layer at all and I am not sure that any authentic specimens occur in the whole Whitby Plant Bed. This simplifies the association.

In the Gristhorpe Bed *N. vittata* is abundant and associated *W. coronata* frequent. *N. major* is occasional only, and there is a single specimen of *W. papillosa*. The block with *W. papillosa* showed no *N. major* however but only *N. vittata* and I do not know if *N. major* occurred near.

COMPARISON. *W. papillosa* differs from *W. coronata* in the larger size of the flower. The floral axis as a whole is more than twice as long (seed-bearing part 33 mm. as against 8 mm.), the exposed corona 4–7 mm. long and tapering as against 2 mm. and cylindrical. The microsporophylls are 20 × 9 mm. as against 15 × 5 mm. and their fertile branches are more slender and diverge more. The micropyle of the seed is strongly papillose instead of being smooth. The interseminal scale heads and micropyles are of about the same size; the cells of the interseminal scale head may be less evenly thickened but this difference is slight. The pollen grains look the same.

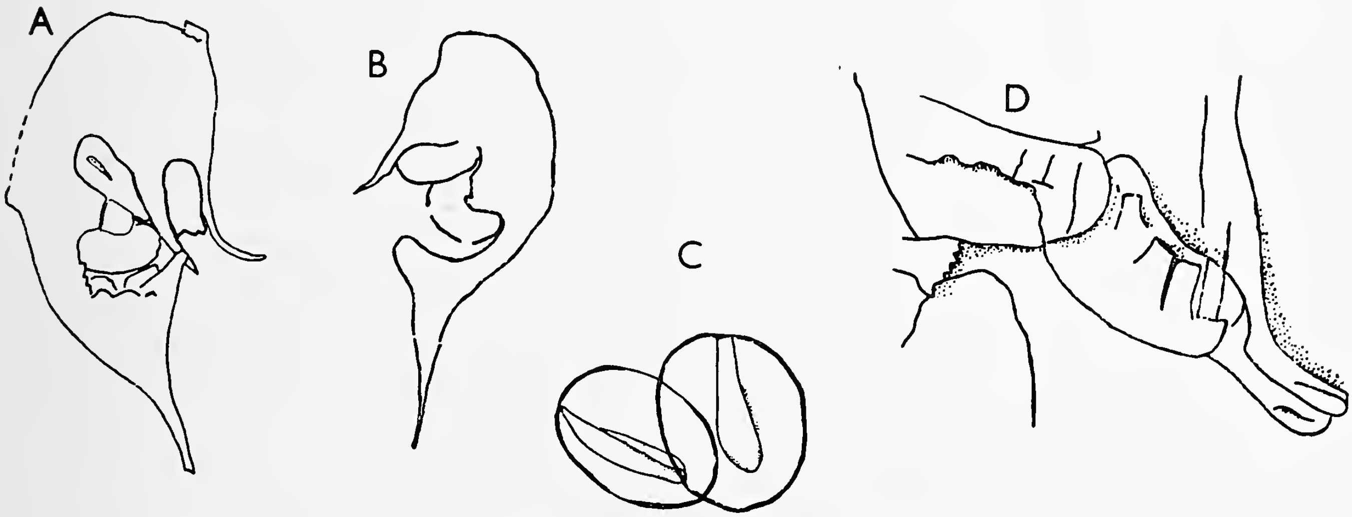

Fig. 64. **Williamsoniella papillosa** Cridland

A, microsporophyll with three fertile branches, V.34252, ×3. B, microsporophyll with two fertile branches, V.34252, ×3. C, pollen grains, V.34254, ×900. D, part of a microsporophyll in balsam transfer, V.34255, ×8.
All figures from Cridland (1957).

Williamsoniella papillosa has a gynoecial axis and corona rather like those of *Williamsonia hildae* and there is a possibility of confusion, though the pollen producing parts (and probably the involucral bracts) are very different. In *W. papillosa* the interseminal scales are smaller and the micropyles much more papillose. Another difference is that the palisade ring at the base of the denuded gynoecium is small and often inconspicuous in *W. papillosa* but large and prominent in *W. hildae*. *W. hildae* has a shorter expanding conical part of the gynoecial axis below the corona. *W. leckenbyi* differs in the same respects as *W. hildae* and in addition has a smaller corona.

OCCURRENCE.

Middle Deltaic	.	Gristhorpe Series, Gristhorpe Bed
Lower Deltaic	.	Whitby main plant bed

Genus BENNETTICARPUS Harris 1932, p. 101

DIAGNOSIS (of 1932). 'This designation is intended for all gynoecia which show definitely Bennettitalean characters, but which are not fully enough known either to be included in or definitely separated from the existing genera.'

Hsü (1948) and Kraüsel (1949) have used this non-committal name.

Bennetticarpus diodon sp. nov.
Pl. 4, figs. 2, 5, 6, 10; Text-fig. 65

DIAGNOSIS. Gynoecium spherical, diameter about 18 mm., apex rounded and unspecialised (base possibly flattened). Gynoecium surrounded by persistent, narrow, incurved bracts.

Interseminal scales uniform, heads polygonal about 0·5–0·7 mm. wide with a longer extension towards a micropyle. Whole surface of scale convex and central region markedly raised to form a pointed boss rising to 300μ above the margins.

Micropyles numerous, each surrounded by 6–8 scales elongated in the micropylar direction, most scales in contact with one micropyle. Scale margins forming conspicuous collars round micropyles. Micropyle projecting 300–400μ, 150μ wide above, slightly wider below, micropylar canal 90μ wide. Cells on exterior of micropyle rectangular with jagged thickenings on lateral walls from which slight ridges extend on to cell surface. Cell surface flat, not thicker in middle. (Other facts about seed not known.)

Bracts surrounding gynoecium linear-lanceolate probably 2 cm. long (base not observed). Width 1–2 mm., tapering above, then becoming filiform, 0·5 mm. wide, apex of filiform extension rounded. Surfaces almost smooth, but not shining.

Cuticle of interseminal scale head 4–5μ thick, divided into central boss, marginal region and depressed edges; edges firmly coherent to next scale and to micropyles. Cuticle of top of central boss much thinner than rest of head; cells typically isodiametric with thickened corners, walls finely marked, straight or minutely sinuous and interrupted. Centre of cell thicker and rays of thicker cuticle extending to cell margins. Cells at sides of central boss slightly elongated, radial-running walls with marked jagged thickenings and cell centre often more strongly thickened and with well-marked extensions towards jags on cell margins. Cells outside central boss mostly rather large and with almost straight strongly marked, more or less pitted walls. Cell surface flat but showing uneven thickening leaving small thinner areas, especially near cell margins. On side of scale next micropyle cells much narrower and usually longer than normal. Margins of scale formed by an inturned epidermis (cells crushed and confused).

Stomata frequent around edges of central boss, mostly orientated with aperture pointing radially. Guard cells somewhat sunken, subsidiary cells small, not papillate.

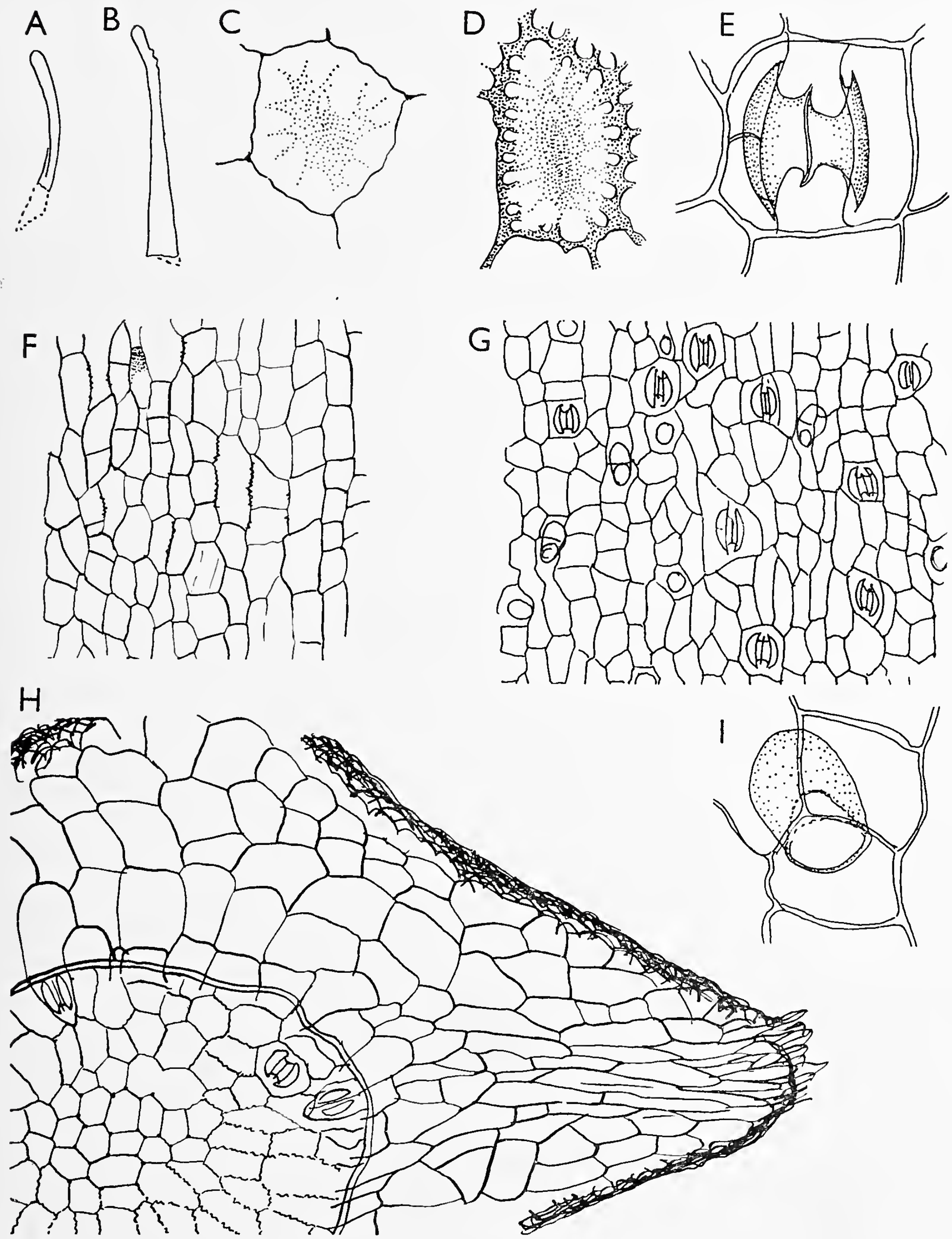

Fig. 65. **Bennetticarpus diodon** sp. nov.

A, B, apices of two bracts, ×4. C, cell of apex of interseminal scale, ×800. D, near cell just outside centre of scale, ×800. E, stoma of bract, one subsidiary cell has subdivided, ×800. F, G, two surfaces of involucral bract, ×200. H, part of interseminal scale, centre in bottom left surrounded by a compression fold, ×200. I, a single sac-like trichome of bract, ×800.

All figures are from the holotype, V.23953. C, D, H are from slide V.23953*a*; E, F, G, I from slide V.23953*b*.

Cuticle of enveloping bracts fairly thick (4–5μ on both sides). Hypodermal cells not observed.

On adaxial side, stomata very few and these ill-formed, trichomes only frequent near margins. Cells polygonal, forming longitudinal files, cells in adjacent files often of very unequal width. Cell outlines often rather indistinct, straight or occasionally minutely sinuous. Cell surface flat, obscurely mottled.

Abaxial side with numerous stomata evenly scattered, not forming files, nearly all orientated longitudinally. Epidermal cells polygonal, outlines very clearly marked, walls straight, cell surface flat, not papillate but mottled. Stomata well developed, not sunken, subsidiary cells small, not papillate. Trichomes numerous, consisting of a basal cell, sometimes an ordinary epidermal cell but sometimes a small cell placed on top of ordinary cells, free part a simple forward-pointing cutinised sac.

The name *diodon* is from *Diodon* the porcupine fish, a small round fish covered with little spines and in some species rather like the present gynoecium.

Holotype. V. 23953. (Pl. 4, fig. 2; Text-fig. 65.)

Description. *B. diodon* is represented by four specimens, all in the Gristhorpe Bed. Of these, two collected by Hamshaw Thomas are tiny fragments of the gynoecium and give no additional information but two are more or less complete gynoecia. All four agree perfectly in their micropyles and interseminal scales.

The holotype, collected by Mr. F. M. Wonnacott in 1935, is compressed laterally and is still surrounded by bracts. Unfortunately its base was lost. Remains of about 8–10 bracts occurred over the gynoecium and at its sides and there must be others beneath.

The second good specimen, collected by Hamshaw Thomas many years ago, is an isolated vertically compressed gynoecium. The core of the gynoecium seems to have decayed and has admitted matrix into the interior. This has resulted in the sides of the gynoecium showing an imprint which gives a kind of radial section showing interseminal scales and seeds in side view. It does indeed look rather like the 'palisade ring' of *W. leckenbyi* but it is not exactly similar because the gynoecial armour extends further downwards. On this radial section the imprints suggesting elongated seeds are up to 1 mm. wide but their full length is not shown.

The cuticle of the bracts is well preserved although the bracts are not particularly robust nor are they fibrous. The stomata are well developed but an unusual proportion are abnormal. An encircling cell is often present (this is scarcely abnormal) but in about a quarter one or other subsidiary cell has divided at right angles to the aperture, but the guard cell itself remains undivided. In some stomata very little is visible of one or other guard cell, but I do not know whether this is because the guard cell is small and badly developed or merely because it is tilted.

Comparison. *B. diodon* is well distinguished specifically from other Bennettitalean gynoecia known in a similar way. Its small size and minutely prickly or mamillate surface are unusual and the thin cuticle of the apex of the interseminal scale is remarkable. The bracts are very narrow and are distinguished by their filiform apices and longitudinal stomata and sac-like trichomes from all other species except *Cycadolepis stenopus*.

Discussion. Plant bearing *B. diodon*.

We have four gynoecia of *B. diodon* all from the Gristhorpe Bed. This bed must be one of the most collected plant beds in the world and I suppose its flora though large must be one of the most known. Since reproductive organs in general are rarer than leaves, it seems very likely that the leaf of the same plant will already have been found in the Gristhorpe Bed.

The specimens are on very small blocks and none have significant associates. Most have *Nilssoniopteris vittata* and *Nilssonia compta* which are abundant in most of the Gristhorpe Bed.

The Gristhorpe Bed has yielded a good many species of Bennettitalean leaves, but some of these are very unlikely to belong to the same plant, being more or less firmly linked with a different gynoecium, or at least with a very different scale leaf. I consider that *Anomozamites nilssoni* is much the most likely leaf to belong to it.

The Bennettitalean leaves of the Gristhorpe Bed (according to my own collecting and that of others, but after rejecting a few records as mistakes) are:

1. *Nilssoniopteris vittata*, here abundant; linked with *Williamsoniella coronata*.
2. *Nilssoniopteris major*, here occasional but abundant elsewhere; linked with *Williamsoniella papillosa*.
3. *Ptilophyllum pecten*, locally abundant here and elsewhere; linked with *Williamsonia leckenbyi* and *Cycadolepis nitens*.
4. *Ptilophyllum pectinoides*, very rare here but abundant elsewhere. Linked with *Williamsonia hildae* and *Cycadolepis hypene*.
5. *Pterophyllum thomasi*, very rare here but locally common elsewhere, linked with *Cycadolepis hallei*.
6. *Nilssoniopteris pristis*, very rare, other organs unknown.
7. *Pterophyllum cycadites*, very rare, other organs unknown.
8. *Otozamites beani*, occasional here, common elsewhere. Other organs doubtful, see below.
9. *Anomozamites nilssoni*, locally abundant here; see below.

I dismiss the first five; the evidence for linking them with another organ is given on the appropriate page. I have nothing to say about the two rare leaves *P. cycadites* and *N. pristis*. *Otozamites beani* has elsewhere been found associated with reproductive organs but the indications are obscure. Once it was found with *Williamsonia himas* (locality unrecorded) and once with *Cycadolepis eriphous* a scale which differs greatly from those round *W. himas*. Thus all I can say is that I see no reason for linking it with *B. diodon*.

Anomozamites nilssoni is firmly linked with *Cycadolepis stenopus* by close association in two localities and by specimens of intermediate form, a *C. stenopus* base bearing a small *A. nilssoni* leaf. *C. stenopus* as we know it differs in shape from the scales around *B. diodon*, for *C. stenopus* is small and narrow while the *B. diodon* scale is long and narrow. I think the gap is caused by failure to collect.

C. stenopus was found in an unusual way—by the deliberate maceration of some blocks of shale containing much *A. nilssoni* in order to look for an appropriate associated scale. The specimens which survived this maceration were sieved off, dried, and picked out. This process greatly favours small organs since they more often remain intact than larger ones.

In such a maceration there are always many fragments which are passed over as of no known interest, and I think that any long *Cycadolepis* bracts of rather fragile substance would get broken and missed unless specifically looked for. At present I have no suitable material for fresh study; more must be sought and examined. A start was made by gently macerating a block of the Gristhorpe shale showing *A. nilssoni* with water (which disintegrates it to mud) and stopping when a suitable specimen was exposed. This gave a *C. stenopus* 17 mm. long, not it is true as long as in *B. diodon* but twice as long as any *C. stenopus* previously seen. I feel sure that suitable search will give what we need.

The original *C. stenopus* scales had very few stomata but the later ones described here have many and these are like those on *B. diodon* scales. Above all, *B. diodon* and *C. stenopus* agree in their sac-like trichomes, which are known in no other scale leaves. This evidence seems to me strongly suggestive but falls short of being acceptable. Still we now know where to look for confirmation (or disappointment if it proves wrong). In the following discussion I use the hypothesis that the two organs are of one plant, but even if this were confirmed I would not put *B. diodon* in *Wielandiella*.

There is no proved distinction of generic value between *B. diodon* and either *Williamsonia* or *Wielandiella*. The differences lie in the androecium, which is satisfactorily known in the *Williamsonia* plant (a separate bell shaped flower here called *Weltrichia*) but in *Wielandiella* apparently at the base of the gynoecium. The facts for *Wielandiella* are not fully clear. Nathorst (1909) figured the cutinised 'palisade ring' of *Wielandiella* (an entirely different structure from the 'palisade ring' of *Williamsonia leckenbyi*). He thought it probably (wahrscheinlich) a ring of reduced microsporophylls, mainly because he obtained much pollen from it though he saw no pollen sacs, full or empty. The second species, *W. punctata* Nathorst 1909, which seemed to support this view, has been shown by Lundblad (1950) to be of very different nature. Thus the androecium of *Wielandiella* is still problematic.

It happens that we do not know the base of the flower of *B. diodon*, but if we did it is possible that we might settle whether it should be placed in *Williamsonia* or *Wielandiella*. This is just the case for which *Bennetticarpus* was created.

OCCURRENCE. *B. diodon* is known only from the Gristhorpe Bed (Middle Deltaic Gristhorpe Series).

Bennetticarpus fragum sp. nov.
Pl. 4, figs. 11, 15, 16; Pl. 6, fig. 3;

DIAGNOSIS (based on a single gynoecium). Gynoecium nearly 3 cm. long, about 2·0 cm. wide near the base, form conical, top bluntly pointed, base rather hollowed. Surface smooth. Gynoecial receptacle 2 cm. × 14 cm., also conical, inner parts largely composed of coarse fibres about 3 mm. × 0·1 mm. running longitudinally in the centre but then arching outwards; outer part of axis largely composed of short thick-walled cells. Seeds and interseminal scales forming rind about 6 mm. thick. Interseminal scales pointing outwards and slightly upwards except at the base of the gynoecium where they point outwards and downwards. Apex of gynoecium formed of ordinary interseminal scales, corona absent. Interseminal scales very slender, head only 150μ wide, forming a thickly cutinised dome about 250μ high, top of dome rounded; cells about 20μ wide, isodiametric, anticlinal walls broad and straight, periclinal walls nearly flat, unornamented. (Stomata not observed.) Margins of dome becoming delicate. Micropyles reaching the surface, not projecting outwards at all but continuing inwards as a well cutinised tube for 500μ long, 200μ wide. Outer cuticle fairly thick, each surface cell bearing a hollow dome 15μ wide and 15–30μ high. Micropylar canal about 100μ broad; cells narrow, straight walled.

Inner part of seed, beneath the micropyle (imperfectly known), including a delicate cuticle of two cell layers (probably nucellus + lining of integument) forming an elongated sac 120μ broad. Both sets of cells with straight walls.

The specific name *fragum* is from the Latin *fragum* a strawberry. The gynoecium of the holotype is the size and shape of a wild strawberry.

HOLOTYPE. V.53392.

DISCUSSION. The holotype is a lateral compression and split longitudinally. Though the base is damaged, I feel sure that the lower backward pointing scales represent the base and that little has been lost.

Though the specimen appeared unpromising, it gave fairly good preparations of interseminal scale cuticles and good ones of the micropyles.

B. fragum may well, when fully known, prove to be an ordinary *Williamsonia*. The holotype may also prove to be of less than full size (half grown abortive gynoecia being frequent in Yorkshire Bennettitales). The form of the interseminal scale heads does indeed rather suggest this, though the preparations, which show them in more or less lateral compression, are not fully convincing.

The specimen is in a fallen block of shale from the Lower Deltaic cliffs near Hawsker at about 54° 28′ 30″ N. This shale '*O. gramineus* Bed' was full of *Otozamites gramineus* but no other Bennettitalean leaves. On other occasions other blocks have been collected around the same place and there must be an extensive bed full of *O. gramineus*, and no other Bennettitalean leaf, so far as I know. This association must not at present be used as evidence that the two organs belong to one plant because there is an equal case for attributing *B. litchi* to *O. gramineus*.

The matter is further discussed on p. 156 where the possibility is also considered that *B. fragum* might be the immature state of *B. litchi*.

COMPARISON. *B. fragum* differs from most Bennettitalean gynoecia in that the micropyles do not project beyond the interseminal scale armour. The inner parts of the micropyles are strongly papillose. Its interseminal scale heads also are very minute but this may be due to the immaturity of the whole gynoecium.

OCCURRENCE. Hawsker *O. gramineus* Bed, Lower Deltaic.

Bennetticarpus litchi sp. nov.

Pl. 4, figs. 14, 17, 18; Text-fig. 66

DIAGNOSIS. (Species based on a vertical compression of a mature gynoecium.) Gynoecium 3·5 cm. wide borne on a peduncle 1·3 cm. wide (upper part unknown). Lower part of gynoecium hollowed round the peduncle. Surface of gynoecium formed by bulging heads of interseminal scales but otherwise smooth; micropyles not projecting and not visible.

Interseminal scales and seeds forming a rind about 12 mm. broad, seed imprints fusiform, sessile, about 1·4 mm. broad in middle. Interseminal scale heads 0·8–1·2 mm. wide, polygonal, often with one or more corners much prolonged (and believed to be pointing towards a micropyle). Head well cutinised, showing a central boss forming a dome 150μ wide and 150μ high surrounded by gently sloping flanges, at boundary with other scales flanges bending sharply inwards but not adhering closely to other scales, Cells of central boss typically small. Lateral walls always prominent, often broad; usually straight but sometimes very finely waved. Surface of cell flat, usually appearing thin but often largely occupied by thick borders to the lateral walls leaving only a thin strip in the cell centre. Stomata occurring on the steep margins of the boss or on the inner parts of the flanges; small, somewhat sunken, often orientated radially. Flanges becoming more thinly cutinised towards margins and cell outlines becoming less broad and cells becoming larger. Flanges divided by radiating ridges to the corners of the scale, ridges to ordinary corners narrow and often indistinct but to extended micropylar corner broad and often strongly marked. At micropylar corner a very small round gap under 100μ wide occurring, but gap occupied only by indefinite cuticle and no micropyle recognised.

No cuticles of micropyles or other parts of seeds preserved.

The name *litchi* was suggested by the fruit wall of the litchi (*Nephelium chinense*) fruit which has a surface suggesting interseminal scales but no micropyles.

HOLOTYPE. V.53394.

DESCRIPTION. The only specimen is preserved in medium grained sandstone as a disc of coal up to 5 mm. thick. Part of this coal was lost in collecting and all the rest was picked off and macerated. It yielded some hundreds of fairly well preserved scale heads, but no part of the seed cuticle. Seeds however appear to be very numerous and about one in three of the corners of interseminal scales have the characteristic form of the extension towards a micropyle. After the coal had been picked off the imprint representing the fruit surface in reverse, showed distinct pits surrounded by extended interseminal scale corners, and I believe these pits represent the position of micropyles.

DISCUSSION. This gynoecium, like *B. fragum*, is associated with *Otozamites gramineus* but in another locality. Where it was found (Beast Cliff *O. gramineus* Bed) this leaf is abundant and no other Bennettitalean leaf was seen. The bed was only accessible for a few metres horizontally and then when again accessible, its flora (or that of another bed at about the same level) is different. Thus the case for considering that the two organs may belong to the same plant is just the same as for *B. fragum* and *O. gramineus*.

The possibility was explored that the two gynoecia might belong to a single species, *B. fragum* being immature, but no good case for this can be made. It is indeed possible that a gynoecium of the shape and size of *B. fragum* could grow into one like *B. litchi*. They seem to have the same somewhat hollowed base, the number of interseminal scales (though only roughly estimated) may be similar, and they agree in the unusual character of having no projecting micropyles. The dome-shaped interseminal scales of *B. fragum* could well develop into the dome of the mature scale of *B. litchi*, the flanges here as in other Bennettitales being formed later. However there is an unexplained difference in the micropyles. In *B. fragum* these are rather thickly cutinised, although concealed inside the armour. Certainly if any such concealed micropyle had been present in *B. litchi* the macerations would have shown it. We would have to suppose that in *B. litchi* the whole micropyle had been extruded and then thrown off—two unusual and entirely imaginary processes, for neither in the 'young' nor in the 'old' fruit do we see anything of the sort. This is regrettable, for if we could have regarded the two gynoecia as stages of a single species various interesting morphological conclusions would have followed and also we could be reasonably sure we have the gynoecium of the *O. gramineus* plant.

B. litchi agrees with the Triassic *B. wettsteini* Kräusel (1949) in showing no micropyles. In *B. litchi* it appears that the micropylar openings have been reduced by the growth of the scales—and very possibly eliminated by being covered over, while we do not know what

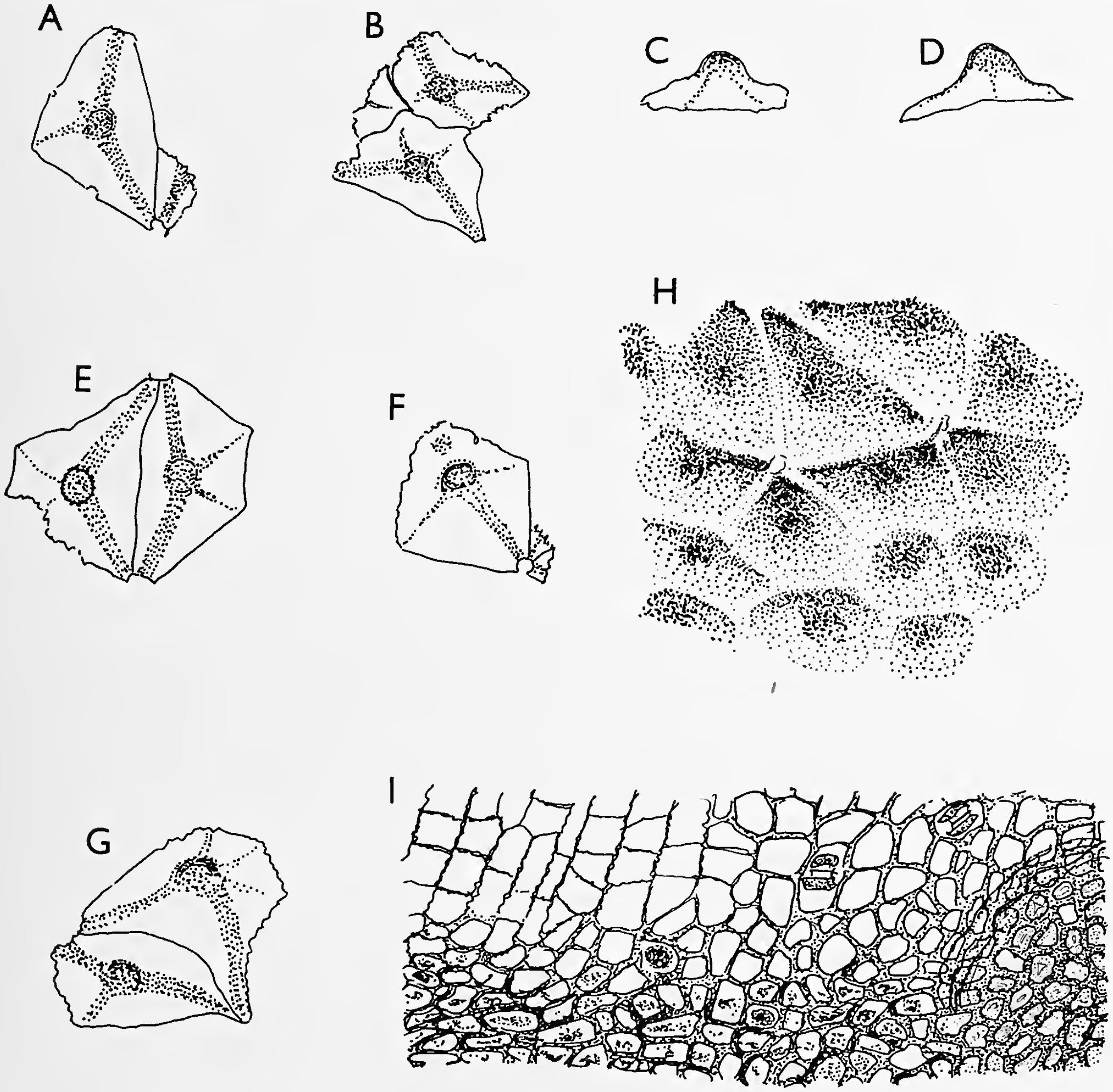

Fig. 66. **Bennetticarpus litchi** sp. nov.

A–G, selected interseminal scales, all ×20. In each the central boss is stippled and also the broad ridges to micropylar corners and narrow ridges to other corners. H, surface of gynoecium, imprint (with reversed sculpture) showing two high points (= pits) corresponding to micropyles, ×20. I, part of an interseminal scale. The central boss is bottom right from which a micropylar ridge extends to the left along the bottom, ×200.

All figures are from the holotype, V.53394. A, B, I, slide A. C, slide C. D, slide D. E, slide E. F, slide F. G, slide B.

has happened to the cutinised micropylar canal, if one existed. In *B. wettsteini* on the other hand all the scales figured are of regular shape and there are no extended corners, and I feel unsure that the two cases are similar.

COMPARISON. *B. litchi* agrees in size and shape and in the general character of its interseminal scales with a number of *Williamsonia* species, particularly *W. leckenbyi* and *W. hildae*. It differs from these in the precise details of its scales and in showing no projecting micropyles, or indeed any part of the seed cuticles.

Genus WELTRICHIA Braun emend.

(*Williamsonia* male flowers of most authors)

1849 *Weltrichia* Braun, p. 709.
1891 *Weltrichia* Braun; Saporta, p. 191, pl. 253–255. This description is taken as the basis of the present treatment.
1909 *Weltrichia* Braun; Nathorst, p. 28. (Critical reconsideration.)
1911 *Weltrichia* Braun; Schuster, in part, p. 8. (Male flowers only, not interpretation.)
1911*a* *Weltrichia* Braun; Nathorst, p. 1, pl. 1. (Further discussion.)

EMENDED DIAGNOSIS. Bennettitalean male flower consisting of a massive cup dividing above into numerous equal lobes or rays; rays of thick substance, tapering to a point. Outer surface of cup and rays without appendages. Cuticles (where known) showing syndetocheilic stomata with single subsidiary cell opposite each guard cell. Inner side of cup and of rays bearing pollen sacs, either directly, or on appendages. Pollen sacs (= synangia) where known consisting of two equal valves, each valve with a single row of microsporangia opening on to inner face. Pollen grains oval, monocolpate.

TYPE SPECIES. *W. mirabilis* Braun 1849.

DISCUSSION. Saporta (1891) was the first to point out that there is no proved difference between *Weltrichia* and the Yorkshire *Williamsonia* flowers we later recognised as male, yet he did not unite the genera. The name *Weltrichia* has been neglected, I suppose partly because Braun's original account has been seen by few and partly because accounts of Yorkshire male flowers (by Williamson, Saporta, Seward and Nathorst) all under the name *Williamsonia* overshadowed *Weltrichia*. Our knowledge of *Weltrichia mirabilis* is less than that of the best known species described as 'male *Williamsonia*', but considerably better than the worst. It is about average. Nothing is known about its cuticle and nothing about the fine details of the (presumed) pollen sacs, a criticism which can be made with equal justice about many Bennettitalean male flowers.

As *Weltrichia* has priority over *Williamsonia* (used for male or female flowers), I follow what appears to me the strict interpretation of the rules and use *Weltrichia* for the male flowers and keep *Williamsonia* for the female ones.

The strange fossil *Cycadocephalus* Nathorst (1902, 1909) has much in common with *Weltrichia*, but as its pollen is entirely different I doubt if it is indeed Bennettitalean.

The male flowers which had been included in *Williamsonia* cover a considerable morphological range mainly in the way in which the pollen sacs are borne, directly on the rays or on pinna-like branches. The pollen sacs too vary from semicircular to elongated. Other variants are sterile appendages of various kinds (*W. santalensis*, *W. setosa*). I considered whether further genera should be made but decided against this because it seems unpractical. Not only does it secure no advantage at our present knowledge to make almost every species into a genus but it also has the grave disadvantage that some of the species are too ill-known to place.

A strange feature of some of the species described here is that they bear inside the cup organs described as 'resinous sacs' where one would expect pollen sacs. Nathorst recognised them in *W. whitbiensis* and called them 'rudimentary synangia' for they continue the pollen sac series into the middle of the cup and they look like pollen sacs. Their extreme resistance to maceration however shows that, however like the normal pollen sacs they may have been at the beginning, they developed differently. The pollen sacs are easily detached, delicate and macerate rapidly. The resinous sacs are firmly attached and very resistant and even after a long time contain much material which continues to resist maceration so that the outer cuticles are hard to separate.

I have preferred the word 'pollen sac' to 'synangia' for the little 2-valved capsule containing pollen because 'synangia' has considerable but insecure morphological implications, particularly in suggesting resemblance to *Marattia* synangia. Similarly I have preferred the purely descriptive term 'ray' to 'microsporophyll' for the segments into which the cup divides.

The following species of *Weltrichia* are recognised here:

1. Species originally placed in *Weltrichia*.
   - *W. mirabilis* Braun 1849, the type species.
   - *W. ovalis* Braun and *W. campanulata* Braun which may be the same as *W. mirabilis*. Rhaetic of S.W. Germany.
   - *W. fabrei* Saporta 1891. Rhaetic of France.
   - *W. oolithica* Saporta 1891. Upper Lias of N. Italy.

2. Species from Yorkshire Lower Oolite and treated here. All but *Weltrichia sol*, originally described in *Williamsonia*.
   - *W. sol* Harris sp. nov.
   - *W. whitbiensis* (Nathorst) comb. nov.
   - *W. pecten* (Leckenby 1864) comb. nov.
   - *W. setosa* (Nathorst) comb. nov.
   - *W. spectabilis* (Nathorst) comb. nov.

3. Species from various regions, originally described in *Williamsonia*.
   - *W. blandfordi* (Feistmantel 1877) comb. nov. Jurassic of Cutch, India.
   - *W. mexicana* (Wieland 1909) comb. nov. Jurassic of Mexico.
   - *W. santalensis* (Sitholey & Bose 1953) comb. nov. Jurassic of Rajmahal Hills, India.
   - *W. alfredi* (Krasser) 1917. Lower Lias of Hungary.

I have omitted flowers which give no clear evidence of having borne pollen sacs. Others may have been missed.

Weltrichia setosa (Nathorst) comb. nov.

Pl. 7, fig. 3; Text-figs. 67, 68

1909 *Williamsonia gigas* Will.; Nathorst, in part, pl. 7, fig. 1 only.
1911 *Williamsonia setosa* Nathorst, p. 7, pl. 4, figs. 1–11. (Fig. 1 is same as in 1909.)
1917 *Williamsonia setosa* Nathorst; Krasser, pl. 2, fig. 3. (Nathorst's 1909 figure reproduced.)
1917 *Williamsonia setosa* Nathorst; Seward, pp. 430, 444. (Discussion.)
1953 *Williamsonia setosa* Nathorst; Harris, p. 47, text-figs. 5 D–G, 6 A–H. (Description and figures repeated here.)

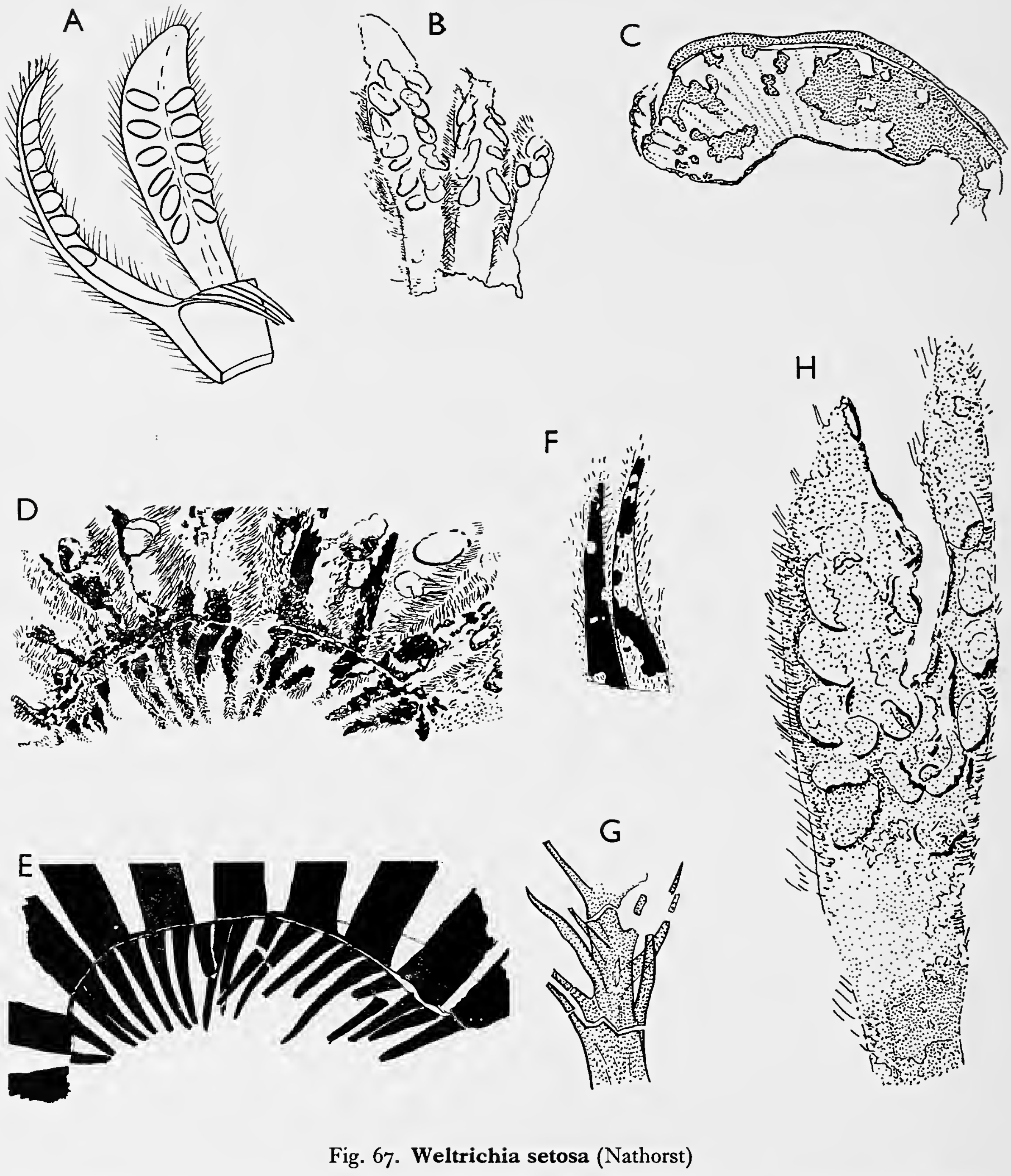

Fig. 67. **Weltrichia setosa** (Nathorst)

A, restoration of part of a flower showing microsporophylls with pollen sacs, cup and inner scales. Slightly enlarged. B, outline of Stockholm specimen (Nathorst, pl. 4, fig. 8) as seen under oil, $\times 1$. C, single pollen sac of same specimen under oil. Note line of junction of valves and faint indications of sporangia, $\times 8$. D, drawing of Stockholm specimen (Nathorst, pl. 4, fig. 2) as seen under oil. Not all the hairs are shown, $\times 2$. E, partial restoration of D, drawn with help of counterpart. F, two of inner scales, from counterpart of 'D', $\times 5$. G, part of a hairy bristle of Oxford specimen in transfer, $\times 100$. H, Oxford microsporophyll (torn above) showing pollen sacs, $\times 2$.

All figures from Harris (1953).

Emended Diagnosis. Male flower, consisting of small cup bearing at its edge a whorl of about 20 rays (microsporophylls) and inside this a whorl of numerous (perhaps about 40) delicate sterile scales. Rays in contact laterally with one another, spreading, but upper parts rather incurved. Length of ray 4–6 cm., width at middle 1–1·6 cm.; base narrowed to about 0·5 cm., apex obtuse. Substance of ray rather thick. Lower side of ray densely covered with bristles 3 mm. long, bristles pointing forwards and outwards and interlocking with those of the next ray. Bristles covered with minute forward-pointing spines 200μ long. Upper side of ray without bristles (except on margin) but with a number of hairs; hairs shorter, thinner and less rigid than bristles and not bearing spines. Upper side bearing pollen sacs (synangia) in two longitudinal rows. Sacs flattened, nearly semicircular, attached at middle of flat side, placed more or less transversely to the ray; free edge pointing outwards and backwards (but sac often displaced in position and often lying very obliquely to the ray axis). Pollen sac 3–7 mm. broad, nearly 2–2·5 mm. from point of attachment to free edge; composed of two equal valves. Valves each enclosing a single row of elongated pollen masses 200μ wide near the base, 300μ wide near the free edge.

Sterile scales moderately thick but much more delicate than rays. Length of scale 1 cm., width about 1·5 mm. at the base, tapering evenly to a point. Margins covered with straight, forward-pointing hairs about 2 mm. long, underside covered with hairs about 1 mm. long; upper side covered with still smaller hairs (about 0·5 mm. long). Hairs of scales tending to be straight but more slender than bristles of rays and simple, without any spine-like outgrowths. Cuticle of scale unknown, probably very delicate.

Cuticle of ray (microsporophyll) rather thin (imperfectly known). One side (probably the lower) showing fairly large rectangular cells, wall straight but with tendency to develop small jagged thickenings. Bristle bases frequent, composed of one or more large cells bearing a thickened ring; bristle itself very thinly cutinised. Other side probably covered with more delicate cuticle with small, straight-walled cells. Stomata not observed.

Pollen sacs covered with very delicate cuticle indeed, but showing small straight-walled cells and occasional unicellular hair bases; occasional stomata present in some parts, showing small but well-thickened guard cells with syndetocheilic subsidiary cells. Microsporangia lined by fairly thick granular cuticle showing strong longitudinal folds, but no cells outline at all.

Pollen grains oval, 37μ × 20μ, with a thin, finely granular wall.

Lectotype. Specimen figured by Nathorst (1909, pl. 7, fig. 1) here designated as lectotype.

Discussion. *Weltrichia setosa* is rare and all the specimens are from the Whitby Plant Bed. None is very well preserved and the study, particularly of cuticles, is incomplete.

The specimen designated as lectotype was collected by Nathorst in 1909, but at first (Nathorst 1909, p. 19) was misinterpreted as the 'apical funnel' of the female *W. gigas*. In 1910 Halle collected a few additional specimens and both these and the original one were described by Nathorst (1911). These specimens are at Stockholm. Much earlier Phillips had collected a single sporophyll, J5019 at Oxford which had been evidently noticed but not named. This though ill preserved gave the cuticle preparations and transfers.

I have collected two specimens in this bed, one of which (Pl. 7, fig. 3) suggests that the cup has neither pollen sacs nor resinous sacs but the evidence is hardly conclusive. The rays are so matted together by the long bristles that it is difficult to be sure where the cup ends.

A third specimen was found in the Cloughton Wyke *Nilssonia* Bed (Sycarham Series). It is less well preserved and its determination is not fully convincing though if it is a known species it must be *W. setosa*. It is associated with two leaves of *Otozamites beani* a species common in this bed, though *O. graphicus* also occurs. In the Whitby Plant Bed both leaves occur also, but in addition a number of other Bennettitalean leaves not yet assigned to a reproductive organ. *O. beani* is hairy on the under side, a possible point of agreement. Thus while I do not assign *W. setosa* to a leaf, it is worth looking for further evidence of association with *O. beani* in particular.

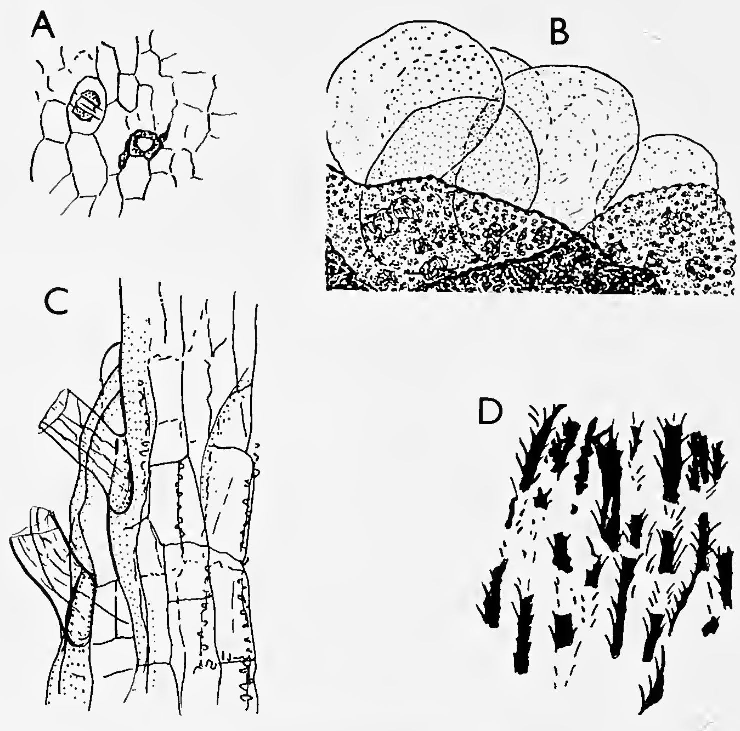

Fig. 68. **Weltrichia setosa** (Nathorst)

A, cuticle fragment, probably from outside of pollen sac, ×200. B, torn preparation from pollen sac showing thick, granular lining cuticle enclosing pollen grains, ×800. C, cuticle fragment, presumably from edge of microsporophyll, showing trichome bases, ×200. D, toothed bristles from transfer of imprint, ×20.

All the figures are of the Oxford specimen and are from Harris (1953).

Nathorst's pl. 4, fig. 1, which gives a view of the centre of the flower suggests a floral cup about 2 cm. wide. It is not known whether it bore any appendages inside, but at the edge there are narrow inward pointing scales and these must have covered the top of the cup. They seem to be twice as numerous as the rays (microsporophylls) but their precise relation to them is not settled. While their morphology is unknown, they may be compared with the scales on the corolla of many Boraginaceae or the appendages of the stamens of some Amaryllidaceae. Nathorst had regarded them as the bases of the microsporophylls but when the specimens were immersed in oil it became obvious that they were different and pointed inwards, not outwards.

W. setosa is distinguished from other species of *Weltrichia* by the inward pointing scales at the top of the cup and by the toothed bristles, or hairy ramenta, on the edges of the rays (microsporophylls).

OCCURRENCE. Whitby Plant Bed, Lower Deltaic.

Weltrichia sol sp. nov.
(*Williamsonia gigas* male flower)
Pl. 5, figs. 1–6; Pl. 7, fig. 6; Text-fig. 69

1900 *Williamsonia gigas* Seward, p. 188, pl. 8, fig. 1. (Specimen however regarded as top of *W. gigas* gynoecium.)
1915*a* *Williamsonia gigas* male flower, Thomas, p. 105, pl. 6, figs. 1, 2; text-figs. 1, 2. See below.

The following are rejected:

1870 *Williamsonia gigas* Williamson, p. 670, pl. 52, fig. 2. (Perhaps *W. whitbiensis*.)
1877 *Williamsonia gigas*, Feistmantel, p. 127, pl. 44, fig. 304. (Distinct.)
1891 *Williamsonia gigas*, Saporta, p. 132, pl. 10, fig. 3. (*W. whitbiensis* but supposed to surmount female flower of *W. gigas*.)

DIAGNOSIS. Flower large (peduncle not known). Cup widely open, height typically 7–8 cm., width of continuous part at top typically about 10 cm., then dividing into about 30 ray-like segments, rays 1 cm. wide at the base, 5–6 cm. long, tapering to a point, width at top of flower up to about 17 cm. (or less because segments may bend inwards). Outer surface of cup and rays hairless but showing longitudinal ridges (probably caused by fibres) and often showing transverse wrinkles.

Inner surface of cup bearing large numbers of 'resinous sacs' but no pollen sacs. Resinous sacs semicircular, typically $1 \cdot 5 \times 1 \cdot 0$ mm., crowded, not forming rows, borne on simple or branched stalks about 1 mm. long. Surface of resinous sacs mainly hairy; interior yielding a spongy but very resistant mass of resin. Pollen sacs borne on short fertile appendages on inner surface of rays, appendages at least 1 cm. long and 1 mm. broad, bearing pollen sacs alternately on the sides (arrangement of appendages imperfectly known, but pollen sacs numerous and crowded). After maturity pollen sacs and appendages often lost.

Pollen sacs (synangia) semicircular, up to about 4 mm. broad, 2·5 mm. high, but sometimes smaller, composed of two valves. Outer cuticle of pollen sac delicate, showing cells with undulating walls but no stomata. Inner cuticles non-cellular, lining the sporangia. Sporangia about 2 mm. long, appearing 300μ wide and in lateral contact when open, number in a full sized valve about 12–15.

Outer cuticle of cup and rays 1μ or more thick. Cells with broad walls, shape square or rounded; not forming obvious files but in parts of rays marked by longitudinal ridges. Stomata varying in frequency in different parts (distribution imperfectly known). In most parts stomata scattered and not forming files, orientation varied but often transverse. On rays, stomata sometimes forming ill-defined longitudinal files and nearly all transverse. Stomatal apparatus superficial or whole apparatus slightly sunken and overlapped by surrounding epidermal cells. Guard cell thickenings well developed, subsidiary cells usually small, mostly

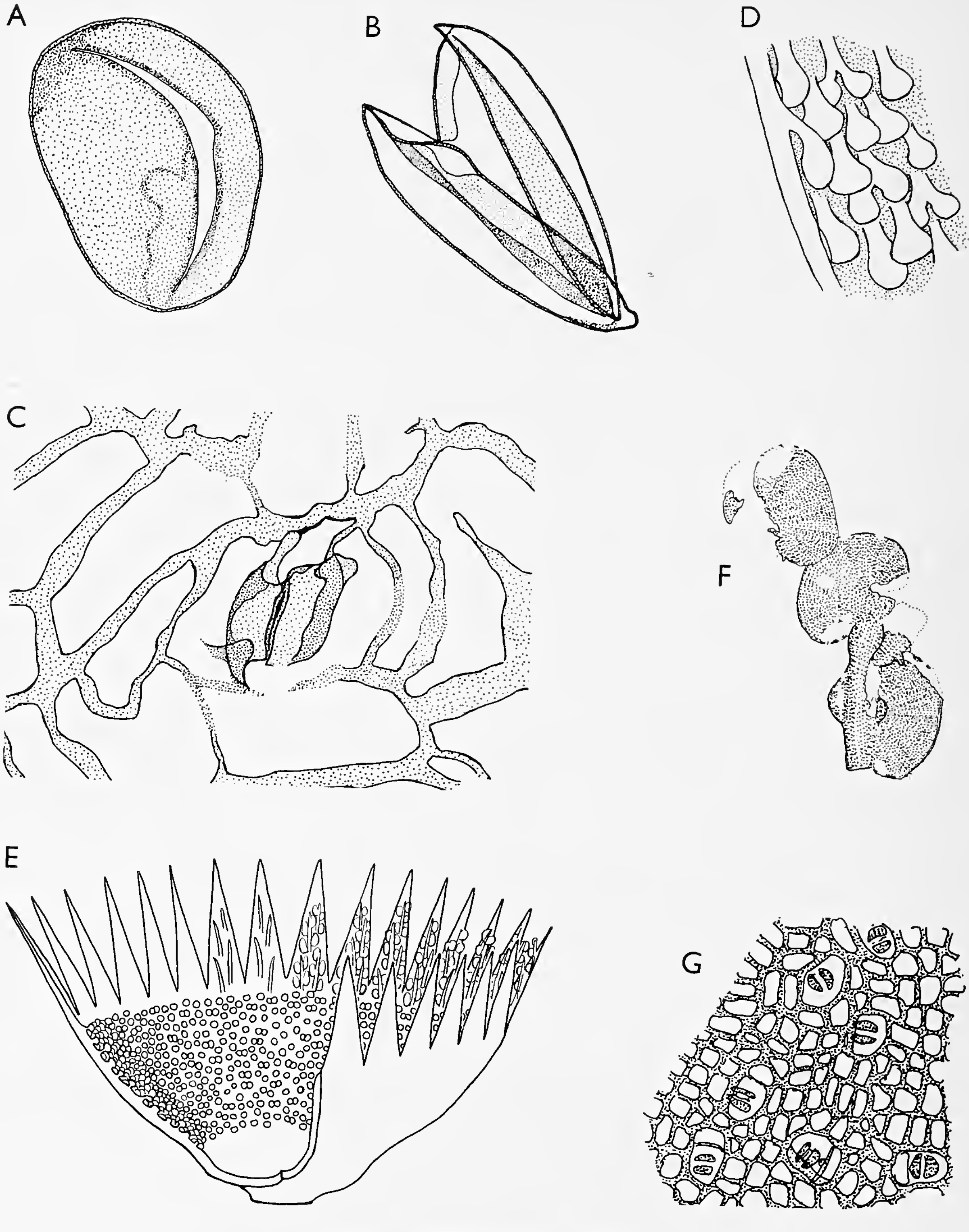

Fig. 69. **Weltrichia sol** sp. nov.
(male *Williamsonia gigas*)

A, B, pollen grains (B is burst), V.53458*a*, ×1000. C, stoma of ray, V.53458*b*, ×1000. D, restoration of 'resinous sacs' inside cup, ×about 5. E, restoration of whole flower showing 'resinous sacs' in cup and some of the pollen sacs on rays, about half natural size. F, pollen sacs, the one on the top left probably belongs to a different fertile branch, ×5. G, cuticle of ray, ×200.

A–E drawings by Miss M. Quin. The specimens A–C are from the Whitby *Zamites* Bed, those in F, G from Haiburn Wyke *Zamites* Bed.

without a papilla but sometimes bearing a papilla which may overlap a guard cell. Occasional stomata showing an encircling cell opposite one of the subsidiary cells. Trichomes absent.

Pollen grains oval with a longitudinal sulcus; length of grain 44–50μ, width 20–30μ (means 46μ long and 24μ wide); wall smooth.

The specific name refers to the resemblance of this flower to a picture of the sun.

Holotype. V.53458.

Discussion. Miss M. Quin drew up an account of this species based on one specimen. Subsequently a few further specimens were found in Museums which fitted readily into her account. Later still, when a search was made of a bed of *Zamites* leaves, additional flowers were found which made it necessary to add to her account.

Wherever I have found *Zamites gigas* leaves abundantly I have found flowers or at least ill preserved flower fragments but in much smaller numbers. As far as I can judge the male and female flowers may be equally frequent but the female are more robust and so better preserved and more easily recognised. I imagine that for some years after 1820 when many dozens, perhaps hundreds of female flowers were found at Saltwick, male flowers also were seen but if so they were thrown away. The only published figure is that of Seward (1900, pl. 8, fig. 1) and there is one other specimen in the British Museum. There is the remarkable K210 (Pl. 5, fig. 1) in the Leckenby Collection at Cambridge.

I think the specimen in the Paris Museum described by Hamshaw Thomas (1915*a*) as male *Williamsonia gigas* was rightly determined but I cannot be certain. It is an ironstone cast and is unlabelled. Since the rock matrix is like that of the numerous female flowers, Thomas felt sure it came from one of the two localities for these flowers and on this presumed association he based his determination. The study of other specimens supports his determination. From Thomas' pl. 6, fig. 2 it looks as though rays were numerous, at any rate over 20 (even though some of his drawings suggest fewer). Then the inwardly projecting branchlets agree with the fertile branches of *W. sol.* So too do the little clusters of pollen capsules. However the size is rather small for *W. sol* (though equally small specimens of *W. sol* do occur) and I cannot account for the rows of dots on the cup, corresponding to the ray midribs.

Certain specimens have been identified wrongly as *W. gigas* male flowers.

The early mistake caused by the idea that the flower we now call *W. whitbiensis* was borne on top of the *Williamsonia gigas* gynoecium caused confusion for nearly a century, and this continued in spite of Williamson's correction. The fact that Williamson thought the female *W. gigas* male added to the difficulty. So too *W. setosa* was for a short time regarded as the male appendage of the top of *W. gigas* (Nathorst 1909), but this he soon corrected (Nathorst 1911).

The present specimens are linked with *Z. gigas* (and *Williamsonia gigas*) on their association. First I would mention the imperfectly localised specimens. There is the holotype on a block of sandstone which includes a *Z. gigas* leaf and no other. Then there is Leckenby Coll. K210 in a very different matrix, an ironstone, which again has *Z. gigas* and no other leaf. We have two groups of localised specimens. There is V.53458 collected in a fallen block of the *Zamites* Bed at Whitby, a bed full of *Z. gigas* and with occasional female flowers but no other Bennettitalean leaf. Then there is a series of male flowers from the Haiburn Wyke *Zamites* bed, found as a result of deliberate search. This locality shows intense localisation both vertically and horizontally and at one point almost the only gymnosperms found were great numbers of complete *Z. gigas* leaves and a few pieces of *Williamsonia* (*Bucklandia*) stem, a few *Williamsonia gigas* flowers and five more or less good specimens of *W. sol.*

As *Zamites gigas* has only a moderate number of Yorkshire localities and the flowers are rare fossils, this repeated association convinced me that the three organs are parts of a single plant species. Earlier collectors were long ago convinced that the female flowers and leaves belonged to the same plants.

Although of less importance, there is distinct resemblance between the stomata of *Weltrichia sol*, *Williamsonia gigas* bracts and to a less extent those of the *Zamites gigas* leaf. In all the whole apparatus tends to be slightly sunken in a shallow, wide pit; an encircling cell may be present and a papilla may occur on one subsidiary cell.

Comparison. *W. sol* is distinguished from all Yorkshire species and indeed nearly all species by its great size. The cup is 7–8 cm. wide and the rays perhaps reached 12 cm. (but when the flower is flattened and split it may seem larger). The Yorkshire *W. pecten* and *W. whitbiensis* must have looked similar on the outside but their size is little more than half and they have about 12–14 rays instead of about 30. On the inside the organisation is different, for in *W. sol* the pollen sacs are not borne directly on the rays but on small appendages and the 'resinous sacs' are more numerous and crowded. *W. sol* is similar in its fertile branches to *W. spectabilis* but they are shorter. We know nothing about 'resinous sacs' in *W. spectabilis. W. setosa* is readily distinguished by its hairy exterior, pollen sacs directly on the rays and the little pointed appendages round the mouth of the cup.

Most of the species from other floras have flowers a good deal smaller than *W. sol*, but *W. santalensis* may be even larger. *W. santalensis* differs in its long pollen sacs instead of semicircular ones and in bearing large horn-like growths on the rays.

Weltrichia spectabilis (Nathorst) comb. nov.

Pl. 7, fig. 8

1909 *Williamsonia spectabilis* Nathorst, p. 6, pl. 1, figs. 1–3, 4a(?), 5, 6; pl. 2, figs. 1–10.
1911 *Williamsonia spectabilis* Nathorst; Nathorst, p. 5, pl. 1, figs. 1–11; pl. 3, fig. 1; text-fig. 1.
1913 *Williamsonia spectabilis* Nathorst; Thomas, p. 230, pl. 24, figs. 1*a*, *b*, 2 (not fig. 3); text-fig. 2.
1933 *Williamsonia spectabilis* Nathorst; Florin, p. 6, text-fig. 1*a*. (Stoma.)

Diagnosis. Flower consisting of a wide cup typically 4 cm. broad and 3 cm. long, borne on a short peduncle. Cup dividing at its top into about 13 rays; rays typically 10 mm. wide below, tapering to 3 mm. at 2–3 cm. from the cup and then continuing as a filiform extension for about 3 cm. (In largest flowers rays 13 mm. at base, tapering to 4 mm. in 4–5 cm. and filiform extension 5–6 cm. long. In smallest flowers parts probably two-thirds of normal size.) Filiform extension curved inwards. Rays sometimes showing a midrib. Substance of cup and rays very thick, conspicuously marked with crowded longitudinal striations, rays showing longitudinal striations and transverse wrinkles. Surface without hairs, inner face of rays bearing fertile branches; fertile branches borne in a longitudinal row on either side of the midrib and at intervals of 3–5 mm. Longest fertile branches (typically 15 mm.) borne at about 2 cm. from edge of cup but branches above and below shorter (in smallest flowers, fertile branches about 10 mm., in largest about 20 mm. long). Fertile branches bearing semicircular or broadly elongated pollen sacs about 1·0–1·5 mm. from base to free edge, 2·5–5·0 mm. from side to side, outer surface of sac nearly smooth, interior showing radiating striations caused by about 14 microsporangia. (Interior of cup not studied, no evidence for existence of 'resinous sacs'.) (Pollen sac presumed to be made up of two equal valves.)

Cuticle of cup and rays of medium thickness, cells mainly almost square, forming longitudinal rows. Walls straight, fairly conspicuous, surface flat. Stomata scattered but mostly transverse, not sunken; guard cells well thickened, subsidiary cells not papillate. Trichome bases not observed. Pollen grains oval, monocolpate, about $60\mu \times 36\mu$, walls thin, smooth. (Grains often split and appearing very narrow.)

HOLOTYPE. Specimen figured by Nathorst (1909, pl. 1, figs. 1–3, 5, 6).

DESCRIPTION. Though Nathorst and Thomas wrote fairly full accounts illustrated by good figures, they gave no diagnosis, so one is constructed here, mainly on the basis of their work. As Nathorst says, *W. spectabilis* is rare. We have the holotype collected by Nathorst from Whitby (Nathorst 1909) and perhaps the one in his pl. 1, fig. 4, but this might be *W. whitbiensis* for it does not show fertile branches. Then there are specimens figured by Nathorst (1911) also probably from Whitby, though I can find no statement. Thomas (1915) figured a fine specimen from Marske Quarry where he says it is 'not uncommon' and the counterpart of this is shown here. It supplied a few additional facts. Thomas's Marske specimen which must have been a good deal larger than those of Nathorst was probably once thick and coaly, but the coal had been oxidised away long ago leaving the fossil as brown stained imprints of the two faces which are somewhat different. In the counterpart figured here there is a very marked groove along each ray which looks like the sharply marked midrib on the adaxial side of *W. whitbiensis*. At the sides of this groove, half way between it and the margin, there is a series of small pits, placed opposite. The lowest are 6 mm. apart and the distance decreases upwards to about 3 mm. I interpret these pits as marking the points of attachment of the fertile branches. The crack through the specimen marks where it was broken and the left half shows no fertile branches and even the attenuated apices of the rays have vanished. The halves were received separately and I determined the left half as *W. whitbiensis* until I found they fitted together. Clearly then, there is a chance that specimens looking like *W. whitbiensis* may be denuded *W. spectabilis*.

This counterpart is superimposed on two leaves of *Otozamites gramineus*.

Leaf of *W. spectabilis*. It is possible that *Otozamites gramineus* belongs to the same plant. Nathorst writes of the association of *W. spectabilis* with '*Ptilophyllum pecten*' at Whitby (properly *P. pectinoides*) and indeed figures this association. He does not mention *Otozamites gramineus* (a species which is also common in the Whitby Plant Bed) and none of his figures show it. At that time he may have regarded it as a synonym of '*P. pecten*'. Thomas also writes about *P. pecten* in the sandstone of the Marske Quarry and figures a characteristic specimen of *O. gramineus* under this name. (Later as I know from what he told me he recognised that he had united many species under *P. pecten*.) As mentioned earlier Thomas' specimen has *O. gramineus* on the same bedding plane. I was unable to collect in the sandstone of the Marske quarry which was abandoned 50 years ago, but there is a large collection in Middlesbrough Museum. Here *O. gramineus* is very abundant indeed (so is *Zamites gigas*) but true *P. pecten* and *P. pectinoides* not represented. This association in two localities is less than convincing but suggests a possibility.

Nathorst (1909, 1911) discussed the comparative morphology of *W. spectabilis* very fully, comparing the pinnately branched ray both with a Bennettitalean leaf and with *Cycadeoidea*, but inevitably it was with the restoration of *Cycadeoidea* and not the strange and compact pollen producing organ itself. We now have *Weltrichia sol* with which to compare it more closely, and their basic structure seems to be the same.

OCCURRENCE. The two localities, the Whitby Plant Bed, and the Marske Quarry sandstone are both at the base of the Lower Deltaic.

Weltrichia pecten (Leckenby) comb. nov.
Pl. 6, fig. 6

1864 *Palaeozamia pecten* Leckenby, p. 77, pl. 9, fig. 4*a*, right. (Refigured by Nathorst 1909, pl. 2, fig. 11.)
1870 *Williamsonia pecten* (Leckenby); Carruthers, p. 694.
1880 *Williamsonia leckenbyi* Nathorst, in part, p. 39, pl. 8, fig. 5, left.
1891 *Williamsonia Leckenbyi* Nathorst; Saporta, p. 161, pl. 248, fig. 1.
1900 *Williamsonia pecten* (Phillips); Seward, in part (?), p. 190.
1909 *Williamsonia pecten* (Leckenby); Nathorst, in part, p. 8. (Reference to Cloughton specimens only), pl. 2, fig. 11 (Leckenby's holotype); pl. 3, figs. 1, 2.
1911 *Williamsonia pecten* (Leckenby); Nathorst, p. 19, pl. 5, figs. 1–8; pl. 6, figs. 1, 2 (middle flower), fig. 3 (left).

DIAGNOSIS. Flower detached without a stalk, consisting of a wide cup dividing at its edge into about 10–12 rays. Cup typically 4 cm. wide (3–5 cm.). Rays typically 3 cm. long, ends incurved. Substance of rays and of cup originally thick but readily rotting away to leave only fibres enclosed in the cuticle. Both surfaces of cup without hairs, showing conspicuous striations caused by longitudinal fibres but without transverse wrinkles. Fibres usually separated from neighbours. Rays bearing two rows of pollen capsules (synangia), rows continued downward into centre of cup by two rows of 'resinous sacs' or 'abortive synangia'; pollen sacs readily falling off at maturity. Pollen sacs semicircular, short stalked typically 3 mm. broad × 1 mm. from base to apex. 'Resinous sacs' smaller and size progressively reduced to centre of cup, firmly attached by a broad base; contents dense and highly resistant to maceration.

HOLOTYPE. Specimen figured by Leckenby (1864, pl. 9, fig. 4*a*, right) and by Nathorst (1909, pl. 2, fig. 11).

DESCRIPTION. *W. pecten* is frequent in the Cloughton Wyke *Solenites* Bed (the main plant bed) and all the specimens previously figured are from there. The specimens collected by Hamshaw Thomas and myself are very like those described by Nathorst (1909, 1911) and there is no need to give figures, which are virtually repetitions. The flower shown in Pl. 6, fig. 6, is better preserved than most, it is small and seems to have only 10 or 11 rays.

In addition there is a single imperfect specimen from the Gristhorpe Bed which seems to be *W. pecten.*

Most of the Cloughton specimens had rotted before preservation and often very little of the substance remains, merely brown cuticles enclosing scattered fibres. Nearly all the specimens are vertically compressed, the small flower figured by Nathorst (1911, pl. 5, figs. 1, 2) being the outstanding exception. Nathorst describes this flower as 'young' and this may be true, but in the collection I have studied small flowers of *W. pecten* seem just as mature as normal or large ones, for all have lost nearly all their pollen sacs.

Many specimens were made into balsam transfers in the hope of seeing well preserved pollen sacs, but all those treated proved to have lost them or shed the few remaining during preparation and the inner surface of the rays merely shows damage or at best little scars. The 'resinous sacs' on the other hand nearly always remain inside the cup. The few pollen sacs of the present collection are like those which Nathorst found attached. The present ones had shed their pollen, but numerous grains of a single kind remain sticking to the granular membrane lining the sporangia.

Discussion. Nathorst described *W. pecten* and the closely similar *W. whitbiensis* very well and the present material of the two which must be as rich as Nathorst's, even with balsam transfers has added scarcely anything. In particular I express full agreement with Nathorst's restoration of *W. whitbiensis* (which would serve just as well for *W. pecten*). This well known drawing has been reproduced by Seward (1917) and by others and there is no need for me to repeat it. Previous writers have agreed in regarding the flower as a whorl of microsporophylls which are concrescent below, an idea which appears reasonable in relation to *Williamsoniella* but for which additional support would be welcome. After all we know nothing of the origin of the Bennettitales.

Comparison. Nathorst only gradually separated this species from *W. whitbiensis* and the differences even now remain vague. Indeed, but for the fact that I feel sure they belong to different 'real' species, I would unite them. In trying to define the differences, I have started, like Nathorst, with the assumption that all the Cloughton specimens are the one species and all the Whitby specimens the other and then that the numerous specimens of both groups that fail to show clear characters are merely ill-preserved. I considered whether some of the differences might be caused by the matrix in which they are preserved (the Whitby rock has coarser grain), but I think not because *W. whitbiensis* also occurs in fine grained shales elsewhere when it still has the same characters.

The differences are:

1. *W. whitbiensis* (as Nathorst remarked) is more 'woody'. *W. pecten* is often preserved as a mere cuticle enclosing a few scattered fibres while I never found *W. whitbiensis* in this state. Moreover the fibres of *W. whitbiensis* are much more numerous and in lateral contact instead of being separated.

2. *W. pecten* may be more widely open when mature as it is nearly always preserved as a vertical compression while *W. whitbiensis* is equally common compressed vertically or laterally and sometimes obliquely. This is true both in coarse and in fine sediments. This statement is based on a considerable number of specimens of each species.

3. It is possible that *W. pecten* flowers tend to be rather smaller (though the size range certainly overlaps). Thus the flower of *W. pecten* in Pl. 6, fig. 6, which has only about eleven rays, may be outside the normal range of *W. whitbiensis*. However most of the *W. pecten* flowers are so poorly preserved that I am unsure of their size and of the number of their rays.

4. Nathorst considered that the tips of the rays are more incurved in *W. pecten* but I am not sure about this for certain specimens of *W. whitbiensis* are strongly incurved, nor do I feel sure about possible differences in the shape of the rays in section (recurving of margins) for this is easily obliterated in compression.

5. Nathorst considered that the synangia in *W. whitbiensis* are more thickly cutinised, but in my specimens they proved similar.

6. The 'resinous sacs' seem rather more strongly resinous in *W. pecten* but this may be an effect of preservation.

7. The cuticles may be slightly different for in *W. whitbiensis* the lower cuticle showed more stomata and with bigger subsidiary cells while the upper had more sinuous walls. However a good many specimens of both gave unsatisfactory preparations and I cannot feel sure that these differences are reliable.

8. The pollen grains inside the opened pollen sacs were compared. Those of *W. whitbiensis* may be a little thinner-walled and smoother, but they looked very similar. The length was reasonably constant but the width varied grossly, no doubt because of distortion. The lengths of two samples of ten grains of each species were measured (from two flowers in *W. pecten*) but two pollen sacs of the same flower in *W. whitbiensis*.

W. whitbiensis	48μ; σ 3μ
	44μ; σ 6μ
W. pecten	44μ; σ 6μ
	45μ; σ 6μ

In each species the longest grain noted was 53μ long and the shortest 35μ in *W. whitbiensis*, 37μ in *W. pecten*. There is no distinction in such data.

Thus the only distinctions which are clear are two obvious but not very satisfactory ones. *W. whitbiensis* is 'woody' while the substance of *W. pecten* though perhaps as thick rots away. And *W. pecten* may be more widely open since it, unlike *W. whitbiensis*, is almost always compressed vertically. Finally there is the fact that *W. whitbiensis* is associated with *Ptilophyllum pectinoides* and *W. pecten* with *P. pecten*.

W. alfredi (Krasser) 1917 from the Lower Lias of Hungary, an imperfectly known fossil, may be very like *W. pecten* and *W. whitbiensis*.

The evidence that *W. pecten* belongs to the same plant as *Ptilophyllum pecten* is merely that of their striking association at Cloughton, where in the main plant bed *P. pecten* abounds in certain layers and here the male flowers also are found. Along with them are *Williamsonia leckenbyi* and *Cycadolepis nitens*. Of other Bennettitalean leaves in this bed, by far the commonest is *Nilssoniopteris vittata*, but we believe we know its flower (*Williamsoniella*). Several other Bennettitalean leaves do occur but they are rare and not associated with the flower.

At the Gristhorpe Bed *Ptilophyllum pecten* is very local. There is nothing to show whether the specimen from Gristhorpe occurs in the particular part of the bed where *P. pecten* is found.

Weltrichia whitbiensis (Nathorst) comb. nov.
Pl. 7, figs. 5, 7, 9, 10

1828 'Head of a plant', Young & Bird, p. 191, pl. 1, fig. 2. (This specimen, which confused the interpretation of *Williamsonia gigas* has been refigured, see Williamson, Nathorst and Krasser below.) This flower has surmounted many restorations of *Williamsonia gigas*.
1870 *Williamsonia pecten* (Leckenby); Carruthers, p. 694.
1870 'Carpellary disc' Williamson, pl. 52, fig. 1.
1900 *Williamsonia pecten* (Phillips); Seward, in part, p. 190, pl. 2, fig. 7 only.
1909 *Williamsonia pecten* (Leckenby); Nathorst, in part, p. 8, pl. 1, fig. 4*b*; pl. 2, figs. 12–15.
1909 *Williamsonia bituberculata* Nathorst, p. 10, text-fig. 1. (Williamson's carpellary disc.)
1909 *Williamsonia gigas* funnel-shaped appendage, Nathorst, p. 12, text-fig. 2.

1911 *Williamsonia whitbiensis* Nathorst, p. 9, pl. 2, figs. 1–15; pl. 3, figs. 2–9; text-figs. 1–3, including *W. bituberculata* (pl. 3, figs. 8, 9).
?1911 Young *Williamsonia* flowers, Nathorst, p. 8, pl. 1, figs. 12–15; pl. 3, fig. 2.
1911 *Williamsonia* sp., Nathorst, p. 16, pl. 3, fig. 10. (Same specimen as Seward, 1900, pl. 2, fig. 7.)
1911 Williamson's carpellary disc, Nathorst, p. 14, pl. 3, figs. 8, 9.
1912 *Williamsonia Whitbiensis* Nathorst; Krasser, p. 968, pl. 11, figs. 13, 14.
1917 *Williamsonia Whitbiensis* Nathorst; Krasser, pl. 3, fig. 6 (Nathorst's figure reproduced); pl. 3, figs. 4, 5 (Krasser's 1912 figures reproduced). The *W. bituberculata* figure reproduced on pl. 1, fig. 3.
1917 *Williamsonia Sewardi* Krasser, pl. 3, figs. 1–3. (*W. pecten* of Seward 1900, pl. 2, fig. 7; pl. 3, fig. 8, reproduced with one new figure.)
1917 *Williamsonia Whitbiensis* Nathorst; Seward, p. 441, text-figs. 555, 556. (Some of Nathorst's figures reproduced; discussion.)
1933 *Williamsonia pecten* (Leckenby); Florin, p. 10, pl. 1, fig. 2. (Stoma.)

DIAGNOSIS. Detached flower with almost no stalk, consisting of a wide cup dividing into 13–16 rays. Cup typically 4 cm. broad, 2·5 cm. deep (largest about 5 cm. broad and 3–4 cm. deep, smallest 3·3 cm. broad). Rays typically 1 cm. wide at the base and nearly 4 cm. long, tapering to the point; apex distinctly incurved and margins distinctly recurved. Substance of cup and rays robust, not readily rotting; outer surface longitudinally striated (striations probably marking crowded fibres). Transverse wrinkles absent, or if present inconspicuous. Hairs absent. Rays bearing two rows of pollen sacs ('synangia'), rows continued into cup as 'resinous sacs'.

DESCRIPTION. *W. whitbiensis* is reasonably common and well preserved at Whitby, mainly in blocks fallen from the upper part of the bed. (Recently this locality has been unproductive.) Scattered specimens have been found in several other localities and at Hasty Bank where it is common, but it is preserved in a very crumbly shale which seldom gives a really good specimen.

Most of the present material adds nothing to the account given by Nathorst (1909, 1911) of this species, though the discovery of specimens in several new localities in association with *P. pectinoides* is useful. However, one specimen, because of its unusual preservation, does give some new facts.

This specimen V.27625 (Pl. 7, figs. 7, 9, 10) from Ravenscar is preserved in a hard sandstone which has saved it from compression but the finer details have been lost. The substance has vanished leaving a cavity which has filled with powdery kaolin. Thus part and counterpart are moulds giving the very different imprints of the inner and outer surfaces. The general shape is similar to that of another uncompressed flower, V.3688, drawn by Seward (1900, pl. 2, fig. 7) and photographed by Nathorst (1911, pl. 3, fig. 10).

The cup is a nearly hemispherical basin. At their bases the rays diverge, but then curve gently inwards so that at their apices they may be diverging only slightly from the vertical. As in some other specimens there is local tearing at the bases of the rays.

The outer mould shows nothing of the pollen sacs but has strong longitudinal ridges, and I presume the grooves between these ridges are the veins though I cannot be certain. The inner mould does not show these veins but on the rays are conspicuous pollen sacs (six pairs on the lower 3 cm. of the longest but incomplete ray). In addition there is a single strong groove representing a midrib passing down each ray and on to the cup. Small and obscure pits on the cup may represent the 'resinous sacs'. This mould of the inner face corresponds to the core seen in V.3688 (mentioned above) where the midribs are plain.

The specimen gives all we know of the vascular system. This then, consists of a large number of equal and nearly parallel bundles in the outer tissues. These bundles run up the cup, forking at various levels and about six pass into each ray. Here they continue almost parallel, and the lateral ones seem to end in the margins. On the inner side is a set of strong bundles running uninterruptedly up the cup and then up the middle of each ray. This bundle looks as though it was the supply of the pollen sacs but no branches to sacs were detected.

This specimen must be very similar to the one described first by Young & Bird (1828) which was later, as the 'carpellary disc', to confuse Williamson's account of *Zamites gigas* and was only satisfactorily placed by Nathorst (1911). The main differences are that the grooves on the outer face are stronger and look more like veins and that the pollen sacs all remain, not just the lower ones. I cannot explain why the vascular bundles should stand out as strong grooves in this specimen (in sandstone) but be so indistinct in specimens in fine shales. Some of the shale specimens however do show less distinct ribs, particularly the midribs on the inner faces.

Plant bearing *W. whitbiensis*. In six localities *W. whitbiensis* is associated with many leaves of *Ptilophyllum pectinoides* and there is no other leaf with which there is any reason to link it. This evidence even in the absence of specific agreement in structure seems sufficient. The other organs of the same plant are *Williamsonia hildae*, *Cycadolepis hypene* and the stem *Bucklandia pustulosa*. We have continuity for the stem, leaves and female flower but we know nothing about the way this almost stalkless male flower was borne.

Occurrence. *W. whitbiensis* has been found in seven localities, all Lower Deltaic. The first of these is in a fallen block of sandstone from Ravenscar where it has no known associates but in the other six *Ptilophyllum pectinoides* is abundant, and sometimes the only recorded leaf.

The localities are:

Ravenscar, fallen block just E. of fault.
Whitby Long Bight Plant Bed, the classic locality and origin of all the figured specimens.
Roseberry Topping Plant Bed.
Hasty Bank Plant Bed.
Hawsker, fallen blocks at Widdy Field at 54° 28′ 12″ N.
Beast Cliff, fallen, *Williamsonia* Bed at 54° 23′ 7″ N.
Beast Cliff, fallen, 'Red House' Plant Bed at 54° 21′ 46″ N.

Genus BUCKLANDIA Presl

1825 *Bucklandia anomala* (Stokes & Webb) Presl, p. 33; for *Clathraria anomala*.
(*Bucklandia* R. Brown 1832, Hammamelidaceae, is a later homonym.)

Whatever the nature of *B. anomala* (see Seward 1917) the name has come to be used for Mesozoic stems of moderate thickness and bearing relatively large leaf scars. They are preserved variously as compressions, as casts or even with cellular structure, and the main thing they have in common is that they are all supposed to belong to Cycads or Bennettitaleans.

Very few stems of this kind have been described from the Yorkshire Deltaics, but they are nevertheless frequent. Collectors have neglected them. Though they make striking fossils they are uninformative and seldom make clear species. For this last reason I have restricted myself to describing only two under specific names and have mentioned two others without names. The two named are *B. gigas* Seward attributed to *Zamites gigas* and *B. pustulosa* attributed to *Ptilophyllum pecten* (and at present indistinguishable from the stems attributed to *P. pectinoides*).

Bucklandia pustulosa sp. nov.

Pl. 6, figs. 2, 4, 8; Text-fig. 59

DIAGNOSIS. Stem of varied size. At its smallest 7–10 mm. wide, nearly straight, but ending at a flower scar and continued by a branch at an angle. Surface showing scattered leaf scars arranged in a spiral. Scars rhomboidal nearly 3 mm. broad by nearly 2 mm. high or in places flatter and only 1 mm. high. Surface also showing scattered rounded lenticels about 1 mm. in diameter. In some specimens surface also showing ill-marked longitudinal ridges (? caused by internal fibres); ridges often 5 mm. long and 0·5–1·0 mm. apart. In the holotype and all other specimens epidermis missing but whole surface (apart from leaf scars and lenticels) formed by a uniform layer of cork. Cells of cork about $40\mu \times 30\mu$, bulging, forming ill-marked longitudinal rows. Internal structure not known but stem apparently woody and fairly compact.

Larger stems known from isolated fragments of bark. With enlargement, leaf scars becoming extended laterally and then not recognisable and number of lenticels increasing to be more numerous per sq. cm. and also more prominent than in small stems.

Large pieces of detached bark no longer showing leaf scars but lenticels still more numerous and prominent and tending to form short vertical files. Cork cells exactly as in smaller stems, longitudinal ridges not seen on surface but surface often marked with short and irregularly placed transverse cracks (of unknown origin). Inner surface showing narrow elongated cells (? phloem). Substance of bark including separate coarse fibres.

HOLOTYPE. V.53464.

DISCUSSION. *B. pustulosa* is very common in the Cloughton *Solenites* Bed with *Ptilophyllum pecten*, large slabs of bark being abundant and pieces overlapping repeatedly in certain layers of rock. The largest pieces seen were 35 cm. long and 15 cm. broad but both must have been larger when preserved for they were broken when collected.

Specimens of all sizes were macerated but none has any cuticle. The first effect of maceration is that the substance crumbles to powder and when the maceration of the powder is completed the chief product is small brown cells—the cork cells. With less full maceration traces of internal tissue can be seen, but nothing clear enough to describe.

The leaf scars do not, unfortunately, show clear vascular bundle prints.

A number of Recent barks were examined for comparison. In some plants (for example woody species of *Paeonia*, *Rubus deliciosus*, *Lavendula vera*) a deep cork is formed early and the outer tissues peel off and are soon lost, but in most woody Dicotyledon stems the epidermis and cuticle are retained for a good many years and merely crack as the surface expands. *B. pustulosa* is evidently a plant in which the surface is thrown off early. Maceration of a number of Recent barks gave consistent results. Where the epidermis is still present the cuticle gave a normal preparation but the deep or superficial cork behaves differently. The cork cell wall substance is as resistant as the cuticle but the cementing matter dissolves so that complete cork cells come apart from one another in the ammonia. This is the same as in our fossil.

The evidence for attributing *B. pustulosa* to the same plant as *P. pecten*, *Williamsonia leckenbyi* and other organs is that of association in one locality and the fact that the leaf scars are suitable. It is powerfully reinforced by the evidence that a very similar slender stem (one I cannot distinguish from *B. pustulosa*) is known to have borne *W. hildae* and *P. pectinoides*, while fragments of bark of broader stems are associated with that leaf and flower in at least three localities.

Bucklandia gigas Seward
Pl. 6, fig. 5

1870 Stem of *Zamia gigas*, Williamson p. 665, pl. 53, fig. 5.
1875 *Zamites gigas* (stem) Saporta p. 56, pl. 11, fig. 1. (Redrawn by Seward 1917.)
1917 '*Williamsonia* (*Bucklandia*) *gigas*' Seward, p. 425, text fig. 541 (specimen in Yates collection, Paris). Specimen figured 'imperfectly', by Saporta (1875).

Diagnosis. Stem 4–5 cm. broad, in old parts denuded and marked with crowded, spirally arranged rhomboidal leaf scars. In younger parts, stem thickly covered with persistent overlapping petioles giving it an apparent width of 8–10 cm. Petioles broken off at about 10 cm. above the base, 4–5 mm. thick, arising at a small angle but usually curving outwards. Petioles showing longitudinal ridges (apparently caused by internal fibres); cuticle well developed, structure apparently dorsiventral. Epidermal cells 30μ wide, walls on one side very prominent and broad, on other side less prominent.

On side with thick walls, cells uniform but on other side a few stomata and a few ramentum bases occurring. Stomata longitudinal, small, with small lateral subsidiary cells. Ramentum bases up to 200μ broad, composed of many narrow cells.

Discussion. I have attributed the species to Seward (1917) but he only gave the name in passing and with a figure and brief description.

The stem figured here shows the top 30 cm. (the lower part being broken off in collecting) Beside it is another, similar stem fragment over 20 cm. long and broken at both ends. Neither stem branches or bears a peduncle. In both the shaggy covering of leaf bases persists to the base unchanged.

The figured stem seems to agree with that of Seward which still bears *Z. gigas* leaves and also has peduncles. Additional reasons for attributing the present specimen to the *Z. gigas* plant are first its close association. The block was collected immediately below the layer of the Haiburn *Zamites* Bed richest in *Z. gigas*. It shows an indistinct imprint of *W. gigas* and on the back many *Z. gigas* rachises lying parallel through current bedding. There is nothing else determinable on the block and in the whole bed there is no other leaf in the least likely to belong to this stem.

Secondly the cuticles of the petiole bases in this specimen match those of the petioles and midribs of *Z. gigas*. (Though ramenta are lacking on the leafy rachis.) This stem differs from that attributed by Williamson to *Z. gigas* which shows the stem surface covered by rhomboidal scars. I suppose Williamson's stem was rightly determined but represents an older stage when all the petioles have fallen off.

The peduncles of *W. gigas* differ considerably from the leafy stem for they are thinner and covered by persistent scale leaves.

Williamson gave restorations of the *Z. gigas* plant as a rather slender unbranched palm bearing the artichoke-like flowers on short (often forked) peduncles near the top. I support this restoration, but I believe that the thick coat of persistent petioles in the upper part would have given it a very untidy aspect, very like many palms. It is not known whether the upright stems continued growing after flowering, but the lack of any specimen showing an old peduncle scar in the lower part suggests that perhaps it did not. Further study of these stems is needed.

Bucklandia sp. A
Pl. 6, fig. 7

This stem is represented by two specimens, very probably from the same locality. Both are preserved in a coarse sandstone. The first collected was found by Sewell at Goathland in 1928 and passed to Hamshaw Thomas. It is 15 mm. wide below, 10 mm. above and resembles the figured specimen except that it has no flower scars and arises as a branch on a larger but similarly marked axis about 20 mm. wide.

The second, collected by me in a small cliff 180 yards N. of the N. end of Goathland Station, in the Sycarham Series. It is about 15 mm. wide and shows two roundish lateral scars which clearly belong to naturally shed branches and strongly suggest the scars of some sort of reproductive organ, cone or flower.

The Sewell specimen has lost all organic substance and the later one, though still with some coal, yielded no cuticle.

There is little reason to attribute *Bucklandia* sp. A to the same plant as a particular leaf. A few specimens of *Pachypteris lanceolata* occurred in the same bed as my specimen and at a rather lower level there is a different bed with abundant *Nilssonia* fragments resembling *N. kendalli*. Both species may have had leaf bases of about the size and shape as the scars on this stem. The large 'cone scars' would seem suitable for a *Beania* or *Androstrobus* or a Bennettitalean flower but not for any organ we know as belonging to *Pachypteris*.

Bucklandia sp. B
Pl. 6, fig. 1

The only specimen is the one figured. It resembles a bent and rather swollen knee and show broad leaf scars, the clearest being 14 mm. × 4 mm. The surface between the scars is smooth apart from slight longitudinal ridges. At the swelling the leaf scars are crowded and flatter than they are above and below. A band of small lumps (possible vascular bundle prints) occurs across the leaf scar but they are not fully convincing. No distinct lenticel was seen. On maceration it gave no cuticles. *Bucklandia* sp. B is associated on the hand specimen with *Nilssonia compta*, the commonest leaf in most of the Gristhorpe Bed. I do not attribute any special significance to this association, though the shape and size of the leaf scars is suitable. A number of other leaf species occurring in the Gristhorpe Bed might equally well belong to it.

Bucklandia sp. B has a good deal in common with the slender state of *B. pustulosa* but differs in its greater width, broader leaf scars and perhaps also in the absence of obvious lenticels, though it is possible that it is only young and that they would be formed later. The Swedish Rhaetic stem, *Clathraria saportana* Nathorst (1878) is even more similar. Nathorst mentions the possibility that it might have borne *Nilssonia pterophylloides* or *Ptilozamites*.

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INDEX

Principal taxonomic names and the page numbers of principal references are printed in **Bold** type.
An asterisk * indicates a figure.

PLATES

PLATE 1

Williamsonia gigas Carruthers

Whitby

FIG. 1. Details of gynoecium from Fig. 7 also immersed in oil. $\times 50$.

FIG. 6. Young flower, dry and as originally exposed, V.53006. $\times 1$.

FIG. 7. Same flower as Fig. 6 immersed in oil and with one of the scales fully exposed at the top and others at bottom left. At bottom right is an organ resembling *Ixostrobus* (to be described later). $\times 1$.

Cycadolepsis thysanota sp. nov.

Whitby

FIG. 2. Scale leaf immersed in oil, V.53450. $\times 2$.

FIG. 3. Holotype specimen, immersed in oil, V.53449. $\times 2$.

Ptilophyllum pectinoides (Phillips)

Roseberry Topping

FIG. 4. Form with pinna bases that are not at all decurrent. $\times 2$.

FIG. 9. Specimen with distinctly decurrent pinnae, V.52964. $\times 2$. Photo retouched by whitening background.

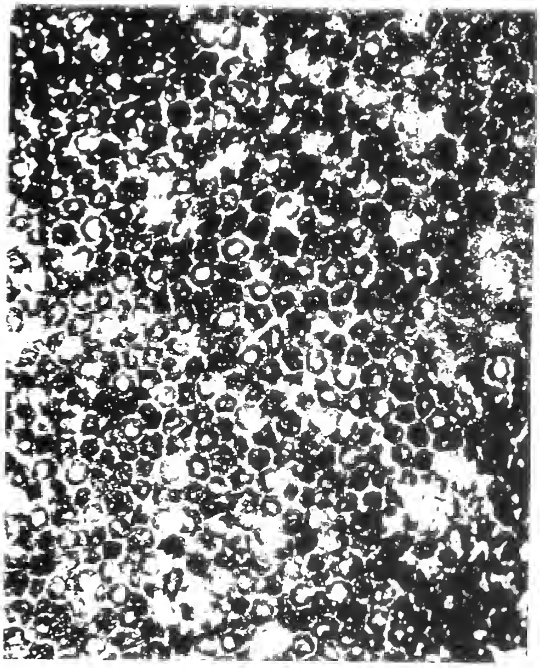
Otozamites anglica (Seward)

Whitby

FIG. 5. Apex of small leaf, V.52866. $\times 1$.

Otozamites leckenbyi sp. nov.

FIG. 8. Specimen K.220 in the Leckenby Collection, Cambridge. $\times 1$.



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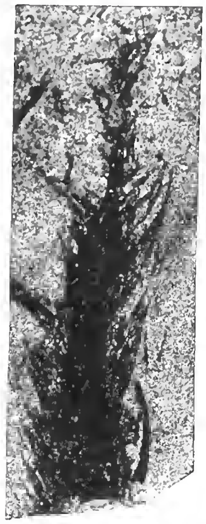

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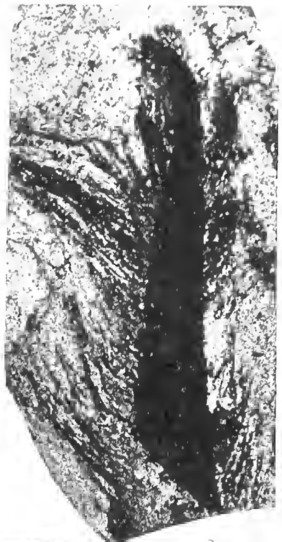

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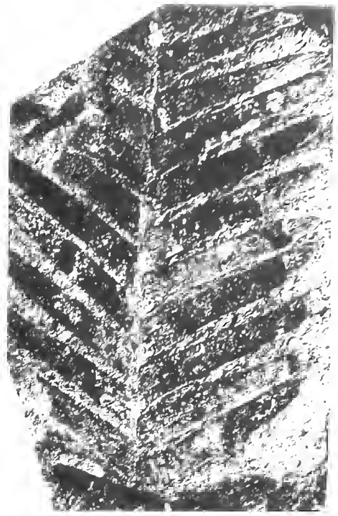

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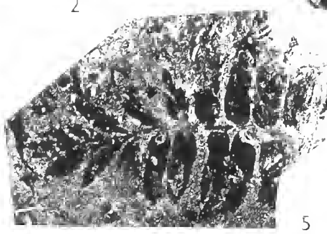

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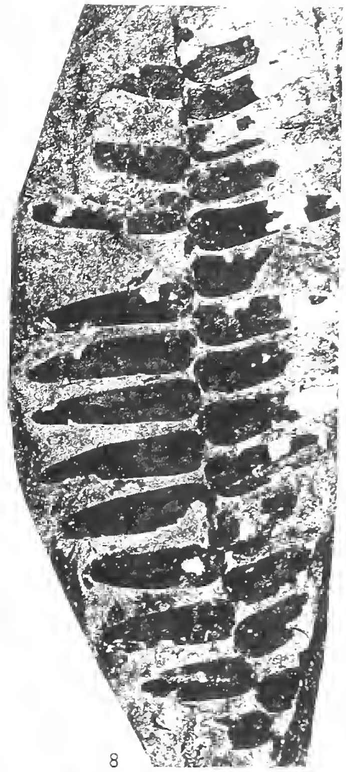

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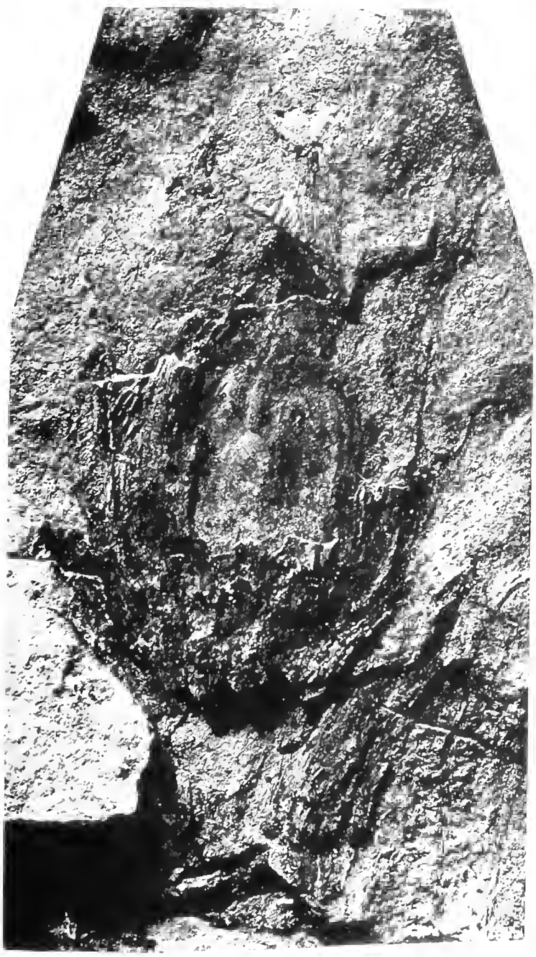

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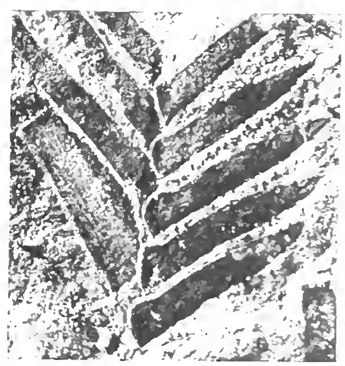

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PLATE 2

Williamsonia hildae sp. nov.

Part and counterpart of two flowers. Marske Quarry

FIG. 1. The upper flower shows the corona and the lower the palisade ring and stalk. The light is from bottom right, V.52976. ×2.

FIG. 2. The upper flower now shows its palisade and the lower the corona. The light is from the top right. ×2.

Williamsonia leckenbyi Nathorst

All from Cloughton, *Solenites* Bed

FIG. 3. Gynoecial axis, the base and some detached fragments of armour are omitted. Photo under oil, V.52988. ×2.

FIG. 4. Broken gynoecial axis. The corona is at the apex and the palisade and some of the peduncle below (small fragments around the axis belong to other plants). Photo under oil, V.52992. ×2.

FIG. 5. Top of gynoecial axis showing projections at the base of the corona, V.52978. ×2.

FIG. 6. Detached fragment of gynoecial armour, cuticle alone remaining. Photo under oil, V.52989. ×2.

FIG. 7. Vertically compressed top of gynoecium (coated with NH_4Cl). The corona (white) is at the top, V.52979. ×1.

FIG. 8. Corona of Fig. 7. ×10. See also Text-fig. 58B.

FIG. 9. Apex of laterally compressed corona, V. 52985. ×10. See also Text-fig. 58A.

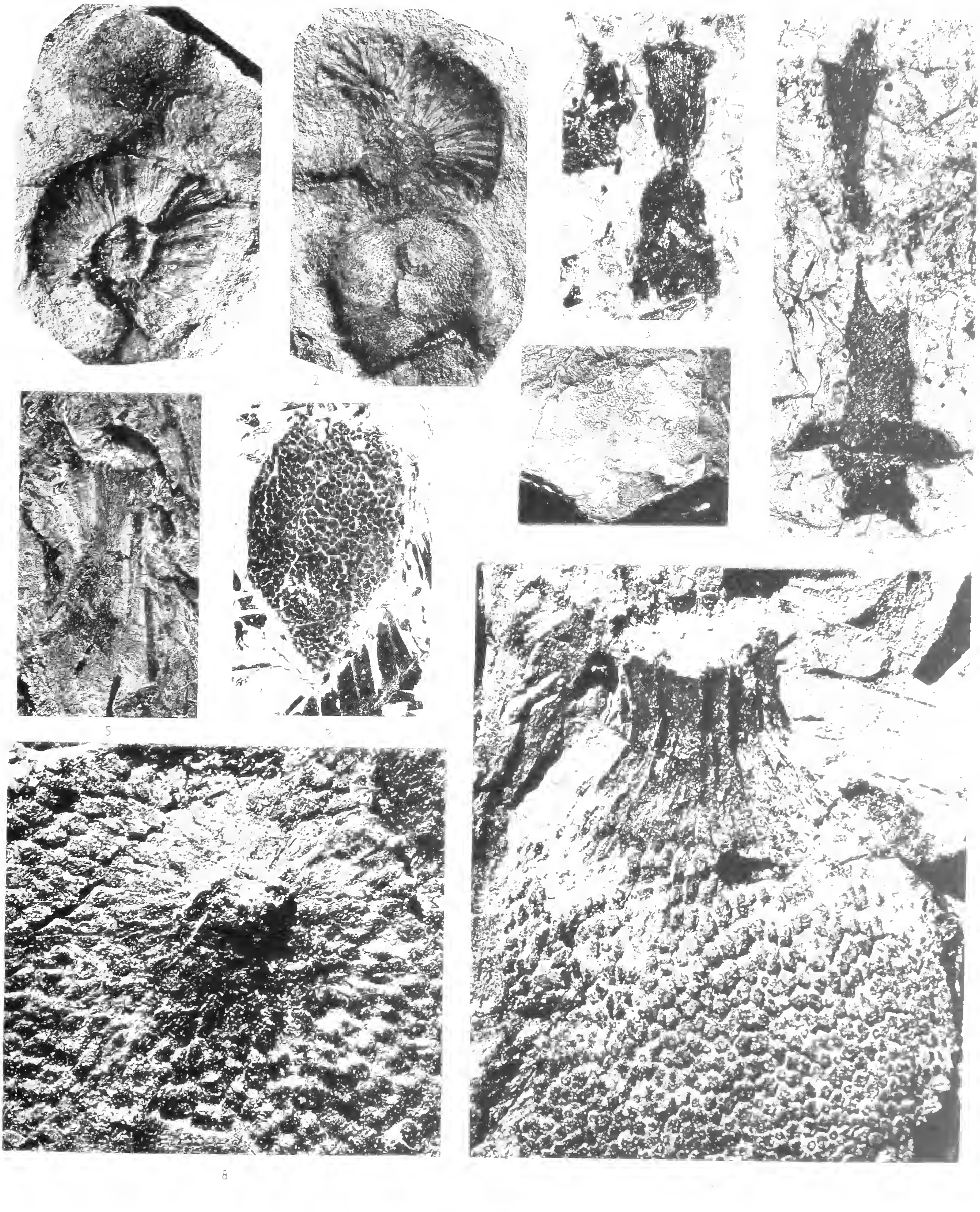

PLATE 3

Williamsonia leckenbyi Nathorst

FIG. 1. Complete gynoecium. Gristhorpe Bed, V.52982. ×1.

FIG. 6. Transversely broken gynoecium showing on left seed imprints. Cloughton Wyke, V.52990*a*. ×2.

FIG. 8. Laterally compressed gynoecium with corona. (Corona subsequently macerated.) Cloughton, V.52993. ×4.

Williamsonia hildae sp. nov.

FIG. 2. Peduncle and lower part of denuded gynoecial receptacle. Most of the palisade ring has broken away. Hasty Bank, V.52977*b*. ×2.

FIGS. 3, 4. Counterpart of specimen in Fig. 2 under different lighting. Fig. 3 shows the palisade ring, Fig. 4 the peduncle scars.

FIG. 5. Base of gynoecium. Whitby Plant Bed, V.52968. ×2.

FIG. 7. Transversely broken gynoecium (resembling Fig. 6). Probably Whitby, V.52969. ×4.

FIG. 9. Apex of gynoecium with corona. Probably Whitby, V.52970. ×4.

FIG. 10. Female flower in bud showing the peduncle imprint (bottom) and overlapping scales. Hasty Bank, V.52973. ×1.

FIG. 11. Same bud as in Fig. 10 but with scales removed to expose the small gynoecium. Note scale scars on peduncle. ×4.

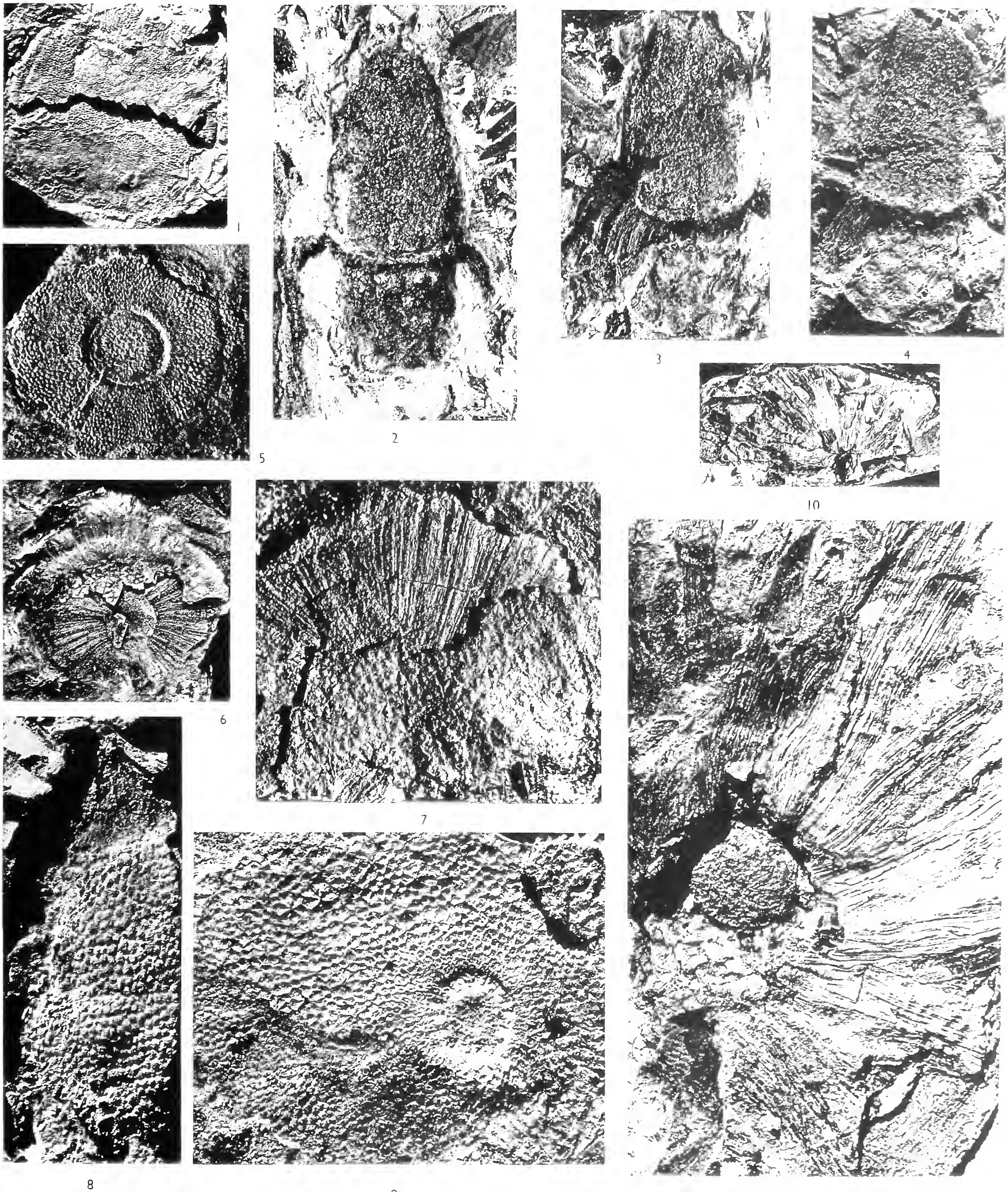
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PLATE 4

Williamsonia hildae sp. nov.

Hasty Bank

FIG. 1. Base of flower with bent back palisade ring and denuded gynoecial axis, V.53409. ×2.

Bennetticarpus diodon sp. nov.

Gristhorpe Bed

FIG. 2. Holotype specimen showing some of the bracts, on the left, V.23953. ×4.

FIGS. 5, 6. Two views of gynoecium under different lighting, V.53396. ×4.

FIG. 10. Part of Fig. 5. ×10.

Williamsoniella coronata Thomas

Gristhorpe Bed

FIG. 3. Two detached microsporophylls, V.53401. ×2.

FIG. 4. Peduncle and gynoecium, V.53403. ×2.

FIG. 7. Peduncle and involucral bracts (gynoecium at deeper level), V.53400. ×1.

FIG. 8. Same as Fig. 7. ×2.

FIG. 9. Small isolated gynoecium, V.53404. ×2.

FIG. 12. Peduncle and gynoecium (slender), V.53402. ×2.

FIG. 13. Forked stem, resembling the stem attributed to *W. coronata* by Thomas, V.53399. ×1

Bennetticarpus litchi sp. nov.

Beast Cliff

FIG. 11. Details from Fig. 18, showing the surface imprint. ×3.

FIG. 14. Counterpart of specimen shown in Figs. 17, 18. The imprint shows spindle shaped seeds, V.53394. ×1.

FIG. 17. Holotype as collected; in the upper part imprints of seeds are seen, V.53394. ×1.

FIG. 18. Holotype after removal of all coal, imprint of base of fruit covered with interseminal scales and showing the large peduncle. ×1.

Bennetticarpus fragum sp. nov.

Hawsker

FIGS. 15, 16. Part (photo under oil) and counterpart (dry) of the holotype specimen, V.53392. ×2.

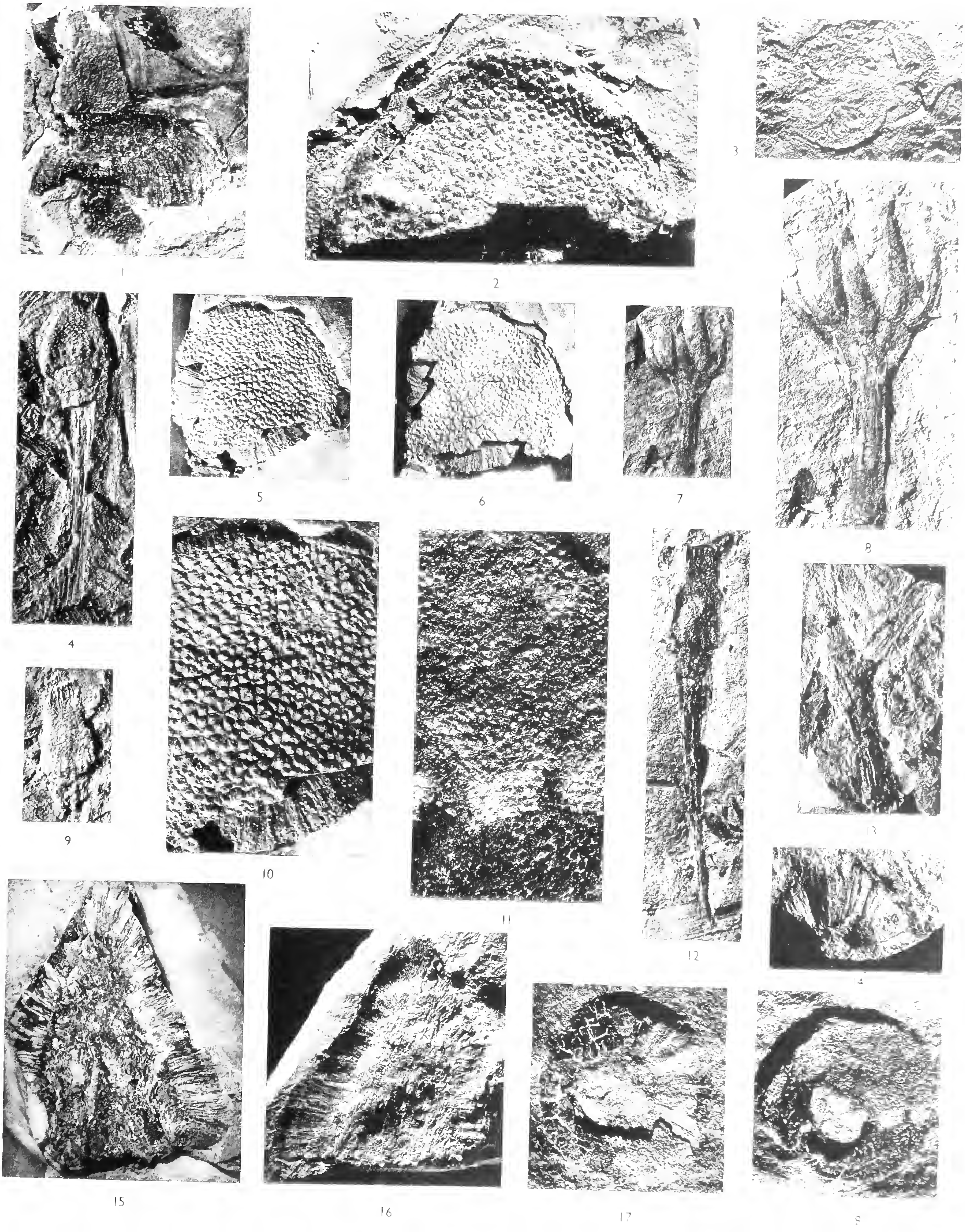
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PLATE 5

Weltrichia sol sp. nov.

(***Williamsonia gigas*** male flower)

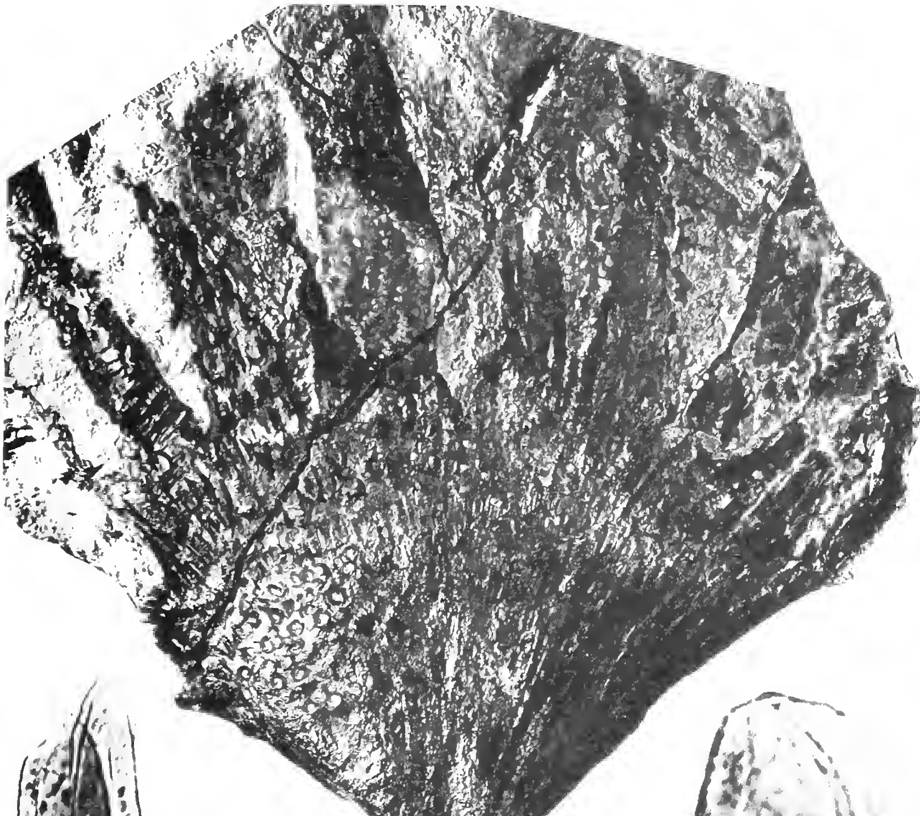
FIG. 1. Ironstone cast of flower, Leckenby Collection, Cambridge, K.210. Labelled *Williamsonia gigas* and also 'Fruits' of *Williamsonia gigas* A.N. Drawing on photograph. ×1.

FIG. 2. Counterpart of Fig. 5 showing imprint of outer surface. The 'resinous sacs' cause slight corrugations. ×1.

FIGS. 3, 4. Pollen grains from the same flower, that in Fig. 3 has split and the halves have curled up separately. Slide, V.53458*a*. ×1000.

FIG. 5. Compressed flower, outer surface (photographed under paraffin). Fallen block, Whitby *Zamites* Bed, V.53458. ×1.

FIG. 6. Same as Fig. 5 but dry and coated with NH_4Cl to show longitudinal ridges in cup.



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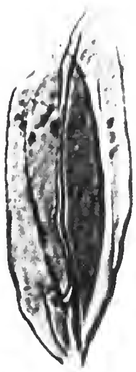

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PLATE 6

Bucklandia **sp. B**

Gristhorpe Bed

FIG. 1. Specimen showing crowded leaf scars at bend (the whole specimen is 13 cm. long), V.53473. ×1.

Bucklandia pustulosa **sp. nov.**

FIG. 2. Lower Deltaic specimen (with *P. pectinoides*). Drawing on a photograph, V.53467. ×1. Beast Cliff *Ptilophyllum* Bed.

FIG. 4. Specimen showing lenticels and underlying fibres. The whole piece of bark is 14 cm. × 11 cm., V.53466. ×1. Cloughton Wyke *Solenites* Bed.

FIG. 8. Bark fragment in which the leaf scar has been stretched by growth to 8 mm., V.53463. ×4. Cloughton Wyke *Solenites* Bed.

Bennetticarpus fragum **sp. nov.**

Hawsker *O. gramineus* Bed

FIG. 3. Micropylar canal and adjacent interseminal scale heads, V.53479*a*. ×100.

Bucklandia gigas **Seward**

Haiburn Wyke *Zamites* Bed

FIG. 5. Upper part of a stem fragment still covered with petiole bases. Drawing on a photograph, V.53468. ×1.

Weltrichia pecten **(Nathorst)**

Cloughton Wyke *Solenites* Bed

FIG. 6. Rather small flower still with some of its organic substance, V.53460. ×1.

Bucklandia **sp. A**

Goathland, N. of Station

FIG. 7. Stem with two flower (?) scars, V.53470. ×1.

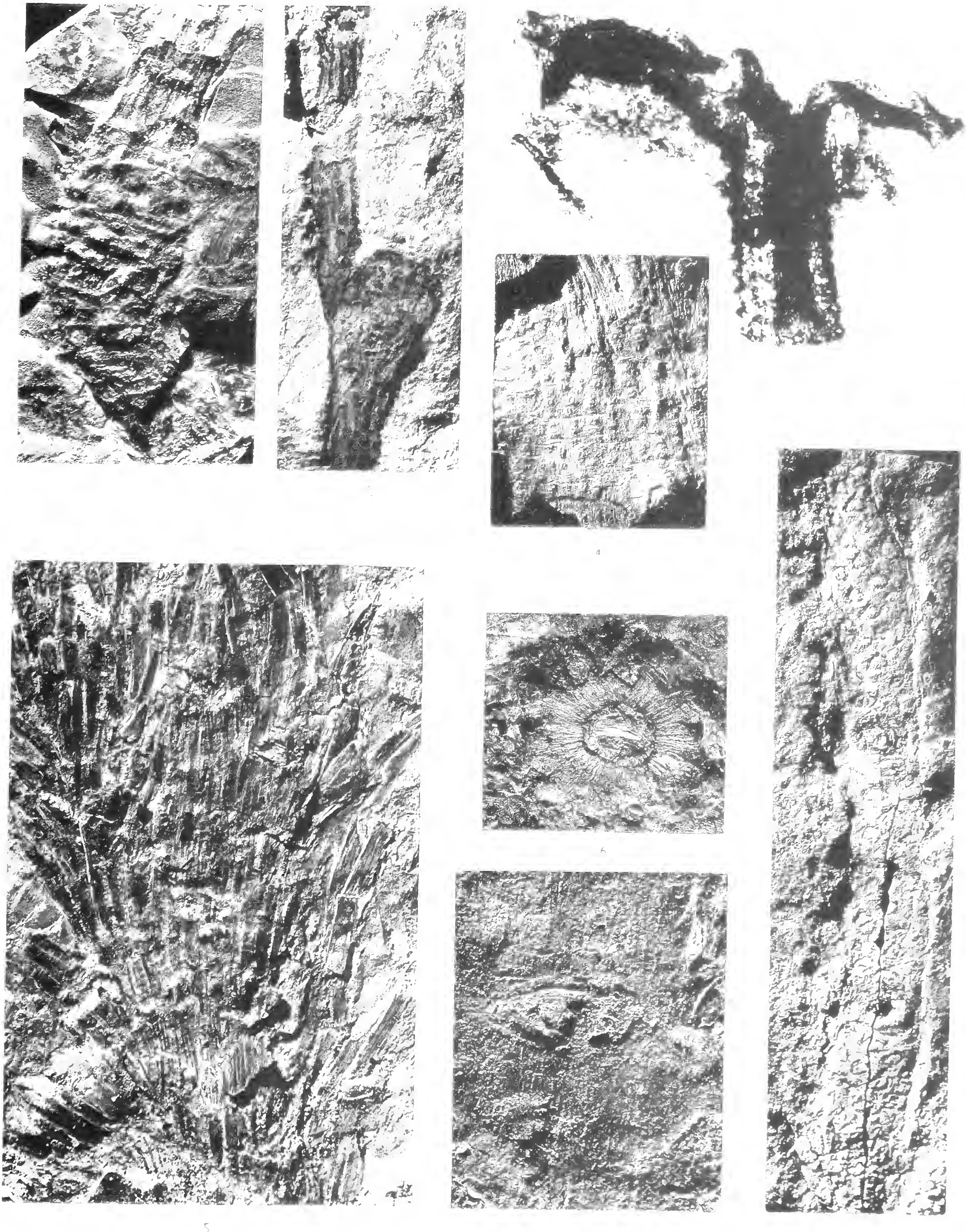

PLATE 7

Williamsonia hildae sp. nov.

Beast Cliff *Ptilophyllum* Bed

FIG. 1. Flower bud still on stem, illuminated obliquely to show imbricate perianth scales, V.53453. ×1.

FIG. 2. Same specimen illuminated vertically, note two damaged leaf rachises, that on the right shows traces of pinnae (*Ptilophyllum pectinoides*).

Weltrichia setosa (Nathorst)

Whitby Plant Bed

FIG. 3. Fragment of cup and rays (seen under paraffin). Some pollen sacs are seen on the right, V.53455. ×1.

Weltrichia whitbiensis (Nathorst)

FIGS. 4, 5. Two views of a nearly undistorted flower. Fig. 4 under oblique lighting to show hollow backs of rays. Fig. 5 under vertical lighting, V.27626. ×1. Beast Cliff *Williamsonia* Bed.

FIG. 7. Part of the specimen seen in Fig. 10, showing pollen sacs. ×1.

FIG. 9. External cast (mould) of specimen in Figs. 7, 10, showing the parallel veins in cup and rays. ×1.

FIG. 10. Internal cast showing pollen sacs and a single midrib in each ray extending down into the cup, V.27625. ×1. Ravenscar.

Weltrichia sol sp. nov.

Whitby

FIG. 6. Transfer of cup and bases of two rays of Whitby specimen, showing resinous sacs. From V.53457. ×2.

Weltrichia spectabilis (Nathorst)

Marske Quarry

FIG. 8. Counterpart of the specimen figured by Thomas (1913) showing some of the rays with fertile appendages but others apparently without. The flower lies on top of leaves of *Otozamites gramineus*, V.53459. ×1.

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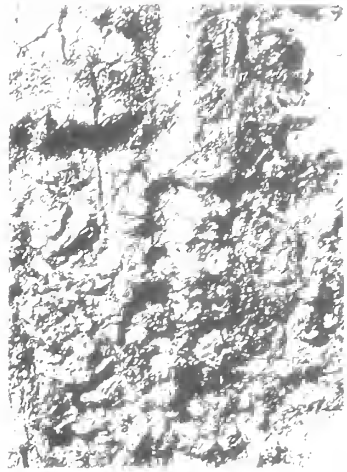

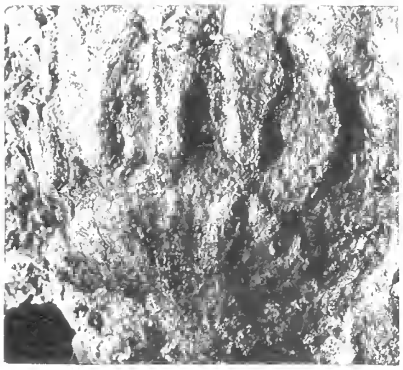

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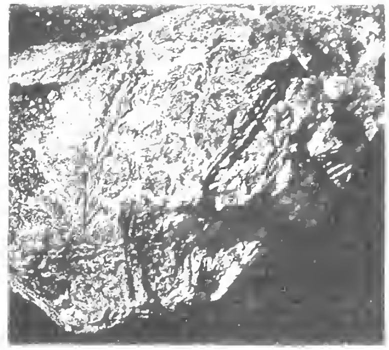

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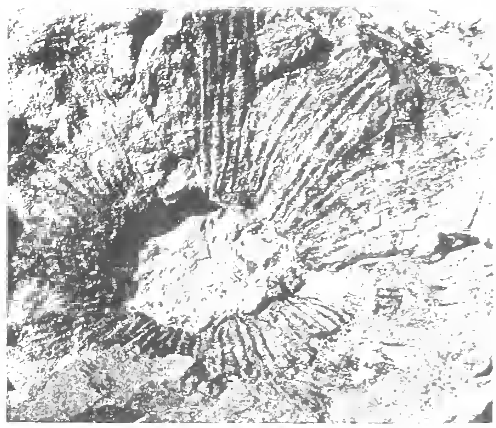

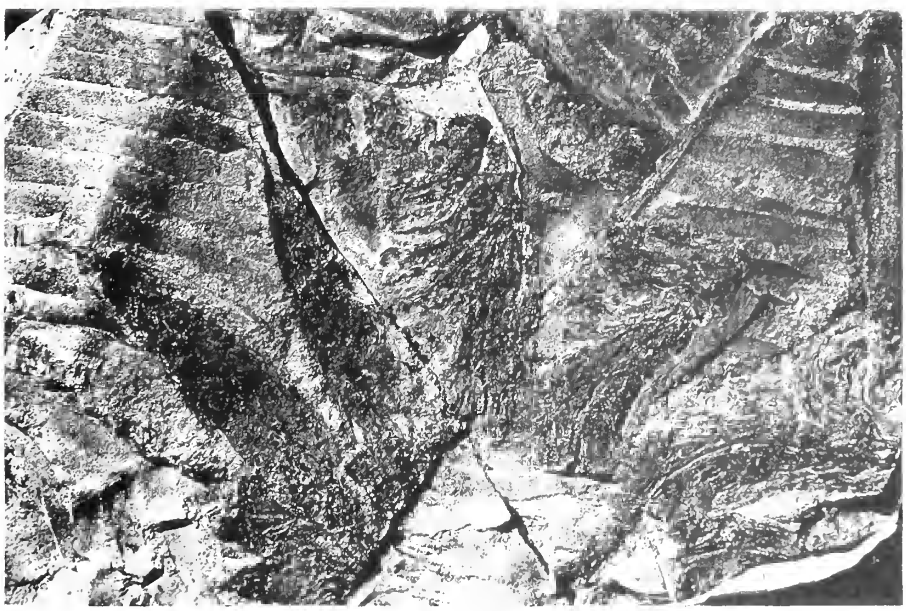

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