THE YORKSHIRE JURASSIC FLORA

V

CONIFERALES

By

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INTRODUCTION

The present volume is the fifth and last of a series on the Jurassic flora of Yorkshire. Amongst those to whom my thanks are due is Dr C. R. Hill, of the Department of Palaeontology, British Museum (Natural History). He has edited the text vigorously and also critically appraised the subject matter. In addition he has provided specimens which gave significant information.

My study of the Yorkshire Jurassic conifers owes much to the work of Rudolf Florin. In particular I was helped by his comprehensive account of the conifer epidermis (1931) and also by his work of 1958 where he described all that was then known about most of the Yorkshire conifers. Originally I planned to follow the latter work, adding only new finds, but eventually, as explained below, I decided to deal differently with some of the species.

The Yorkshire conifers may be divided into three groups according to how well the plants are known, the least-known species being represented merely by fragments of leaves. There are better-known species where the material consists of more or less intact, though sterile, leafy shoots. The best-known species have leafy shoots linked directly or indirectly with female fructifications and sometimes also with male cones.

Florin described the species known from leaf fragments under the comprehensive form genus Elatocladus Halle 1913 and I can see no better course than this. Indeed since there is little to add to his descriptions I merely refer to his work. He placed the best-known species, those with cones, in ordinary genera and ascribed these to families as is the usual procedure, and this again I follow. But I differ in my treatment of the sterile shoots. He and others, including myself, had placed each of these species in a genus, and the genera were considered natural though of course incompletely known. Some of these genera were adopted from earlier work and new ones also described, the total number being considerable. There are reasons, however, both theoretical and practical, for preferring a small number of artificial form-genera for such shoots until their reproductive organs become known (Harris 1969). A theoretical reason is that in the living conifers the combination of characters of gross shoot form and of epidermal structure does not always characterize a conifer genus uniquely, as for example in Podocarpus. The main practical reason is that the combinations of characters defining the various genera of sterile fossil shoots are almost impossible to remember: nearly 300 generic names have been published, mostly poorly characterized and imperfectly distinguished from earlier described genera. Thus when someone has to describe a new conifer he very likely neglects the past and makes yet another genus, a course which leads to no useful end.

I also differ from Florin in treating the Taxaceae as a family of the Coniferae (Coniferopsida) and not as a separate class of equal rank, the Taxopsida. This is because an evolutionary origin of Taxus can be imagined from the primitive conifer Lebachia (Harris 1976), a possibility which makes complete separation seem unnecessary. Again there is also a practical reason, for as Florin made clear, there is no character or group of characters by which a fossil needle-leaved shoot can be reliably classed as a conifer or a taxad.

Since 1958 only a few new species of Yorkshire conifers have been discovered though there has been notable progress with the fructifications of those already known. Florin knew of about three species of shoots linked with a female fructification, whereas we now have nine and for
some the male cone also. This advance has resulted mainly from later collecting, some of it directed deliberately. I have no doubt that continued work on these lines will be rewarding.

I give below a list of the families in alphabetical order. It includes only about half the total number of species, placed either firmly or tentatively in these families. As I have no basis for an opinion about the families of the remaining species they are not listed.

**Araucariaceae**
Araucaria phillipsii (Carruthers) Harris, i.e. Brachyphyllum mamillare L. & H. with Araucarites phillipsii Carruthers.

**Cephalotaxaceae** (sterile shoots)
Elatocladus (Thomasiodendron) zamiioides (Leckenby) Seward.

**Hirmerellaceae** (formerly Cheirolepidiaceae)
Brachyphyllum crucis Kendall, with its male cone described by van Konijnenburg-van Cittert.

Hirmerella kurrii (Schimper) Harris, i.e. Pagiodyllum kurrii (Schimper) Salfeld and Hirmerella estonensis (Kendall) Harris.

Hirmerella maculosum (Kendall) Harris, i.e. Pagiodyllum maculosum Kendall and Hirmerella kendalliae Harris. Possibly also the following sterile shoots: Pagiodyllum ordinatum Kendall, P. insigne Kendall, Brachyphyllum ardicum Harris and Geinitzia rigida (Phillips) Harris.

**Pinaceae** (Abietaceae of some authors)
Pityocladus scarburgensis Harris and Schizolepis lassokuperianus Braun.

**Podocarpaceae**
Scarburgia blackii (Harris) Harris, i.e. Cyparissidium blackii (Harris) with Pityanthus scalbiensis van Konijnenburg-van Cittert and Scarburgia hilli Harris.

**Podozamitaceae**
Lindleycladus lanceolatus (L. & H.) comb. nov. (sterile).

**Taxaceae**
Marskea jurassica (Florin) Harris.

Possibly also the following sterile shoots: Torreya gracilis Florin, Torreya valida Florin, Elatocladus (Tomharrisia) ramosus (Florin) Harris and Elatocladus (Bartholinodendron) punctulatus (Florin) Harris. E. ramosus may be linked with Poteridion haleli Harris.

**Taxodiaceae**
Elatides williamsonii (L. & H.) Nathorst.

Elatides thomasi Harris.

Possibly also the following sterile shoots: Pagiodyllum (Farndalea) fragilis (Bose) Harris and Elatocladus (Sewardiodendron) laxus (Phillips) Harris.

Unknown family
Bilsdalea dura Harris and Trulla nitens Harris.

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**Key to the form-genera of Yorkshire Conifer shoots**

1. Leaf contracted basally and then expanded to form a blade .................................................................................. 2
   Leaf contracted gradually from a broad base ................................................................................................................. 4

2. Lamina with a single vein ........................................................................................................................................ 3
   Lamina with several veins ................................................................................................. Lindleycladus (Podozamites)

3. Leaf very long (length up to 100 times width), mainly crowded on dwarf shoots ................................................. Pityocladus
   Leaf length seldom over 20 times width, all leaves on long shoots ................................................................. Elatocladus

4. Leaf length at least five times its width .................................................................................................................. 5
   Leaf length under five times its width ..................................................................................................................... 6

5. Leaf flat in section .................................................................................................................................................. 7
   Leaf round or rhomboidal in section ..................................................................................................................... 7

6. Free leaf longer than width of its basal cushion ................................................................................................. Brachyphyllum
   Free leaf shorter than width of its basal cushion .................................................................................................... 8

7. Free leaf appressed to stem .................................................................................................................................... 8
   Free leaf diverging from stem
INTRODUCTION

(8) Free leaf thin, flat, twisted into horizontal plane . . . . . . . . . . . . . Elatocladus
Free leaf thick vertically, not twisted . . . . . . . . . . . . . . . . . . . Pagiophyllum

Notes on key

(1) Leaves at the sides of the stem may appear to have a constricted base if they are twisted so that the lamina is held horizontally. The true width of the leaf base is seen in a leaf borne on the top of the stem.

(3) Pityocladus (very rare in Yorkshire) has not yet been found with leaves still attached.

(5) Leaves twisted basally into the horizontal plane are flat in section in all Yorkshire species. With leaves not so twisted compare the apparent width of a leaf compressed at the side of the stem with the apparent width of one compressed on top of the stem. If they are equal the thickness equals the width (Walton 1936).

(6 & 7) If the free leaf is pressed close to the stem it may be difficult to distinguish from its basal cushion. Normally however there will be a little matrix trapped between the adaxial leaf surface and the stem and this can be degaged by dissection. Also the cuticle of the adaxial leaf surface ends where the leaf joins the stem, and this junction can be revealed by maceration.

This key omits three genera or form-genera of later Jurassic floras because they are unknown in Yorkshire. These are Cupressinocladus with scale leaves (or short needle leaves) borne in opposite pairs or occasionally in whorls of three or more, Pinus with needle leaves borne in pairs, threes or fives on caducous dwarf shoots and Sciadopitys with peculiar double needles borne on long shoots in the axils of scale leaves. In fossil material the double needles are found detached and then they are to be distinguished from detached Elatocladus leaves by special details. A single cuticle fragment from Yorkshire was regarded by Florin as possibly Sciadopitys but scarcely establishes the occurrence of the genus.

Finally I emphasize that some of the species have variable foliage and occasional specimens overlap the boundary of another form-genus. Their identity is shown mainly by the numerous associated specimens of normal form.
SYSTEMATIC DESCRIPTIONS

Form-genus **BRACHYPHYLLUM** Lindley & Hutton *ex* Brongniart

1828a *Brachyphyllum* Brongniart: 109. (Definition, but type species not described)
1836 *Brachyphyllum* Lindley & Hutton: pl. 188.

**Emended Diagnosis.** Shoot, bearing leaves helically (spirally). Leaf composed of a basal cushion tapering into a small free part, length of free part (upper surface beyond leaf cushion) or total height of leaf and cushion (outwards from shoot) less than width of leaf cushion.

**First Described Species.** *Brachyphyllum mamillare* Lindley & Hutton.

**Discussion.** The basis of the diagnosis is from Kendall (1947) but modified by the omission of certain details. Though emphasizing that *Brachyphyllum* was probably heterogeneous, Kendall tried to give it precision by adding several cuticle characters to the basic ones of shoot and leaf form. These additional characters would make the genus more natural but since I here treat *Brachyphyllum* as an artificial form-genus, I now consider this undesirable (Harris 1969). The genus as here defined includes *B. mamillare* of the Araucariaceae and also *B. muensteri*, the foliage of *Hirmerella muensteri* which has very different male cones. Certain specimens of *Brachyphyllum* with unusually long leaves overlap the boundary of *Pagiophyllum*. Such leaves are rare in *B. mamillare* but commoner in *B. crucis* and common still in *B. muensteri*. On the other hand occasional shoots of *Pagiophyllum maculosum* have leaves short enough to fit *Brachyphyllum*.

**Key to normal specimens of the Yorkshire species of Brachyphyllum**

1. Leaf + cushion nearly as long as broad
   - Leaf + cushion usually twice as long as broad
   
2. Free part of leaf usually over 1 mm long, margin usually thin and microscopically frilled
   - Free part of leaf under 1 mm long, margin thick, entire

All three species have rather thick cuticles though that of *B. mamillare* is often fragile. *B. expansum*, which occurs in the Jurassic of the English Midlands (Kendall 1949) has not been found in Yorkshire. Its fragments resemble *B. crucis* and its leaves have a frilled margin but it is distinguished by its strongly papillose subsidiary cells.

*Branhphyllum mamillare* Lindley & Hutton (foliage and male cone) and
*Araucarites phillipsii* Carruthers (female cone and scale)
Figs 1–5; Pl. 1, figs 1–14

The following are Yorkshire specimens of shoots:
1829 *Thuites expansus* Phillips: 147, 153; pl. 10, fig. 11. (Rough sketch)
SYSTEMATIC DESCRIPTIONS

1835 *Thuites expansus* Phillips; Lindley & Hutton: pl. 167. (Good figure)
1836 *Brachyphyllum mammillare* Lindley & Hutton: pl. 188. (Good figure, Brongniart's name used)
1837 *Brachyphyllum mammillare* L. & H.; Lindley & Hutton: pl. 219. (Good figure)
1870 *Brachyphyllum mammillare* Bronniart; Schimper: 335 in part, excluding some of the cited specimens.
1870 *Brachyphyllum philippii* Schimper: 335. (New name for specimens of Lindley & Hutton 1835, 1836, 1837)
1875 *Brachyphyllum mammillare* Lindley & Hutton; Phillips: 229, Lign. 59. (Diagram)
1875 *Thuites expansus* Phillips; Phillips: 229; pl. 10, fig. 11. (Rough sketch, as 1829)
1884 *Brachyphyllum mammillare* Bronniart; Saporta: 326; pl. 162, figs 3–7.
1900 *Brachyphyllum mammillare* Bronniart; Seward: 297; pl. 10, fig. 1. (Good figure)
1919 *Brachyphyllum mammillare* Bronniart; Seward: 320. (Discussion of Yorkshire and other material)
1947 *Brachyphyllum mammillare* Bronniart; Kendall: 230, text-figs 1, 2. (Leaves, cuticle, figures reproduced here)
1947 *Brachyphyllum scalbiensis* Kendall: 235, text-figs 3, 4. (Leafy shoots, cuticle)
1949 *Brachyphyllum mammillare* Bronniart; Kendall: 152, text-figs 2b, c, e, f, 4. (Restoration, cuticle and other organs; figures mostly reproduced here)
1958 *Brachyphyllum mammillare* Bronniart; Florin: 369. text-fig. 6a. (Shoot in association with cone scales)

Male cone (Yorkshire):
1949 *Brachyphyllum mammillare* Bronniart; Kendall: 160, text-figs 3A–E, 4. (Figures mostly reproduced here)
1958 *Brachyphyllum mammillare* Bronniart; Couper: 129; pl. 27, figs 1, 2. (Pollen from Kendall's preparations)
1971 *Brachyphyllum mammillare* Bronniart; van Konijnenburg-van Cittert: 51; pl. 11, figs 1–6. (Male cone and pollen)

Female cone scale, *Araucarites philippii* Carruthers. The following are Yorkshire specimens:
1829 'Winged seed', Phillips: 190; pl. 10, fig. 5. (Also as 'Cycadites' on p. 150)
1869 *Araucarites philippii* Carruthers: 6; pl. 2, figs 8, 9. (Not fig. 7, described as a rolled cone)
1875 *Araucarites philippii* Carruthers; Phillips: 229; pl. 10, fig. 5. (As 1829)
1884 *Araucaria philippii* (Carruthers) Schimper: 254. (The name here refers to the cone scale only)
1900 *Araucarites philippii* Carruthers; Seward: 285; pl. 10, fig. 4. (Good specimen)
1919 *Araucarites philippii* Carruthers; Seward: 263, text-fig. 740, 9. (As 1900 but reduced)
1949 *Araucarites philippii* Carruthers; Kendall: 154, text-figs 1. 2A, D, 3F. (Figures reproduced here)
1952 *Araucarites philippii* Carruthers; Kendall: 588, text-fig. 3C. (Figure reproduced here)
1958 *Araucarites philippii* Carruthers; Florin: 369, text-fig. 6b, c. (Scales in association with foliage)

A moderate number of Jurassic shoots from various parts of Europe and Asia have been identified more or less firmly with *B. mammillare*. Some do look like it and may well prove to agree in fine details but are not accepted until their cuticles have been studied.

'B. sp. a., cf. *B. mammillare*' Seward (1904) from the English Midlands might equally well belong to *B. expansum* (Sternberg) whilst specimens described by Saporta (1884) from the Upper Jurassic of France as *B. gracile* and *B. nepos* match forms of *B. mammillare*.

From various parts of the USSR, specimens determined as *B. mammillare* by Turutanova-Ketova *et al.* (1963) and by Baranova, Burakova & Bekasova (1963) match certain Yorkshire specimens, though one so determined by Sikstel' & Khudaibergyev (1968: pl. 23, fig. 9) differs in its distally thickened shoots. Specimens from the Rajmahal Hills, India, determined by Bancroft (1913) and by Sahni (1928) have narrower leaves than most Yorkshire specimens and according to Ramanujam (1957) are associated with *Araucarites cutchensis* scales. Bose & Maheshwari (1974) record *B. mammillare* as an Indian species.

**EMENDED DIAGNOSIS** of shoot (*Brachyphyllum mammillare*). Main stems (rare) thick, leaves large, branching probably radial. Lateral branches caducous, richly and pinnately branched in one plane, branchlets arising at 50°, gradually tapering and ultimately 1–2 mm wide, often curved. (No resting buds present, no regions of arrested growth apparent on lateral branch systems.) Leaves pointing radially, arranged in a simple helix, parastichies mostly 2 + 3 but 3 + 5 on thickest stems and reduced to 1 + 2 near apex.
Fig. 1. *Brachyphyllum mamillare* Lindley & Hutton

Fig. 2. *Brachyphyllum mamillare* Lindley & Hutton

A, cuticle showing thickenings on surface of cells, V.27221a, × 200. B, single stoma from same leaf, × 400. C, cuticle of leaf with small, thick-walled cells, K.818a, × 200. D, stoma of K.823a, × 400. E, fragments of lower and upper cuticles of K.823a, × 10. Stomatal apertures shown as short lines; stomata where aperture not seen shown by dots. F, reconstructed transverse section through stoma in which subsidiary cells have ridges. G, reconstructed section where they have no ridge. All figures are from Kendall (1947), those in C–F originally determined as *B. scalbiensis*. 
Leaf together with rhomboidal basal cushion typically 1·5 mm long \( \times \) 2·0 mm wide but up to 4 mm \( \times \) 3 mm, rarely larger. Free part arising from whole of basal cushion, pointing outwards and upwards, height of free part almost equalling its width. Free part nearly square in section, lateral angles sharp, outward angle fairly sharp but inward angle more rounded. Leaf apex rounded or obtuse, lateral edges approaching apex at an angle of 80°–110° but occasionally at 70° or even less. Apex of leaf typically placed immediately above top of cushion but exceptionally and on larger shoots projecting 1–2 mm above cushion. Leaf surface normally almost smooth but sometimes (especially in longer leaves) showing furrows (stomatal grooves). Leaf margins normally entire and not scarios, but longest leaves with narrow scarios edges in upper part.

Cuticle of leaf and cushion about 4 \( \mu \text{m} \) thick but rather fragile, stomata equally common over whole surface or fewer on adaxial surface of small leaves. Stomata forming irregular longitudinal files in short leaves but regular and conspicuous files in longer leaves; files slightly sunken in longer leaves but not in short ones. Stomata unevenly placed in files, often encircling cells of adjacent stomata in contact but not shared. Stomata amphicyclic or imperfectly amphicyclic, irregularly orientated, guard cells at bottom of a wide pit, guard cell surface and aperture thinly cutinized; pit formed from subsidiary and encircling cells usually narrow (in radial direction), subsidiary cells sometimes showing an ill-marked ridge concentric with the pit margin, encircling cells unspecialized. Polar subsidiary cells like lateral ones.

Ordinary epidermal cells of all surfaces typically isodiametric, forming longitudinal files. Anticlinal walls broad or very broad, prominent, uninterrupted, corners of cells rounded. Surface of cell unpitted, often thickened in middle region to form an ill-defined papilla. Scarios margins of leaf (where developed) consisting of a single layer of cells, each cell projecting as a tooth. (Trichomes absent.) Hypodermal cells not usually preserved but occasionally visible between stomatal files.

**Diagnosis** of male cone. Cone borne singly at end of a leafy twig, falling after loss of pollen but not breaking to pieces; cone after shedding pollen about 12 mm \( \times \) 6 mm, rather delicate. Surface covered by slightly imbricating distal ends of microsporophylls; ends rhomboidal, very slightly longer than broad, arranged helically (perhaps in \( 8 + 13 \) parastichies). Distal end delicate with thin margins but a median longitudinal ridge. Horizontal limb slender but expanding as it joins the distal end. Pollen sacs elongated, typically 1·3 mm \( \times \) 0·3 mm but sometimes shorter, number per microsporophyll probably 3 (manner of attachment not known). Cuticles of distal end very delicate, showing cells with straight, finely-marked walls (and possibly stomata). Compressed pollen grains rounded, diameter typically about 70 \( \mu \text{m} \), extremes noted in about 100 grains 56–84 \( \mu \text{m} \), wall inaperturate. Exine 1–2 \( \mu \text{m} \) thick, consisting of a nexine which may be separated by shrinkage from the sexine; sexine smooth, up to 1 \( \mu \text{m} \) thick, sexine about 1 \( \mu \text{m} \) thick and finely marked with granules about 1 \( \mu \text{m} \) wide.

**Emended diagnosis** of *Araucarites phillipsii* (female cone, cone scale and seedling). Mature cone oval, 6 cm \( \times \) 3·5–4·0 cm, composed of an axis about 4 mm wide and numerous cone scales forming a helix (perhaps \( 21 + 13 \) parastichies). Cone at maturity falling to pieces and scales normally found separately. Cone scale up to 17 mm \( \times \) 15 mm but usually about 15 mm \( \times \) 13 mm, often smaller and disproportionately narrower; always wedge-shaped, widest point just below apex. Apex pointed, sharp, directed upwards at right angles to the almost horizontal scale, 1·0–1·5 mm long and 1·0–1·5 mm broad at its base. Margins of scale showing membranous wings, basal part thicker, almost as thick as broad. Ligule delicate, 1–2 mm high and up to 6 mm broad. Seed typically 12 mm \( \times \) 8 mm in full-sized scale, embedded in middle region of scale.
Fig. 3. *Brachyphyllum mamillare* Lindley & Hutton

A, restoration of shoot, × 5. B, shoot showing decussate leaves, V.58801, × 4. C, D, male cones embedded in bakelite resin and ground away to give sections; sporophyll stalks are seen at x, V.27579a, × 5. E, drawing of two microsporophylls from V.56932, Pl. 1, fig. 14, top left. Obscure elongated bodies are pollen sacs. × 20. F, details of sculpture at edge of typical pollen grain, showing pitting. × 3200. G, shoot with male cones, Oxford Museum, J.933, × 1. H, group of pollen grains. The folds are caused by flattening and the dots are shading. V.27554a, × 400. All figures except B, E and F are from Kendall (1949) by permission of *Annals of Botany.*
Cuticle of erect apex of cone scale resembling that of *B. mamillare* leaf. Cells nearly isodiametric, anticlinal walls thick, periclinal walls often thickened in centre. Stomata frequent, scattered, somewhat sunken, orientation varied. Guard cells surrounded by irregular ring of subsidiary cells of rather varied size, terminal subsidiary cells not specialized, papillae absent. Encircling cells occasional, unspecialized. Outer cuticles of rest of scale showing mostly elongated, straight-walled cells, stomata probably absent. Nucellus well cutinized at its micropylar end, composed of elongated cells with minutely crenulate walls. Megaspore membrane well developed.

Seedling showing an extended radicle, probably epigeal.

**Lectotypes.** Shoot figured by Lindley & Hutton (1836: pl. 188); female cone scale figured by Carruthers (1869: pl. 2, fig. 8).

**Discussion.** The name *B. mamillare* refers to the leafy shoot. It is here extended to cover also the male cones as these are known attached to the shoot and have never by themselves received a name.

There has been divergence over the spelling of the specific name. Brongniart gave *mamillare*, whilst Lindley & Hutton used *mammillare*, though this latter spelling is an error. The Latin word *mamma* is correct and from it come numerous words with *mm*, but the diminutive *mamilla* is also correct and from this comes the adjective *mamillaris*.

The specific name as well as the combination are generally attributed to Brongniart but since he left the species as a *nomen nudum*, the annotated figure of Lindley & Hutton under this name constitutes the first description. Fortunately their figure is good. Earlier they figured two Yorkshire specimens as *Thuites expansus* Phillips but I assume these were wrongly determined specimens of *B. mamillare*.

Though the cuticle of *B. mamillare* is thick it is often difficult to prepare. It is fragile when sufficiently macerated and matter from the leaf interior often survives maceration and disfigures it. Indeed the cuticle seems chemically peculiar, for I found that I could get coherent cuticles by gentle maceration though these were still dark brown. After further oxidation in the acid they became light brown and looked satisfactory until placed in ammonia, when they swelled and cracked and gave poor mounts. When macerated in acid until yellow they swelled in ammonia to double their size or broke up.

Cuticles from specimens of *B. mamillare* collected at various localities all behaved in just this way but those of other species behaved differently. For instance an equally thick cuticle of *B. crucis* can be oxidized in acid until pale yellow, after which in ammonia it swells only a little and remains tough.

The shoots of *B. mamillare* at some localities have decayed before preservation and the soft tissues have vanished. In these the xylem core formed about one-third of the width of the whole shoot. In the cortex there are some solid-looking oval sclereids measuring 120 mm × 35 mm. Such sclereids occur widely in *Araucaria* and they look similar in *A. cunninghamii* D. Don, but those of *A. excelsa* (Lambert) R. Br. are hollow and those of *A. araucana* (Molina) K. Koch are branched.

*Brachyphyllum scalbiensis* Kendall was mainly distinguished by its longer, more pointed leaves which are often long enough to extend slightly beyond their own basal cushions. The leaves and cuticles show well-marked stomatal grooves. The leaf margins are sharp and often scarious in the free part, a feature not normal in the short-leaved form of *B. mamillare*. The original *B. scalbiensis* specimens were from two Upper Deltaic localities whilst *B. mamillare* is widespread in Upper, Middle and Lower Deltaic rocks. Further collecting however has made the two species impossible to separate. The three distinguishing characters—long leaves, marked stomatal
Fig. 4. Araucarites phillipsii Carruthers

A, lower surface of cone-scale, x 2, edge of coaly substance shown by thin black line, edge of impression in matrix by broken line, double lines near apex representing folds, V.27551. B, transfer preparation of specimen in A, showing base of ligule (unstippled area represents crack in substance). C, double-seeded scale, a mineralized root passing through centre shown white. V.27600, x 1. D, double-seeded scale showing two apices, V.27563, x 1. E, V.27546, x 1. F, cuticle of ligule, V.27560b, x 200. G, reconstructed longitudinal section of cone-scale, endosperm shaded, substance of nucellus and of scale stippled, x 2. H, reconstructed transverse section of cone-scale, shading as in G, x 2. I, cone-scale, V.27575, x 1. J, seedling, Oxford Museum J.5007, x 1. The lateral root-like bodies may not be continuous with the cone-scale. K, cuticle of pointed apex of cone-scale; anticlinal walls closely stippled, thickened periclinal walls lightly stippled. V.27560a, x 400. L, cuticle of outside of cone-scale, V.27574b, x 200. All figures are from Kendall (1949).
grooves and scarious lateral angles—vary independently in each local population. Moreover in localities where leaves of the *scalbiensis* form occur, shorter-leaved shoots also occur, in the Lower as well as the Upper Deltaic. The most that can be said is that at certain localities, e.g. near Scalby Ness (Upper Deltaic) and at Hasty Bank (Lower Deltaic), shoots of *scalbiensis* character are more frequent than they are at most localities. A Hasty Bank shoot with exceptionally long leaves is shown in Pl. 1, fig. 9, and this specimen is of *Pagiophyllum* form.

The fragment shown in Fig. 3 b is the only specimen with decussate leaves out of a very large total number. The leaves along the top look less prominent than the lateral ones but this may be due to compression. The leafy shoot shown in Fig. 3 g, bearing numerous male cones, is the only one of its kind, though detached male cones rather larger than these have been found in many localities where *B. mamillare* and *A. phillipsii* are abundant.

Kendall’s detached cones showed the cone axis, long horizontal sporophyll stalks and overlapping upturned distal ends but had lost most of their pollen. Subsequently male cones with better-preserved microsporophylls were found at Haiburn Wyke. Their distal ends are nearly square, with corners pointing up and down, and seem to be in 8 + 13 parastichies. One of these cones, split longitudinally, shows that the horizontal limb is attached to a considerable part of the distal end, not just its basal corner. One cone although nearly empty of pollen has a few ripe but intact sacs, and a macerated fragment yielded a block which separated in ammonia into three long, parallel masses of pollen. Very possibly there were originally three pollen sacs per microsporophyll.

Van Konijnenburg-van Cittert (1971) described the pollen of *B. mamillare* in detail and compared it with Recent pollen of *Araucaria araucana* (Mol.) K. Koch. In *A. araucana* after preparation suitable for comparison with fossil pollen, she observed many grains with a nexine separate from the sexine. We do not know the state of these grains before preparation but I suggest that separation and shrinkage may have been pathological, perhaps induced by bad weather. A sample of *A. araucana* pollen I examined showed very few grains with a shrunk nexine. Her observations nevertheless demonstrate that the two layers have the capacity to separate easily, both in the living and fossil species. As she pointed out, a fossil grain with a
shrunken nexine may appear saccate and could be confused with pollen of other fossil genera, but normal grains agree with *Araucariacites australis* Cookson, of world-wide distribution and ranging from the Triassic onwards.

The wall of the empty pollen sacs shows elongated cells 20 μm wide crossed by transverse bars 5 μm apart. Similar cells occur in many conifer pollen sacs. In addition to this membrane the pollen sacs yield a tapetal membrane marked with plaques 1–4 μm wide and similar plaques often adhere to the pollen grains.

Every observed feature of the male cone matches living species; its form, phyllotaxis, the form of the microsporophyll, the probably three narrow pollen sacs and the pollen grains themselves. A petrified male cone attributed to *Brachyphyllum* from the Indian Jurassic, described by Bose & Hsü (1953), differs from *B. mamillare* in its more massive microsporophylls and in the pollen grains which are only 30 μm wide.

No female cone has yet been found attached to a *B. mamillare* shoot, and the cone and cone scales are attributed to the same plant on the evidence of association and agreement in cuticle structure. Early writers considered the cone scale Araucarian but thought the shoot unrelated, perhaps akin to *Cupressus*, and it was Kendall (1949) who first pointed out the association. She recognized this association in 13 localities, usually in the same bedding plane and often as the only species present. Subsequently the organs have been found together in many more localities and Florin’s (1958: 369, text-fig. 6) is typical. Neither organ shows any other suggestive association. The agreement in structure between the leaf-like upturned tip of the cone scale and the foliage leaf is impressively close.

Intact cones are rare, the specimen figured here (Pl. 1, figs 10, 11) being the only one known to me. It is preserved in ironstone (sideritic mudstone) and as is usual the external cuticles in contact with this matrix have been destroyed, though the internal ones, nucellus and megaspore membrane, were preserved and normal. The matrix has prevented the usual compression and many cone scales are seen in longitudinal or oblique section and so look unusual. They are also slightly less than the normal size; I suppose this cone was detached and preserved a little before it was mature and for this reason did not disintegrate as did the ripe cones. Its main value is to show the size of the cone and to confirm the guess already made that it was organized as in *Araucaria*.

A few cone fragments are known. One of these (Kendall 1952) is a sort of transverse section and since its scales are rather small I suggest that it may be the detached top of a cone; the top of the cone of *Cedrus* falls off as a piece in this way. I do not accept the specimen (in Manchester Museum) figured by Carruthers (1869: pl. 2, fig. 7) as an eroded cone of this species; it looks like a stem of some very different plant.

**Comparison.** The species of *Araucarites* cone scales are distinguished from one another by the size and proportions of their parts. Unfortunately the scales at the ends of a cone differ from those of the middle region and extend the form range, thus blurring specific distinctions. The cuticle is very helpful but has been described in less than half the species.

Seward (1904) described cones of *Araucarites* from marine Jurassic rocks, mostly from the south or midlands of England. Of these the most comparable seems to be *A. ooliticus* (Carruthers), which is of slightly younger age. Allowing for its different preservation, more or less petrified with calcium carbonate, the cone scales may be like those of *A. phillipsii* but no precise comparison can be made.

Numerous *Araucarites* scales called *A. brodiei* Carruthers occur in the nearly contemporaneous ‘Stonesfield Slate’ of the English midlands. If the collection includes two species, the
smaller scales (Seward 1904: pl. 12, fig. 2) may be the same as A. phillipsii. But the large narrow scale (Seward 1904: pl. 12, fig. 5) is well outside the range of Yorkshire A. phillipsii. No cuticles are preserved in this material.

A. phillipsii differs from nearly all Jurassic species in having a remarkably small apical scale extension. Thus A. cutchensis, which is rather similar, usually has a longer apical extension but it may be broken off, as has perhaps happened with the scales figured by Arber (1917) and by Oishi (1940). The Indian material of A. cutchensis has recently been revised. Pant & Srivastava (1968) described specimens with well-developed cuticles even on the inner parts of the scale where in A. phillipsii the cuticle is delicate. The stomata are also more numerous and more protected. Bose & Maheshwari (1973a) renamed this A. pantiana and limited A. cutchensis to specimens of rather poor preservation and no cuticle. They describe it as having no ligule. They also describe two other species. Three of the four Indian species have a longer apex than A. phillipsii though A. sehoraensis Bose & Maheshwari looks similar but is stated to have no ligule. A. phillipsii has a well-developed but delicate ligule which is not apparent in a scale viewed from below until exposed in a transfer preparation. The cuticle seems similar and with similarly distributed stomata, but their figures suggest less sunken stomata and a less regular ring of subsidiary cells.

The superficially similar Yorkshire cone scale Araucarites estonensis Kendall is discussed on p. 37.

**Occurrence.** Brachyphyllum mamillare is one of the commonest plants in the Yorkshire Deltaics and occurs at all levels without marked changes in frequency. Often it occurs as the only species, covering a bedding plane along with its female cone scales and male cones, but often it is also associated with pinnae of Coniopteris hymenophylloides (Brongniart) Seward. Its occurrence suggests that it was a species growing in the delta itself and often deposited near where it grew. It is met with in the rich plant beds and also in the moorland coals. On the other hand it is not particularly common in beds of partly marine origin, nor is it common in micaceous shales with drifted Pagiophyllum fragments and supposed to represent the flora of land above flood-plain level. But in both, occasional specimens occur.

**Taxonomic position.** I am fully satisfied that Brachyphyllum mamillare belongs to the same plant as Araucarites phillipsii. Thus reconstructed the plant agrees in all known characters except the shape of its leaves with living Araucaria, particularly the section Eutacta, and I thus suggest that the name Araucaria phillipsii (Carruthers) Schimper could be used for the whole plant. Living Araucaria includes species with leaves of several shapes though none are like Brachyphyllum. Its leaf is as though the elongated tapering needle of Araucaria excelsa (Lambert) R. Br. were reduced in length to a low four-sided pyramid. In the Jurassic there were several Araucaria species with leaves of this shape and this might justify their being placed in a distinct section of the genus. Clearly the Jurassic Araucaria had a wide distribution and only later did it become extinct in the northern regions. We do not know where the family originated.

It is worth mentioning evidence of taxonomic value that we still lack. We have no attached female cone and no direct evidence that the leaf had just one vascular bundle. It is likely that the microsporophyll has three pollen sacs but this needs confirmation. Above all we need to know the wood anatomy of a well-grown, mature stem.
Fig. 6. Brachyphyllum crucis Kendall

**Brachyphyllum crucis** Kendall

Figs 6, 7

1947 *Brachyphyllum crucis* Kendall: 240, text-figs 5, 6. (Shoot form, cuticle; specimens from ‘Oxford Clay’, Callovian, Wiltshire)

1952 *Brachyphyllum crucis* Kendall: 590, text-figs 4, 5. (Shoot and cuticle, Bajocian, Yorkshire)

1971 *Brachyphyllum crucis* Kendall; Van Konijnenburg-van Cittert: 59; pl. 14, figs 3–6; pl. 15, figs 1, 2, 4; pl. 16, fig. 1; text-figs 8, 9. (Yorkshire male cones and pollen)

1972 *Brachyphyllum crucis* Kendall; Van Konijnenburg-van Cittert: 28; pl. 1, fig. 3. (Male cone)

**Emended Diagnosis.** (Main stem unknown.) Lateral branches (rarely preserved) 5 mm thick, their leaves like those of smaller shoots. Smaller shoots caducous, rarely much branched and any branches borne irregularly and at a small angle. Commonest type of shoot nearly straight, 1–3 mm wide, with no branches but often with small buds. No specialized resting bud produced, but leaves towards shoot apex relatively short, basal leaves of a branch sometimes short and occasional zones of long shoots bearing shorter leaves.

Leaves in a simple helix, parastichies 2 + 3 (but reduced to 1 + 2 in smallest shoots); exceptional shoots with decussate leaf pairs. Large shoots with basal cushions up to 4–5 mm × 3 mm, free leaf commonly 2–3 mm long, merging into cushion, small shoots with cushions about 1.5 mm × 1.0 mm and free leaves about 0.5 mm long, but some shoots having longer free leaves. Leaf apex in surface view commonly obtuse, sometimes acute, sometimes rounded, rarely curved inwards (when it appears truncate). Leaf crescent-shaped in section, adaxial surface of leaf concave, abaxial surface strongly convex but not keeled, merging into cushion. Margins of cushion with vertical or overhanging edges. Margin of free leaf commonly scarious at least in apical part, no longer scarious where free leaf joins the cushion, continued by angular cushion margin. Some leaves, particularly long ones, with only slightly or not at all scarious margin. Leaves thickly cutinized, showing epidermal cells and stomata.

Shoots of juvenile type occasionally preserved, their leaves up to 7 mm long, slender (0.4–0.8 mm wide), diverging from stem and often falcate, vertical thickness about equal to their width, lateral angles sharp but upper and lower surfaces rounded. Apex acute, lateral edges not scarious even at apex. Cuticle of normal thickness and resembling that of normal leaves, stomata rather sparsely scattered on both surfaces.

Cuticles of leaves of all types and of basal cushion thick, usually 6 μm (in folds) but sometimes thicker, tough and resistant to maceration but often delicate at base of adaxial part of leaf. Stomata scattered over both surfaces of leaf and over leaf base but sometimes avoiding middle region, rather sparse on leaves of all types.

Stomatal index about 4–5 on abaxial surface, varying on adaxial surface of different leaves from 0 to more than 5. Stomata scattered, not forming longitudinal files, spacing uneven and occasionally two with lateral subsidiary cells in contact; guard cell orientation random. Subsidiary cells 4–6, uniform, forming a ring but occasionally ring narrowed in longitudinal direction. Inner part of subsidiary cells forming a pit which may be shallow or moderately deep, but edge forming a rim which may be raised 20 μm above the general surface and may be divided to form large, low papillae. Surface of subsidiary cells outside rim never thickened to form a papilla, often rather thinner than general surface, sometimes finely marked with radial striations. Guard cell poles concealed under subsidiary cells. Encircling cells commonly forming complete ring, typically elongated tangentially, but sometimes encircling cells unspecialized and ring incomplete.

Scarious margin of leaf normally forming a frill 100–150 μm wide. Inner part of frill composed of two layers of cells, outer part a single layer of columnar cells. Edge entire or
Fig. 7. *Brachyphyllum crucis* Kendall

A–D, shoots with juvenile foliage. A, leaves very slender, V.58815, ×2. B, shoot showing transition from mature foliage, V.58814, ×1. C, small shoot, V.56923, ×1. D, two shoots, one possibly showing reversion to mature foliage but attachment of branchlet not certain, V.58817, ×1. E, shoots with leaves becoming short, V.56927, ×1. F, details of slender shoot, V.58804, ×4. G, shoot with short leaves, V.56926, ×1. H, two shoots each with a zone of shorter leaves, V.56925, ×1. I, unusually large and richly branched shoot, the woody core exposed in places, V.58813, ×1. J, details from I showing the decussate leaves on one branchlet, ×2. K, details of main shoot of I, ×2. L, two shoots perhaps originally joined, V.56924, ×1. The specimens in C, E are from Westerdale, Esklets Crag, that in H from Farndale, Hillhouse Nab. The rest are from Hasty Bank.
irregularly notched, never regularly dentate. In leaves with an undeveloped frill, edge of leaf sharply angular.

Epidermal cells up to twice as long as broad, usually almost isodiametric, arranged in longitudinal files. Anticlinal walls straight, forming prominent ridges up to 6 μm broad, but sometimes thin, unpitted or with occasional pits. Periclinal walls flat, centre not thickened, surface sculpture of fine striations or granules. Hypodermis developed generally except under stomata, its cells typically isodiametric and 40–50 μm broad; outlines marked by fine, straight ridges. Inner tissues of leaf and cushion dense, one vein present.

**Holotype.** Yorkshire Museum, specimen labelled ‘A’.

**Discussion.** Kendall based *B. crucis* on three shoots from the marine Oxford Clay of Christian Malford, Wiltshire, and the species was named after the locality. Later (1952) she reported a specimen from the marine ‘Forest Marble’, Bathonian, of Filkins, Oxfordshire, and others from various levels in the Bajocian of Yorkshire. Considering the material as a whole there is some variability; apart from size of shoot, and individual leaves, for example, there are leaves in which the marginal frill is poorly developed and such leaves are commoner in some Yorkshire localities than others. I also note some variability in the thickening of the subsidiary cells, both in Kendall’s original specimens and those from Yorkshire.

Ordinarily preserved specimens show nothing of the vascular tissue of the leaf, but in some detached leaves 2 mm broad, which had decayed somewhat before preservation, there is a single median strand 0-3 mm broad which I interpret as the vascular bundle. Tracheids could not be distinguished.

Numerous well-preserved shoots of *B. crucis* are now known, particularly from Hasty Bank. Most of these are thin and simple or sparingly branched. Many show an undamaged apex where the leaves become progressively shorter and I imagine that these shoots were caducous. The specimen shown in Fig. 7 i–k is exceptional, however, and was doubtless still larger when deposited in the plant bed; its main axis may have been of unlimited growth. It shows a xylem core which is 2 mm thick, but its almost equally thick side branches have a core only 0.7 mm thick. This specimen is remarkable also in bearing a small shoot with paired leaves, the 9 upper pairs alternating at 90° (strict decussation) whereas the basal leaves are in pairs at a smaller angle or not in pairs at all. No other shoot of *B. crucis* with decussate leaves has been observed.

Decussate phyllotaxis is a rare variant and thus an unimportant character in *B. crucis*. It suggests, however, a possibility that a related species might show it frequently, even normally, and the Jurassic shoots with this phyllotaxis, *Cupressinocladus ramonensis* Chaloner & Lorch (1960) and *C. micromerum* (Heer) Piao (see Teixeira 1948, Piao 1974) may possibly belong to the Hirmerellaceae and not to Cupressaceae.

The discovery of good shoots of juvenile type at Hasty Bank is interesting as they are of *Geinitzia* rather than *Brachyphyllum* form. They occur with great numbers of normal shoots and their identity is confirmed by transitional forms (Fig. 7 b). Possibly the mature tree produced occasional juvenile shoots as do some modern conifers (*Juniperus sabina* L.). Heterophyll is also known in the related fossil *Tomaxella biforme* Archangelsky (1966) but there the *Geinitzia* form predominates.

**Comparison.** *B. crucis* in its typical form is well distinguished from most shoots of the *Brachyphyllum* group by its strongly developed scarious leaf margin, by its thick cuticle with scattered stomata and also by the complete absence of epidermal papillae. The absence or weak development of papillae on subsidiary cells distinguishes it from *B. expansum* (known from
contemporaneous rocks in the English midlands). Another difference is that *B. expansum* commonly dropped richly and regularly branched shoot systems like a *Chamaecyparis*.

*Brachyphyllum trauti* Barale & Contini (1973) from the Bajocian of Doubs, France, is based on a branched shoot which resembles certain specimens of *B. crucis* in appearance, in leaf form and in the abaxial cuticle. Like some leaves of *B. crucis* it has few adaxial stomata. The stomata themselves look similar but encircling cells are only occasional. Many epidermal cells show a pale central area, not observed in *B. crucis*, but their fine sculpture is similar.

*B. mamillare* is readily distinguished by its shorter leaf cushions rising to an outward-directed free point. The cuticles show different cellular details and in addition a fully cleared cuticle of *B. mamillare* is usually grey-brown and fragile while one of *B. crucis* is yellow-brown and tough.

*B. ardenicum* is compared on p. 22.

The longest-leaved shoots fall well within the form-genus *Geinitzia*. *G. rigida* in particular may be similar but the occasional trichomes on the leaf edges distinguish it. *Pagiophyllum ordinatum* has well-marked stomatal files and no scarious leaf margin, and its leaves are much thicker vertically. The Liassic *Pagiophyllum peregrinum* shares these differences.

The four species of *Brachyphyllum* described by Archangelsky (1963) from the Lower Cretaceous of Argentina are all rather similar in form and cuticle. Three (*B. bretii, B. mirandai, B. irregulare*) agree in their marginal frills and in having adaxial stomata. Of these *B. bretii* differs in its obvious stomatal files, *B. mirandai* also in its files (though they are less obvious) whilst *B. irregulare* with scattered stomata is most similar. It differs in its flatter subsidiary cells which are concentrically rather than radially striated.

None of the four species of *Brachyphyllum* described by Wesley (1956) from the Upper Lias of north Italy is very similar. *B. praetermissum*, the least different in form, has no adaxial stomata or marginal frill but has papillate subsidiary cells. *B. kendallianum* has similar stomata but they form files; there are no stomata on the adaxial surface, there is no marginal frill and the leaf is shorter.

Two species with similar shoots are *Hirmerella muensteri* (Schenk) Jung (which includes *H. rhaetoliassica* Höhhammer 1933, see Jung 1967, 1968) and *H. airelensis* Muir & Van Konijnenburg-van Cittert (1970), but they are microscopically distinguishable from *B. crucis*. *H. muensteri* (cuticle preparations of German specimens in the British Museum) has nearly all its stomata in well-marked files and only rarely a slight scarious fringe at the leaf apex. Most leaves do not show any papillae though the whole cell surface may bulge, but a few do have distinct solid median thickenings which are to be termed papillae if they project outwards. A single specimen from the English Lower Lias (Wood 1961) is similar to *H. muensteri*.

*H. airelensis* which is contemporaneous with *H. muensteri* has papillae on some leaves but not on others. Its stomatal files are less definite than in *H. muensteri* but more definite than in *B. crucis*. Some leaves at least have a scarious apical margin. Muir & van Konijnenburg-van Cittert identify specimens described by Lemoigne (1967) without names from a locality near Airel with *H. airelensis*. If all Lemoigne’s material belongs to this species it is at least as variable as *B. crucis*. Another Lower Liassic shoot which is probably a *Hirmerella* (though this was not realized) is *Brachyphyllum scottii* Kendall (1949a) from western Scotland. It has very short leaves with no frill, scattered stomata and very strongly developed papillae. We need to know more about the range of cuticle and leaf form in these Rhaeto-Liassic species before they can be separated satisfactorily from one another but the Middle Jurassic *B. crucis* does seem distinct from them all.

*Brachyphyllum ekaistomum* Sukh-Dev & Bose (1974) has leaves and cuticles like the forms of *B. crucis* with short leaves, but is distinct. The parastichies (probably 6 + 8) are higher than in
equally thick shoots of *B. crucis* and the abundant Indian material includes no long-leaved forms. Sukh-Dev & Bose considered that *B. ekaistomum* might be podocarpaceous, but the Hirmerellaceae is another possibility.

*Brachyphyllum sarvum* Barnard & Miller 1976 from the Elburz Mountains of Iran and of similar age to *B. crucis* is so similar that certain preparations of leaf cuticles of the two are indistinguishable, but a difference can be recognized in the adaxial cuticles when a larger number of leaves are compared. In *B. crucis* the adaxial cuticle commonly extends back for 1 mm from the marginal frill and in its outer part it is like the abaxial cuticle and may bear 10–20 stomata. Only in an occasional leaf are there just a few stomata, or none. In *B. sarvum* it only extends about 0.5 mm, its cells are often crushed and stomata (if recognized) are very few and ill-formed. Barnard & Miller (1976: 108) stated a difference in the stomata, papillose in *B. crucis*, not in *B. sarvum*, but there is no reliable distinction. In Kendall's three original Callovian specimens (1947) the ring round the stomatal aperture was sometimes distinctly lobed, described as ‘papillae’, but in her later (1952) Bajocian specimens it was more often without lobes. Even in *B. sarvum* some stomata have a discontinuous ring which could be described as unevenly developed papillae.

The whole of our information on the male cone is that provided by van Konijnenburg-van Cittert (1971, 1972). I quote her diagnosis verbatim.

‘Male cone 7 mm long, 3.3 mm wide; microsporophylls borne spirally, consisting of a rather slender stalk and a sporophyll head 0.3–0.7 mm high, 0.5 mm broad, rhomboidal in outline; outer cuticle of sporophyll head about 4 µm thick; normally some scattered stomata present, stomata sunken; guard cells surrounded by a ring of subsidiary cells; stomatal pit oval to circular; papillae of subsidiary cells forming a thickened ring around the guard-cells; periclinal walls of subsidiary cells marked with fine striations running radially from centre of stomatal apparatus, encircling cells indistinct, epidermal cells rectangular, 15–20 µm wide, 20–40 µm long with thick walls, arranged in longitudinal rows; margin of microsporophyll head scarios; microsporophyll bearing two pollen sacs, pollen grains spherical with somewhat flattened poles, equatorial diameter 35 µm (extremes 30–40 µm); exine divided into two caps by an indistinct equatorial belt, 5 µm wide; exine of the caps 1–2 µm thick, baculate, striae of the equatorial belt not very distinct, usually 8 striae, sometimes up to 12; distal cap separated from the equatorial belt by a distinct thin region (rimula) 1–2 µm wide; distal pole with a circular thin area about 9 µm in diameter, proximal pole with a triangular thin area extending over the largest part of the pollen grain (in polar view).’

**Discussion.** Van Konijnenburg-van Cittert discusses the various male cones yielding Classopollis pollen and also discusses similar dispersed pollen grains. She points out that *B. crucis* pollen changes its aspect during maceration. At first the girdle shows no striations and the grains look like *Circulina*, but with further maceration striations become visible and the grains then look like *Classopollis multisstriatus* Burger.

Like many fossil male cones, that of *B. crucis* is incompletely known but its attribution seems to me to be secure. The specimens were found at Hasty Bank on blocks with *B. crucis* shoots and no other conifer. It is also linked by agreement in structure. The sporophyll ends are very like the cuticle of a leaf in their stomata and scarios edge. The cuticle is 4 µm thick, remarkably robust for a male cone.

There is still conflict of opinion about the organization of the microsporophyll in different species of the Hirmerellaceae. The evidence indicates variation in number of pollen sacs from 2 to 8. *H. muensteri* was originally believed to have a radially symmetrical ring (as in *Taxus*) and this has been reaffirmed by Jung (1968). Harris (1957) interpreted it differently. I argued that there were about 6 sacs below the sporophyll forming a semicircle and that the top of the
supposed ring was provided by sacs of the sporophylls above. I adhere to this view, which would bring *H. muensteri* into line with other species and conifers generally except *Taxus*. *Brachyphyllum crucis* is described as having just two pollen sacs and certainly not a ring. Male cone fragments from Wales, with leaves determined as *H. muensteri* by Harris (1957) and attributed to though not categorically identified with *H. airelensis* by Muir & Van Konijnenburg-van Cittert (1970), have denuded dorsiventral microsporophylls on which there would only be space for two, or at most three, of the associated pollen sacs. The *H. airelensis* male cone (Muir & Van Konijnenburg-van Cittert 1970) has two (or three?) pollen sacs—a difference from *H. muensteri*.

Other male cones providing *Classopolis* and therefore presumed to be of the Hirmerellaceae are *Masculostrobus rishra* Barnard (1968) from Iran, which has dorsiventral microsporophylls with 6–8 pollen sacs on the under side, and *Tomaxellia biforme* Archangelsky from the Lower Cretaceous of Argentina, which has small cones yielding *Classopolis* but in which the organization of the microsporophyll is unknown.

The most detailed account available of the pollen of *B. crucis* is by Van Konijnenburg-van Cittert (1971). Pettitt & Chaloner (1964) give fine details of the wall of the Welsh *Classopolis* grains from intact pollen sacs. It agrees with the dispersed grain *C. torosus* (Reisinger) Couper.

**Occurrence.** In Yorkshire *B. crucis* ranges throughout the Deltaic series (Bajocian and Bathonian) but is more abundant near the base of the series than higher up. It is also known from the marine Bathonian of Oxfordshire and the marine Callovian of Wiltshire. It is, however, unknown in the richest plant beds at Cloughton and Grinsthorpe and is very rare in the Middle Deltaic coals. Many fragments are from rocks of partly marine origin or close to a marine horizon and all the intact shoots are from beds with marine microfossils (acritarchs and *Tasmanites*) or with *Pachypteris papillosa* (Thomas & Bose) Harris, itself strongly associated with marine microfossils. However, it occurs also in localities in which no marine influence has been recognized and it is thus not yet to be taken as an indicator of a salty habitat. Further work is needed.

**Localities:**

Wiltshire: (Marine) Callovian ‘Oxford Clay’ *jasoni* or *dunkeri* Zone, Christian Malford (Kendall 1947).

Oxfordshire: (Marine) Upper Bathonian ‘Forest Marble’, Filkins (Kendall 1952).

Yorkshire: *B. crucis* occurs in marine beds, in beds of partly marine origin (with land plants and marine microfossils) and in ones of fresh-water origin. Certain shales bordering a marine rock have been counted as part of the marine rock.

<table>
<thead>
<tr>
<th>Marine localities</th>
<th>Fresh-water localities</th>
</tr>
</thead>
<tbody>
<tr>
<td>Upper Deltaic</td>
<td>1</td>
</tr>
<tr>
<td>Grey Limestone</td>
<td>–</td>
</tr>
<tr>
<td>Grinsthorpe Series</td>
<td>6</td>
</tr>
<tr>
<td>Millepore Bed</td>
<td>–</td>
</tr>
<tr>
<td>Sycamore Bed</td>
<td>5</td>
</tr>
<tr>
<td>Eller Beck Bed</td>
<td>1</td>
</tr>
<tr>
<td>Lower Deltaic</td>
<td>7</td>
</tr>
</tbody>
</table>

Thus of all its localities 25 are marine or close to a marine horizon whilst 19 are, so far as we know, without marine influence.

**Taxonomic position.** I am convinced that the shoots and male cones belong to one species, though continuity has not been demonstrated. On this basis the species is probably to be placed in the Hirmerellaceae, discussed on p. 51.
Brachyphyllum ardenicum sp. nov.

Fig. 8

Diagnosis. Ultimate shoots (the only part known) cylindrical, about 2–3 mm wide (branching unknown). Leaves forming simple helix, probably with 1 + 2 parastichies, each basal cushion surrounding two-thirds of stem. Largest leaf and cushion 7 mm × 3 mm but most about 3 mm × 1.5 mm. Free part of leaf 0.5–1.5 mm long, margins continued on cushion as overhanging edges. Leaf apex pointing forwards, close to stem, surface of cushion rounded. Margins of cushion rounded in section in basal part, becoming angular at middle and sharply angular in free leaf, not scarious but marginal cells sometimes forming minute solid projections.

Cuticles tough, thickness measured in folds up to 15 μm. Stomata absent from adaxial leaf surface, widespread on abaxial surface and cushion but fewer below and fewer in middle region than towards sides. Stomata forming well-marked longitudinal files but scattered near cushion base. Files on general level but individual stomata sunken in pits, unevenly spaced in their files and separated by ordinary cells. Encircling cells absent (or not recognizable with certainty), guard cell orientation varied, subsidiary cells 4–6, forming a ring; surface sloping inwards to form wide pit up to 50 μm wide and 25 μm deep. Surface of subsidiary cells tending to be thicker towards outer margin of pit but thinning inwards. Subsidiary cell surface varied; smooth, granular or radially striated. Outer wall of subsidiary cells at general level, inner wall heavily thickened, 10 μm broad but not raised, forming a rim which is even or lobed but not forming papillae. Guard cells thinly cutinized. Trichomes absent from surface.

Epidermal cells mostly longer than broad, often 2–4 times longer, rectangular, forming longitudinal files. Anticlinal walls broad, prominent, straight but often with distinct lateral nodules or tooth-like extensions onto the surface; periclinal wall flat and without any local thickening but often with numerous pits 2–3 μm wide. Hypodermis occasionally seen as faintly marked elongated cells between files.

Holotype. V.57498, Fig. 8 D.

Name. The specific name is from Arden, the district that includes two of its localities.

Discussion. The material consists of numerous fragments isolated by bulk maceration and nearly all are separate leaf and leaf base cuticles. Many are folded in a way that shows that they encircled more than half the stem, as in the restoration (Fig. 8 a). In this the species differs from normal shoots of B. mamillare, B. crucis and most other species.

Comparison. Brachyphyllum ardenicum has short free leaves which point forwards, not outwards as in B. mamillare; its cuticle is far more robust, its cells are often elongated and its stomata monocyclic. Short-leaved forms of B. crucis are more similar but they differ in the leaf having a marginal frill and in their scattered stomata. The short-leaved forms of Geinitzia rigida are even more similar but have a more extensive adaxial cuticle, often with stomata and usually also with marginal trichomes. The cell walls of G. rigida are never jagged.

Occurrence. B. ardenicum is known from five localities only, four in the Lower Deltaic and one in the Sycarham Series. It was nowhere recorded as the commonest species and its associates are fragments of tough cuticles of more widespread species. Nothing unusual was noticed among the associated miospores.
Form-genus *Pagiophyllum* Heer 1881

**Emended Diagnosis.** Shoot, bearing leaves in a helix; leaf about as broad as its basal cushion, length exceeding width of cushion. Blade not or scarcely narrowed at its base, in section broader horizontally than thick vertically.

**First described species.** *Pagiophyllum cirinicum* (Saporta) Heer (1881: 11), for *Pachyphyllum cirinicum* Saporta (1879: 402).
Discussion. The diagnosis differs from that of Kendall (1948) mainly in omitting details of the cuticle.

The sole distinction of *Pagiophyllum* from *Brachyphyllum* is its longer free leaf, and occasional specimens of both genera transgress the arbitrarily defined boundary. *Geinitzia*, as defined here, has leaves as thick vertically as they are broad laterally. Earlier authors had made no definite distinctions between these three genera, and species which I now place in one or another were formerly included in many different genera implying family or generic affinities. I presume *Pagiophyllum* includes plants of diverse families though some species certainly belong to the Hirmerellaceae.

All but one of the Yorkshire species have numerous Yorkshire localities ranging through the Bajocian and Bathonian, but the exact occurrence is different for each. Nearly all the specimens are fragments of tough cuticles, certainly broken before deposition, and differences in their mechanical properties seem unlikely to explain their different occurrence. I think it more likely that they reflect differences in where and how the plants originally grew. This is discussed further under each species.

Key to the Yorkshire species of *Pagiophyllum*

All field determinations require confirmation based on the cuticle.

1. Free leaf commonly over 5 mm long
   - Free leaf commonly under 5 mm long
     - Leaf apex commonly obtuse (no stomata above)
       - Leaf apex acute, stomatal pits on both surfaces
         - Leaf concave above, over 12 mm long
           - Leaf convex above, seldom over 12 mm long
             - Apical angle under 30°, stomata papillate
               - Apical angle over 30°, stomata not papillate
                 - Leaf convex above, length four times width
                   - Leaf concave above, length under four times width

2. *P. maculosum*

3. *P. insigne* 

4. *P. kurrii* 

5. *P. ordinatum* 

6. (Geinitzia rigida) 

7. *P. fragilis* 

This key does not satisfactorily place the very long-leaved main stems of *Pagiophyllum kurrii*. It might also include long-leaved forms of *Brachyphyllum mamillare* and of *B. crucis*.

Kendall (1948), while recognizing that *Pagiophyllum* as revised by her might be heterogeneous, pointed out certain *Araucaria*-like features in their leaves. Two of the five species described here, *P. maculosum* and *P. kurrii*, are now known to have female cones like those of *Hirmerella*, so these are not araucarian. Some of the others have a leaf epidermis which somewhat resembles these two, as does *Geinitzia rigida* (formerly included in *Pagiophyllum*), but *P. fragilis* is very different.

*Pagiophyllum insigne* Kendall  
Figs 9, 10

1948 *Pagiophyllum insigne* Kendall: 78, text-figs 1–3. (Description and figures repeated here)

Diagnosis (modified from Kendall). Ultimate shoots straight, rarely branched. Axis about 3 mm wide, leaves forming a loose, simple helix with $2 + 3$ parastichies. Shoot apex with shorter leaves (but not forming a resting bud and no regions showing short leaves).

Leaf base cushion normally concealed, about 5 mm $\times$ 2.5 mm, bulging and rounded, free leaf borne at its apex. Leaf blade projecting radially at about 50° to axis, lanceolate, apex curving
slightly forwards, typically 12 mm long by 6 mm wide near middle, contracting to 4 mm wide near base, tapering to sharp point at apex. Substance about 1.3 mm thick. Upper surface of leaf concave, lower surface very convex, forming an obtuse keel. Margins entire, not scarious, but leaf surfaces meeting at acute angle.

Cuticles about 6 μm thick on each side of leaf. Stomata frequent on both sides but often fewer on keel and absent near margins and at apex, forming longitudinal files one stoma wide, only a few stomata occurring out of a file. Files evenly spaced and separated by about five files of ordinary cells. In their files stomata fairly evenly spaced, commonly separated by 2–5 ordinary
epidermal cells; subsidiary cells of adjacent stomata rarely in contact. Orientation of stomata irregular, mostly oblique. Stomatal files not sunken, but individual stomata sunken about 40 μm below general epidermal level. Guard cells large, 60–90 μm long by 38 μm wide, surface and aperture thinly cutinized; aperture about 40 μm long, curved, the middle being at a deeper level than ends. Upper margin of pit sometimes as wide as guard cell surface but often contracted and round or oval, orientation if oval independent of guard cell orientation. Subsidiary cells about 6–8, forming an irregular ring, lateral walls inconspicuous, inner margin forming the pit and usually overhanging guard cells. Surface not thickened or papillose. Wall of pit rather thickly cutinized. Encircling cells seldom present.

Ordinary epidermal cells similar on both sides of leaf, arranged in longitudinal files about 20 μm wide. Those cells in stomatal files are approximately square, those between files rectangular and about 32 μm long, but near margins and apex of leaf often longer. Anticlinal walls of epidermal cells obscurely marked, about 10 μm wide; lateral and end walls similar. Periclinal walls flat, without a papilla, unpitted, sometimes showing obscure longitudinal ridges. Hypodermal cells slightly cutinized, about 16 μm wide by about 170 μm long; end walls oblique. (T.)ichomes absent.)

Holotype. V.24696.

Discussion. P. insigne is rare. It is represented by four good shoots, collected by F. M. Wonnacott from the Gristhorpe Bed on one visit, and by a single leaf fragment from the somewhat older Sycarham Series at Hagg Beck, Bed D. It is exceptional in being represented by good specimens though not by numerous and widespread fragments, unlike the other species of Pagiothyllum which have many localities yielding fragments.

The four shoots are in a similar matrix and might originally have been joined, though the blocks cannot be fitted together. I presume that the species was originally rare and that a tree dropped its shoots directly into the Gristhorpe lagoon or the river feeding it. I do not think it was one of the species of higher ground that provided scattered cuticle fragments.

The stoma is here interpreted differently from Kendall (1948). She noted that the outlines of the epidermal cells, particularly of the subsidiary cells, were obscurely marked. However, they become more distinct with further maceration and I now consider that the subsidiary cells form both the surface just outside the pit and also the sloping or vertical sides of the pit. Encircling cells (which Kendall considered to be present round the pit) are rarely present. I give restorations of two stomata, one with the pit mouth only slightly constricted, the other more constricted and overhanging the guard cells. This is similar to the interpretation now given for the stoma of P. maculosum but I can find no very similar stoma among living conifers.

Comparison. Most Pagiothyllum shoots have shorter leaves than P. insigne. The possibility was considered that P. insigne might represent the unknown main stem of P. maculosum, but normal shoots of P. maculosum are unknown in the Gristhorpe Bed and though the stomata are somewhat similar the cuticles differ in other respects. The adaxial cuticle of P. maculosum has scarcely any stomata and its epidermal cells have central thin ‘spots’. Pagiothyllum ordinatum and P. kurrii have different stomata and differ also in their very thick leaves. P. veronense Wesley from the Italian Upper Lias looks similar but has shallow, scarcely constricted stomatal pits.
Fig. 10. *Pagophyllum insigne* Kendall

A, B, cuticle of holotype, V.24696c; hypodermal cells shown by broken lines, × 400; B, × 200. C, imaginary transverse section through E. D, similar section through A. E, stoma of rather open form, V.24697a, × 400. Figures A, B are from Kendall (1948).
Fig. 11. *Pagiophyllum kurrii* (Schimper)


*Pagiophyllum kurrii* (Schimper) Salfeld (shoot) and *Hirmerella estonensis* (Kendall) comb. nov. (female cone)

Shoot and leaf, Figs 11–13; Pl. 3, figs 4, 5

1843 *Araucaria peregrina* Lindley & Hutton; Quenstedt: 267. (German specimens)
1846 *Araucaria peregrina* Lindley & Hutton; Kurr: 9; pl. 1, fig. 1. (German)
1849 *Moreauta Kurrii* Pomel: 331 (nomen nudum, in list).
1858 *Araucaria peregrina* Lindley & Hutton; Quenstedt: 272; pl. 34, figs 1–3, 7. (German)
Emended diagnosis. Main shoots (rarely preserved) with an axis 1 cm thick; straight, seldom branched. Leaves borne helically and rather sparsely, in 2 + 3 parastichies, each at top of a bulging basal cushion; free parts stiff, nearly square in section, projecting radially, somewhat reflexed; length up to 40 mm, width and thickness at base 3 mm, tapering evenly to a sharp point. Intermediate shoots with axis about 6 mm thick, leaves at right angles to stem and 30 mm long. Ultimate shoots shed intact, usually straight, simple or sparingly branched, stem including leaf bases up to 3 mm wide. Apical leaves small (but not forming a bud and no bud scales present below). Leaves persistent, helically arranged in 2 + 3 parastichies, projecting evenly on all sides, overlapping and usually concealing basal cushions of leaves above. Free part of leaf typically 10 mm × 4 mm (range 14 mm × 5 mm to 6 mm × 3 mm, but still smaller at stem apex). Lateral margins curving downwards to form sides of basal cushion, upper surface running straight to top of cushion, lower surface bending sharply to form surface of cushion; cushion extending about 2 mm downwards, only slightly broader than free part of leaf. Leaf apex usually curved forwards, normally acute but occasionally obtuse. Substance of leaf very thick, vertical thickness typically about half of horizontal thickness but occasionally nearly equal to it. Lower surface of leaf strongly convex, upper surface moderately convex, both surfaces rounded and with no ridge along mid-line. Leaf margins forming sharp angles but not scarious. Surfaces of lamina smooth, stomata obvious as pits in files.

Cuticle about 6 µm thick on both sides of leaf. Stomata present in about equal numbers on both surfaces, concentration typically 25 per mm² evenly distributed over most of leaf and of cushion, but fewer at apex, at margins and at base of cushion. Stomata placed in well-marked longitudinal files but some occurring out of a file on basal cushion and exceptionally also on free leaf. Stomatal files usually separated by 4–6 files of ordinary epidermal cells, not sunken and not grouped into bands. Stomata rather closely spaced in their files, usually separated by 1–3 unspecialized epidermal cells. Apertures variably orientated.

Guard cells about 30 µm below general level, 60–75 µm long, aperture 28–36 µm long, the middle being at a deeper level than the poles; surface of guard cells thinly cutinized. Subsidiary cells forming regular ring, usually about six, occasionally more. Outer edge of each subsidiary cell separated from adjacent epidermal cells by deep trench with thinly cutinized base. Outer vertical wall of trench appearing in compression very thick and sometimes slightly raised above general surface. Subsidiary cell surface thickened as it approaches centre of apparatus, forming a firm ring. Each subsidiary cell bearing on its surface near and over this ring a conspicuous solid papilla which is upright or oblique and converging over stomatal aperture. Papillae of very varied size but a typical and well-developed one 36 µm long, its base 16 µm wide, then narrowed to 8 µm but expanding above to a rounded head; heads usually projecting above rest of epidermal surface. Depth of stomatal pit about 30 µm. Encircling cells absent (or if present occasional and doubtfully recognizable).

Epidermal cells of both surfaces similar, arranged in longitudinal files, cells of stomatal files
often square but with somewhat rounded corners, width about 25 μm, cells between stomatal files often somewhat longer than broad and occasionally 60 μm long. Anticlinal walls prominent, about 10 μm wide, uninterrupted; surface wall smooth, bulging slightly but not thickened to form a papilla. Hypodermal cells marked by thin ridges of cuticle (but originally thick-walled and in more than one layer), those between stomatal files about 15 μm wide, elongated and with pointed ends, those of stomatal files about 40 μm × 30 μm. (Trichomes absent.)

Type specimen. Kurr, 1846: pl. 1, fig. 1, selected by Schimper (1870).

Discussion. Pagiophyllum kurrii with its turgid, almost succulent small shoots and its main shoots with long needles must have looked a striking plant. Heterophylly has been observed also

Fig. 12. Pagiophyllum kurrii (Schimper)
A, upper and lower cuticles of one leaf, ×5; dots representing stomata. B, stomata near fold in cuticle, showing pits and papillae, ×200. C, cuticle, ×200. D, imaginary transverse section through a stoma; cuticle shown black, dotted cell walls imaginary, ×200. E, stoma; the margin of the pit formed by encircling cells is slightly overhanging, hypodermal cell-outlines seen as faint ridges represented by broken lines, ×400. Figures A–C, E, are from Kendall (1948), based on cuticles from Yorkshire Museum specimen 'B'. Fig. D, reconstructed from various preparations, is new.
in the related *Tomaxellia biforme* Archangelsky (1966), but there the long and short leaves both occur on the same shoot systems, rather as in *Juniperus sabina* L.

The identification of the Yorkshire material named *P. connivens* with the German *P. kurrii* increases our knowledge. The shoots look similar but Kräusel (1923), who examined the cuticle, gave a figure which seemed outside the range of *P. connivens* as it showed many more than the usual six stomatal papillae. The Director of the Institut und Museum für Geologie und Paläontologie der Universität Tübingen kindly lent me one of the German specimens, the original of Salfeld's pl. 19, fig. 1. It is preserved in a hard limestone and Salfeld's figure is remarkably accurate. The upper leaf surface is strongly convex, projecting well above the lateral margins, just as Salfeld's figure implies. The stomata are seen as pits which form crowded files on both surfaces, as in a typical Yorkshire shoot of *'P. connivens'*, but it proved very difficult to prepare a cuticle. A minute fragment previously unexposed was macerated. The substance was thick and oxidized only very slowly, remaining tough like horn. Though some solution took place in ammonia much internal tissue persisted and it was difficult to separate the cuticles. A few stomata showed their papillae clearly and their number (about six) was the same as the subsidiary cells, but in addition there were extraneous drops of solidified oil resembling papillae. In all respects apart from preservation the cuticle agreed with the Yorkshire specimens. Though I have not seen Kräusel's preparation, I think that if it was preserved in the same way as the present one, mistakes would have been likely, and I suggest that some of his papillae may be in fact extraneous globules of hardened oil. Leaves preserved in marine limestones rather frequently seem to be oil-imregnated and it is difficult to prepare their cuticles.

The German specimens of *P. kurrii* are of Upper Liassic (Lias ε) age, similar to the holotype of *P. connivens* (Upper Lias *serpentinus* Zone at Whitby), but most of the Yorkshire material is younger, being Bajocian or Bathonian.

In diagnosing *P. connivens*, Kendall described the lateral angles of the leaf as rounded and the upper and lower as sharp, but this was a verbal slip and is here corrected. Leaves compressed in various planes show their shape clearly, with sharp lateral angles, a moderately bulging upper surface and a strongly bulging lower surface. In the Yorkshire material the leaf substance has usually decomposed and nothing remains of the vascular tissue. The shoot must in life have looked unlike that of any existing conifer but more like some dicotyledon with thick, succulent leaves.

Kendall based her *P. connivens* on three shoots and a few cuticle fragments. Her holotype seems to be the specimen which Fox-Strangways (1892) called *Pachyphyllum peregrinum*, of the *serpentinus* Zone. Apart from this specimen the species was unknown to earlier workers, but shoots have now been found in a good many localities and isolated leaves are often abundant, being amongst the most widespread of Yorkshire fossils.

All the shoots known to Kendall were ultimate ones and she called them slender, but later a few thicker ones were found. One of these, from Haiburn Wyke, has an axis 6 mm thick. Its leaves diverge widely, making the shoot 20 mm wide, but they are short, though on the same block there is an isolated leaf 20 mm long and 4 mm wide below. A fallen block below Hawsker, of Lower Deltaic or Sycarham age, gave many *P. kurrii* shoots, ranging from the ordinary small ones to long thick ones with stiff and slightly reflexed leaves 40 mm long; Fig. 13 f–h.

The stoma is here interpreted somewhat differently from Kendall (1948). I doubt if the cells occasionally opposite a subsidiary cell are true encircling cells. In a new reconstruction of the stoma in section (Fig. 12 d) I show the trench round the subsidiary cell-group as very deep and the cuticle at its bottom as thin. This trench is near the outer edge of the subsidiary cells. The next cells are ordinary epidermal cells, not encircling cells. The depth of the trench varies as
Fig. 13. *Pagiophyllum kurrii* (Schimper)

Fig. 13. Pagophyllum kurrii (Schimper)
F–H, shoots from a single fallen block at Hawsker. F, large shoot with reflexed leaves 4 cm long; also basal portion of leaf of Zamites quiniae Harris. V.58330. G, similar large shoot with two smaller ones originally attached, V.58329. H, medium-sized shoots with straight leaves about 3 cm long, V.58327. All figures ×1.
does the thickness of the radial walls between the subsidiary cells. Often in poor preservation
the cuticle of the trench breaks and the whole middle part of the apparatus is lost. I cannot find
any living conifer with a stoma just like *P. kurrii*.

**Comparison.** *P. kurrii* is at once distinguished from all other Yorkshire species of
*Pagiophyllum* by its characteristic stomata, and these distinguish it too from the Lower Liassic
*P. peregrinum* (see Kendall 1948) which has no papillae. Other species with leaves of similar
shape but no stomatal papillae are *P. sewardi* Kendall (1948) and *P. veronense* Wesley (1956).
*Voltzia ribeiroi* from Portugal (Teixeira 1948), with similar leaves and similar stomatal papillae,
is distinguished by its papillose ordinary cells; see p. 36 for further discussion. There are
*Pagiophyllum* shoots described by Saporta (1884), under the specific names *P. rigidum* and *P.
peregrinum*, from the French Jurassic which look similar but their cuticles are unknown.

**Occurrence.** Yorkshire hand specimens are distributed as follows, most occurring in
sandy beds:

<table>
<thead>
<tr>
<th>Horizon</th>
<th>No. of localities</th>
</tr>
</thead>
<tbody>
<tr>
<td>Upper Deltaic</td>
<td>1</td>
</tr>
<tr>
<td>Middle Deltaic Sycarham Series</td>
<td>2</td>
</tr>
<tr>
<td>Lower Deltaic</td>
<td>9</td>
</tr>
<tr>
<td>Upper Lias (serpentinus Zone), Whitby</td>
<td>1</td>
</tr>
</tbody>
</table>

In addition leaves or leaf fragments have been found by bulk maceration in 73 localities
distributed as follows:

<table>
<thead>
<tr>
<th>Horizon</th>
<th>No. of locs</th>
<th>% of all locs with determinable plants</th>
</tr>
</thead>
<tbody>
<tr>
<td>Upper Deltaic</td>
<td>4</td>
<td>3%</td>
</tr>
<tr>
<td>Grey Limestone or just below it</td>
<td>6</td>
<td>(all)</td>
</tr>
<tr>
<td>Gristhorpe Series</td>
<td>12</td>
<td>9%</td>
</tr>
<tr>
<td>Millepore Bed</td>
<td>1</td>
<td>–</td>
</tr>
<tr>
<td>Sycarham Series</td>
<td>20</td>
<td>28%</td>
</tr>
<tr>
<td>Eller Beck Bed</td>
<td>1</td>
<td>–</td>
</tr>
<tr>
<td>Lower Deltaic</td>
<td>28</td>
<td>13%</td>
</tr>
<tr>
<td>Upper Lias</td>
<td>1</td>
<td>–</td>
</tr>
</tbody>
</table>

*Pagiophyllum kurrii* is particularly well suited to being recovered and identified from bulk
macerations. Its relative abundance in the Sycarham Series is noteworthy because that stage is
rather barren; fragments of *P. kurrii* are also the chief species recovered from the Grey Limestone.
Fragments often accompany those of the equally tough cuticles of *P. maculosum* and *Geinitzia
rigida*, no doubt partly for mechanical reasons. *P. kurrii* is, on the other hand, unknown in the
rich plant beds of Whitby, Cloughton and Gristhorpe, and it is very seldom met with in the
Middle Deltaic moorland coals or in the partly marine beds just above the Lias. I once thought
it might represent the upland flora washed down as fragments from distant high hills but I now
consider this not necessarily so. A few metres elevation above the flood plain would be enough
to provide a habitat with a soil which was strongly contrasted with that of the flood plain itself,
being leached and acid instead of irrigated and base-enriched.

**Male cone**

Fig. 14 B–D, F, I

In 1952 Kendall described two detached male cones from an old quarry on Eston Moor. The
block of sandy shale also showed many *P. kurrii* shoots and when macerated in bulk it gave in
Fig. 14. Reproductive organs associated with Pagiphyllum kurrii (Schimper) at Eston Moor
A, female cone-scale, holotype of Araucarites estonensis Kendall. The dotted lines are very indistinct impressions on the matrix and some are doubtfully real; V.29497, ×2. B, C, two male cones, V.29562, ×3. D, margin of microsporophyll, V.29561b, ×400. E, stoma from lower part of membranous wing on left of A; V.29497a, ×400. F, pollen grains from male cone, V.29561c, ×400. G, cuticle from distal part of membranous wing on left of A, V.29497b, ×400. H, mutually adherent cuticles from lower part of ‘seed’ of A, V.29497c, ×400. I, cuticle of microsporophyll, hypodermal cells represented by broken lines; V.29561a, ×400. All figures are from Kendall (1952).
addition a few fragments of *P. maculosum*. There was little else. The rock was weathered and the specimens were miserably preserved but she was able to obtain minute fragments of cuticle from both cones. The cones merely show their size and shape and the upturned ends of microsporophylls, and it is impossible to see how the pollen sacs were borne. On the free upturned ends of the microsporophylls the cuticle is about 2 \( \mu \)m thick and shows the clearly-marked outlines of somewhat elongated cells, in some places continuous though other preparations show them as a row of dots. In places the surface wall is marked by parallel striations. The margin shows irregular teeth 10–15 \( \mu \)m high, the extensions of single cells. Stomata are rare and the few seen are round with papillose subsidiary cells.

The pollen sacs have shed their pollen though one preparation believed to be a pollen sac tapetum shows many similar-looking round pollen grains. Kendall noted their size and thick walls but no other features. Couper (1958) however, who re-examined her preparations, was able to recognize the characteristic features of *Classopollis* and I concur, though the preservation is poor.

It is interesting that Teixeira (1948: pl. 2, fig. 12, 12a) found a male cone like that of *P. kurrii* with his *Voltzia ribeiroi* (which I suspect is closely related). We have no details. *P. connivens* of Markova (1961) merely refers to dispersed *Classopollis* grains resembling Couper’s figures of pollen from the Yorkshire *P. kurrii* male cones.

*Hirmerella estonensis* (Kendall) comb. nov. (Female cone)

![Image](14, E, G; Pl. 1, figs 19–21)

1952 *Araucaries estonensis* Kendall: 583, text-fig. 1A–D. (All figures represent the holotype, now regarded as a *Hirmerella* bract scale. Figures reproduced here in Fig. 14A,E,G,H.)

**Emended diagnosis.** Separate bract scales and ovuliferous scale known only. Bract scale 1–2 cm long and up to 1·5 cm broad, lower part wedge-shaped, rounded angles at its top contracting to obtuse or acute point. Substance fairly thick in middle but thinning to margins and apex. Cuticles fairly thick; in marginal and apical parts showing isodiametric thick-walled cells, those near apex often with a solid papilla; cells in lower parts of scale elongated. Stomata frequent near margins and apex (distribution on the two surfaces unknown), scattered, orientation varied. Subsidiary cells about six, equal, forming a ring; encircling cells normally absent. Subsidiary cells separated from rest of epidermis by a deep trench thinly cutinized at its bottom, inner part forming a thick ring and each cell bearing a papilla. Papillae typically with elongated stalks converging over the aperture and ending in an enlarged round head, but form varied. Elongated hypodermal cells present, marked by delicate cuticles.

Ovuliferous scale wedge-shaped, about 1·5 cm long, 0·8 cm broad above. Lateral margins straight, apical margin rounded, divided into four (or five) rounded lobes each about 1·5 mm long and 1·5 mm broad or rather broader. (No other details known.)

**Holotype.** V.29497.

**Discussion.** There are four specimens, the two described by Kendall and two found later which include the only ovuliferous scale. The quarry on Eston Moor which provided the material was abandoned long ago and the fossils in the flaggy sandstone are severely weathered. Several layers are fossiliferous, *P. kurrii* being widespread and *P. maculosum* occasional. The layer that gave the female cone scales contained many *P. kurrii* shoots and nothing else determinable, although the small male cones described by Kendall were from nearly or exactly the
same place. The bract scale described by Kendall as the holotype of *Araucarites estonensis* gave fairly good cuticle preparations, but the cuticle of the more recently collected one (Pl. 1, figs 20, 21) is poorer and the ovuliferous scale (Pl. 1, fig. 19) is replaced by an oxidized iron mineral giving no fine details. Kendall’s stomata agree with those of *P. kurrii* and nothing else in the Yorkshire flora, so I am convinced that *H. estonensis* belongs to it. She interpreted it (with my agreement) as a cone scale of *Araucarites* and regarded the confused cuticles at its base as those of the seed, but I now think they may be extraneous adherent fragments. The holotype had markings suggesting a single seed, though the recently-collected nearly complete bract (Pl. 1, figs 20, 21) shows nothing like one. Although these bracts are of different size and shape, the differences are no greater are met with in *H. kendalliae*.

The ovuliferous scale (Pl. 1, fig. 19) merely shows its outline and I cannot be sure whether one of the lobes is very broad or is really two lobes close together. The identification rests on its general resemblance to a *Hirmerella* cone scale.

*Hirmerella estonensis* is imperfectly known. Still, assuming my ideas are right, it does fit the general picture of a *Hirmerella* and also of the reproductive organs attributed to *Voltzia ribeiroi* by Teixeira (1948) which are in some respects very similar to this species.

Affinity of *Pagiophyllum kurrii*. If, as I believe, the male cone and the female cone scales described here belong to *P. kurrii* then it has no near affinity with *Araucaria* but on the contrary is close to *Hirmerella muensteri*.

*Pagiophyllum ordinatum* Kendall
Figs 15–17

1948 *Pagiophyllum ordinatum* Kendall: 104; text-figs 11, 12. (Cuticles only)

**Emended diagnosis.** Ultimate shoots slender (not flattened), occasionally branched, scarcely tapering (leaves near apex not much smaller and not forming a protected bud). Width of shoot typically 10–15 mm but sometimes more; axis 2–3 mm wide, its surface forming convex leaf bases but usually concealed. Leaves borne helically in 2 + 3 parastichies, free part typically 10–12 mm long, 5 mm wide and 3 mm thick, but some leaves larger; diverging from stem at 60°–70°, curving forwards slightly and apex often pointing adaxially. Apex obtuse, rarely acute. Blade attached to top of cushion, lanceolate and widest at its base, both surfaces rounded and strongly convex; margins strongly angular (but not scarios), in lateral compression converging and meeting over adaxial surface just below apex. Leaf surfaces smooth apart from stomatal pits, internal substance dense (details apart from hypodermis unknown).

Cuticle on both surfaces of leaf tough, about 6 μm thick. Stomata numerous, evenly distributed on both sides but avoiding middle region at leaf base, placed in files a single stoma wide, very few stomata out of their files except at leaf base. Stomatal files separated by about three files of ordinary epidermal cells, many files ending below apex. Neighbouring stomata of a file separated by 1–3 ordinary cells, rarely with subsidiary cells in contact. Guard cells irregularly orientated, sunken in deep, rounded pits. Pits compound, outer part formed by edge of encircling cells, inner part formed by subsidiary cells. Outer pit 50 μm wide, 30–50 μm deep, sides vertical or overhanging. Inner wall of encircling cells thick and usually raised. Subsidiary cells with thinly cutinized surface but thickly cutinized near inner pit over guard cells. Inner pit of stoma rounded or oval, typically 30 μm wide (24–44 μm), shallow, but ring of cuticle round pit sometimes considerably raised. Encircling cell pit, if strongly overhanging, concealing thin outer
surface of subsidiary cells. Subsidiary cell surface sometimes radially striated. Guard cells thinly cutinized (often not preserved). Outer encircling cells occasionally present, unspecialized. Ordinary epidermal cells of both surfaces rectangular, arranged in longitudinal files, corners seldom rounded. Cells in stomatal files often extended transversely, those between files square or moderately elongated. Anticlinal walls usually prominent, about 6 μm wide, sometimes interrupted by pits, occasionally cuticle almost evenly thick and anticlinal walls inconspicuous. Periclinal cell walls sometimes marked with faint striations, usually smooth and flat but sometimes convex and slightly thicker in middle of cell (though not papillose). Hypodermal cells 16 μm wide, their walls faintly marked.

**Holotype.** V.27424.

**Discussion.** Kendall based this species on cuticle fragments from four Upper Deltaic localities. Since then a few hand specimens have been collected at two Lower Deltaic localities and these have added considerably to knowledge. Cuticle fragments have also been found throughout the Deltaic series.

The main differences between the present account and Kendall's are additions arising from
hand specimens, whilst the stoma is differently interpreted as a result of better material. Laterally compressed stomata seen in folded leaves were very useful.

Comparison. *Pagiophyllum ordinatum* looks very like *P. kurrii*, but the leaf base cushion is shorter in *P. ordinatum*. Both have thick leaves, convex on both sides and with sharp lateral margins. They are readily distinguished by the stomata which though similarly constructed are conspicuously papillose in *P. kurrii* but not papillose at all in *P. ordinatum*. As Kendall says, the stomatal files of *P. ordinatum* are often more regular, their stomata are more crowded and the stomatal pits larger.

*P. veronense* Wesley from north Italy agrees with *P. ordinatum* in the form of its leaf, but the leaves are less crowded. Though the stomata are in similar strongly-marked files, the cuticle differs in being thinner and in showing elongated epidermal cells with conspicuously pitted anticlinal walls.

*P. peregrinum* (Lindley & Hutton) of the Lower Lias (Seward 1904, Kendall 1948) has rather similar shoots, thick leaves and somewhat similar stomata but the leaves of *P. ordinatum* are nearly always longer in relation to their width.

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Fig. 16. *Pagiophyllum ordinatum* Kendall

A, cuticle from middle of leaf, each dot representing one stoma, V.27423, ×5. B, cuticle from near leaf apex of holotype, showing stomata, V.27424, ×5. C, cuticle from base of leaf, V.27424, ×5. D, upper and lower cuticles of one leaf, V.27425, ×5. E, cuticle in which epidermal cell outlines are prominent and the subsidiary cell thickenings nearly fill the pit; hypodermal cells shown by broken lines; V.27425, ×400. All figures from Kendall (1948).
Occasional shoots of *Brachyphyllum crucis* with unusually long leaves may look similar but are distinguished by the concave upper surface of their leaves, the marginal frill and scattered distribution of the stomata.

The classification of *P. ordinatum* is open but its similarity to *P. kurrii* suggests that they may be related. Kendall (1948) considered the possibility that both might be araucarian but we now realize that there is a strong case for linking *P. kurrii* with *Hirmerella*.

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**Fig. 17. Pagiophyllum ordinatum** Kendall

A, reconstructed transverse section through a stoma like one of those shown in B, ×400. Cutinized walls solid black, imaginary uncutinized walls dotted. In some stomata the subsidiary cell thickenings extend further out. B, cuticle in which the cell outlines are inconspicuous and the subsidiary cells exposed and only lightly thickened. Westerdale, Esklets Crag, V.57390, ×400.
**Systematic Descriptions**

**Occurrence.** *P. ordinatum* fragments occur at all levels in the Deltaic series.

<table>
<thead>
<tr>
<th>Horizon</th>
<th>No. of locs</th>
<th>% of productive locs</th>
</tr>
</thead>
<tbody>
<tr>
<td>Upper Deltaic</td>
<td>16</td>
<td>14%</td>
</tr>
<tr>
<td>Grey Limestone (or next to it)</td>
<td>4</td>
<td>(most)</td>
</tr>
<tr>
<td>Grinstead Series</td>
<td>12</td>
<td>9%</td>
</tr>
<tr>
<td>Millepore Bed (or next to it)</td>
<td>1</td>
<td>-</td>
</tr>
<tr>
<td>Sycarham Series</td>
<td>9</td>
<td>13%</td>
</tr>
<tr>
<td>Lower Deltaic</td>
<td>11</td>
<td>5%</td>
</tr>
</tbody>
</table>

The two localities giving hand specimens, Westerdale Esklets Crag and Farndale Hill House Nab, happen to be ones with microfossils of marine origin and follow the early Bajocian transgression that produced the Dogger (of British usage). *P. ordinatum* is also remarkably abundant as fragments in the micaceous shales just above the Grey Limestone. Apart from this its distribution has much in common with that of *P. kurri*, though it is less frequent and has more Upper Deltaic localities. I imagine that it grew on land above the flood plain and not on the delta.

**Pagophyllum maculosum** Kendall (shoot) and

**Hirmerella kendalliae** sp. nov. (female cone)

Shoots. Figs 18, 19; Pl. 1, figs 15–17; Pl. 3, figs 6, 7

1948 *Pagophyllum maculosum* Kendall: 95, text-figs 9, 10A, B. (Isolated leaves and cuticle)
1952 *Pagophyllum maculosum* Kendall; Kendall: 590, text-fig. 3A, B. (Shoots)

**Emended Diagnosis.** Ultimate shoots (only part known) slender, not flattened, seldom branched (apex not tapering and not forming a specialized resting bud). Width of leafy shoot 6–10 mm, axis about half as wide. Leaves in a simple helix with 2 + 3 parastichies, usually enveloping stem closely, free part diverging at 30°. Leaf ovate or triangular ovate, apex blunt (rarely acute), in lateral compression typically appearing acute with apex curved upwards or slightly adaxially. Leaf widest at base or just above it, basal cushion 2–3 mm long, adaxial surface attached in an arched line. Leaf bases normally concealed by leaves below. Large leaf commonly up to 10 mm × 5 mm, upper surface 5 mm long, but leaves often relatively shorter (e.g. 4 mm × 3 mm) and upper surface only 1–2 mm; occasionally longer and relatively narrower. Lower surface of leaf strongly convex, rounded throughout or slightly keeled distally. Upper surface flat or slightly concave near apex, more concave near base with the next leaf above fitting into the concavity. Leaf substance very thick, veins not indicated on either side. Margins of leaf sharp, not scarious, occasionally marginal cells heavily thickened and projecting 20–30 μm.

Cuticle up to 6 μm thick on both sides. Stomata distributed over most of the under surface of lamina and on basal cushion, but upper (adaxial) surface normally with none, exceptionally with very few scattered stomata.

Upper (adaxial) cuticle much smaller in area than lower, shorter and narrower, commonly paler and slightly thinner. Epidermal cells typically 48 μm wide and about 30 μm long. Anticlinal walls broad, uninterrupted, often ill-marked and no darker than cell interior. Periclinal wall nearly flat, usually with sharply-defined thin area in middle. Hypodermal cells forming a complete layer except under stomata, usually conspicuous and often better marked than epidermis, cells typically 160 μm long × 16–60 μm wide, walls sharply marked, straight, uninterrupted, ends of cells pointed.
Stomata widespread on abaxial cuticle but often avoiding leaf margins and median region, usually placed in fairly well marked longitudinal files but becoming scattered near leaf base, files separated by about four files of ordinary epidermal cells. Stomata unevenly spaced in their files, more frequent near apex, separated by 2–7 ordinary epidermal cells, rarely with subsidiary cells in contact. Stomatal files not sunken but guard cells sunken to about 30 μm below the general level, apertures irregularly orientated. Guard cells typically 60 μm × 30 μm long, surface of stomata thinly cutinized except at aperture. Stomatal pit formed by a ring of 4–6 subsidiary cells, polar cells not distinguished. Subsidiary cells strongly thickened especially towards

Fig. 18. Pagiophyllum maculosum Kendall
A, B, shoots; Riksmuseum, Stockholm, nos 198 and 201, ×2. C, adaxial cuticle (spots not apparent), V.27402, ×200. D, abaxial cuticle (spots obvious), V.27400, ×200. E, cuticles of holotype leaf. Each dot is one stoma, the broken lines representing the restored outline damaged in preparation; V.27399, ×5. F, stoma, V.27401, ×400. G, opened cuticle of a leaf, dots representing stomata, V.27404, ×5. H, abaxial cuticle, V.27402, ×200. In C, D, H the hypodermal cell outlines are represented by broken lines though they are really continuous. Figs A, B from Kendall (1952); C–H from Kendall (1948).
their outer ends which are normally raised above the general level; their surface thick, sloping obliquely downwards to make a conical pit and then vertical or overhanging for a short distance above guard cells; anticlinal walls usually conspicuous. Encircling cells normally present but unspecialized and often difficult to recognize. Epidermal cells of a stomatal file irregular in shape and often extended transversely, cells between stomatal files square or slightly elongated, forming well-marked longitudinal files. Anticlinal walls broad, prominent, not interrupted by pits, corners of cells somewhat rounded. Periclinal walls flat or slightly raised, not papilllose but often with a rounded thin area in middle of cell. Hypodermal cells often less conspicuous than on upper surface, those of non-stomatal regions similar to those of upper (adaxial) surface but shorter and broader in stomatal files.

**Holotype.** V.27399.

**Discussion.** Kendall based *P. maculosum* on the cuticle of isolated leaves obtained by bulk maceration. Intact shoots were only recognized later, in material collected many years before by Nathorst. Subsequently a moderate number of shoots have been found in various layers at Cloughton Wyke. Indeed one of these, the *Zamites* Bed, is full of isolated leaves and has also yielded a very few larger pieces. Most of the other specimens are from the Cloughton cliff in otherwise barren rocks, and the exact levels could not always be determined. Thus the number of localities is uncertain.

None of these shoots is branched and the longest fragment (Pl. 1, fig. 16) is only 6 cm (most are much less). One tapers to the base (Fig. 19 n). The leaves diverge only slightly from the stem or are close to it and each leaf closely covers the base of a leaf above. I believe the upper surface is always hollow, at least in its basal part. (Kendall thought it was slightly convex.) The cuticles of separate leaves are distorted in compression, because of the original curved shape, and the flat or hollow upper epidermis is about a third or half as wide as the convex lower one. Thus dorsiventral compression may cause strong longitudinal folds in the abaxial cuticle, or alternatively the adaxial may split lengthwise and gape widely. Along the midline the upper epidermis only extends from the leaf apex to where the leaf joins the stem, that is about a third the way from the apex to the lower end of the leaf base cushion, but along the sides the upper epidermis extends very far back, the line of junction of leaf and stem being strongly arched. The smallest shoot found is only 3 mm wide and its leaves only just overlap, so that this specimen might have been included in *Brachyphyllum*.

The new material has made a fuller description possible and corrected certain details. Occasionally pale stomata do occur on the upper side, for example the leaf in Fig. 19 b has at least three. The pale spots on the epidermal cells which Kendall earlier called papillae prove to be thin areas on the surface wall without any projecting papilla surmounting them. The present interpretation of the stoma also is rather different, for I believe that the stomatal pit is usually widely open at its outer end, and here the cuticle is thickened and raised to form a low rampart. This new interpretation is based partly on stomata which have been compressed laterally. Occasionally the rampart is strongly developed and also constricts the mouth of the pit as in Kendall's text-fig. 9 e, but such stomata are unusual.

**Occurrence.** Leafy shoots forming hand specimens occur as follows:

- Middle Deltaic Grishorpe Series: 4 localities
- Middle Deltaic Sycarham Series: 2 localities
- Lower Deltaic: 1 locality
Fig. 19. *Pagiophyllum maculosum* Kendall

All the Middle Deltaic localities are at the foot of the cliff just north of Cloughton Wyke. The Lower Deltaic one is Nathorst's 'New Layer' at Whitby which has not been found since he collected there.

Cuticle fragments are widespread and often abundant. They are distributed as follows:

<table>
<thead>
<tr>
<th>Horizon</th>
<th>No. of locs</th>
<th>% of productive locs</th>
</tr>
</thead>
<tbody>
<tr>
<td>Upper Deltaic</td>
<td>2</td>
<td>2%</td>
</tr>
<tr>
<td>Grey (Scarborough) Limestone or just below it</td>
<td>6</td>
<td>(all)</td>
</tr>
<tr>
<td>Gristhorpe Series</td>
<td>51</td>
<td>34%</td>
</tr>
<tr>
<td>Millepore Bed or adjacent Deltaics</td>
<td>4</td>
<td>(all)</td>
</tr>
<tr>
<td>Sycarham Series</td>
<td>24</td>
<td>34%</td>
</tr>
<tr>
<td>Eller Beck Bed or adjacent Deltaics</td>
<td>2</td>
<td>(nearly all)</td>
</tr>
<tr>
<td>Lower Deltaic</td>
<td>14</td>
<td>5%</td>
</tr>
</tbody>
</table>

Though *P. maculosum* is sometimes found with fragments of other *Pagiophyllum* species its distribution is different. It is absent from just above the Scarborough Limestone, e.g. at Upper Kirk Moor where several other conifers are abundant. It is the most frequent *Pagiophyllum* in the Gristhorpe Series, especially in the moorland coals (23 of its Gristhorpe Series localities refer to macerated coals). Unlike *P. ordinatum* and *P. kurrii* it is commoner in the two divisions of the Middle Deltaic than in the Lower or the Upper Deltaic. It clearly grew near enough to river channels and to *Equisetum* swamps during the Middle Deltaic to provide many separate leaves and occasional intact shoots.
**Hirmerella kendalliae** sp. nov. (female cone)

Figs 20–23; Pl. 1, figs 18, 22

**Diagnosis.** Cone probably terminal on a rather stout leafy shoot; cylindrical, length exceeding 2.5 cm (base alone known), width about 1.5 cm. Cone scales forming a helix, parastichies possibly 2 + 3. Cone axis in lower part 2 mm thick.

Bract scale ultimately separating from ovuliferous scale; adaxial surface strongly concave in longitudinal direction (base at nearly 90° to upper part), slightly concave transversely. Middle region fairly thick and with ill-marked keel on abaxial surface, becoming thin towards margins; margins sharp but not scarious. Scale as a whole broadly rhomboidal with lateral angles extended into acute points and apex more or less extended and acute, attachment region at base rather small. Whole scale up to about 8 mm long × 15 mm broad.

Surfaces finely striated especially below (mainly by longitudinal fibres). Adaxial surface mainly or entirely lacking stomata, epidermal cells isodiametric, bulging, forming longitudinal files, surface occasionally showing a thin spot. Hypodermal fibres well marked. Abaxial surface with numerous stomata in lateral and apical regions but scattered rather than in files, stomata sparse in middle and basal parts. In lateral region, epidermal cells and stomata indistinguishable from those of the *Pagiophyllum maculosum* leaf but in middle and basal region anticlinal walls of epidermal cells often indistinct and surface wall often bulging as a dome, frequently with a pale spot (thin area) at its top. Hypodermal cells conspicuously outlined in the cuticle and occurring generally except under a stoma. Interior of scale containing round or angular sclereids about 50 μm wide (vascular tissues and resin ducts not recognized).

Ovuliferous scale falling and preserved separately after maturity. Form flattened, substance very thick in whole of middle region and moderately thick at edges. Length about 7 mm, width about 8 mm, apical and lateral margins bearing 10–12 lobes of various sizes and some overlapping others. Largest lobes nearly 2 mm × 2 mm and semicircular, situated near middle of distal margins, but lobes on lateral margins smaller and relatively narrower.

Cuticles well developed over both surfaces. Distal lobes with up to 100 stomata per mm² on one surface but usually none on the other, lateral lobes with fewer stomata or none; a few scattered stomata present on main part of scale just below distal lobes but none elsewhere. Lobes with numerous stomata having them scattered rather than in files but in other respects cuticles like those of *P. maculosum*. Epidermal cells more or less isodiametric and with bulging surface (but not fully studied).

Scale enclosing two cutinized seed megaspores in its proximal part and also delicate internal cuticles (their nature not yet understood). Outer one of these cuticles showing obliquely elongated cells often with very broad but weakly marked anticlinal walls; inner with longitudinally orientated cells, cells often side by side in packets, their anticlinal walls marked by a fine, conspicuous ridge, their surface wall often showing dark spots, possibly oil drops. (Pollen grains of *Classopolis* adhere to this membrane.)

**Holotype.** V.57395; slides V.57396–V.57410; Figs 20 G, H; 21 A, B; 22; 23.

**Name.** The species is named in honour of Mabel W. Kendall.

**Discussion.** The information given in the diagnosis was obtained with difficulty from some unsatisfactory specimens found in a single locality, an upper mudstone layer of the Cloughton Wyke *Zamites* Bed which outcrops just below the Millepore Bed. This bed is full of fragments of *P. maculosum* and contains a huge number of *Classopolis* grains, but plant fragments exceeding
Fig. 21. *Hirmerella kendalliae* sp. nov.

A, holotype cone, V.57395, ×3. B, diagrammatic analysis of A, indicating bract scales only. Parts still present indicated by a firm outline, fibre orientation shown by striations; regions represented only by imprints shown as blank spaces and purely imaginary parts represented by broken lines. C, possible form of whole cone-scale as seen from above. Overlapped parts shown by dotted lines. The stippled area marks the extent of the internal double cuticles; seed megaspores shown solid black. D, rather small ovuliferous scale, coaly matter outlined in ink and imprints where coal has fallen off marked by broken lines. V.58359, ×4. E, transversely broken and compressed cone, V.57414, ×4. F, part of same specimen in balsam transfer (drawing reversed), ×4. L1–L6 are leaves of a *P. maculosum* shoot; O1–O5 are ovuliferous scale lobes, B1–B5 are fragments of various bract scales (B1, B2 possibly belong to a single scale).
Fig. 22. Hirmerella kendalliae sp. nov.

A–C and D, E, two adjacent cone scales of balsam transfer of holotype, V.57395. The lower surfaces of the bracts are shown in A and D, whilst deeper-lying lobes are exposed in B. Crumbs of coal were dissected away from each scale and their position recorded. They were then macerated and the cuticles from each crumb mounted separately. Figs C, E are reconstructions based on these macerations, the obliquely stippled areas showing the extent of the internal double membrane and the oval shapes the positions of the shrivelled seed megaspores. All the parts recognized are illustrated, those at the highest level shown by solid outlines, those at lower levels by broken lines where overlapped. (The right side of the bract scale of A–C, which is seen only as an imprint, is also shown as a broken line.) All drawings are ×6 approx.
1 cm in length are unusual. Other species occurring as occasional small fragments are *P. kurritii*, *Brachyphyllum mamillare* and *Zamites gigas*. Though cuticles are well preserved the rock splits almost as readily in any direction and the coaly substance of the plants is crumbly. The bed was quarried away on repeated visits whenever it was exposed by coastal erosion and the reproductive fragments obtained resulted from deliberate search.

All the nearly complete bract scales have been figured. Most showed their lower surface unless the coal had fallen away to give the imprint of the upper surface. Transfers were attempted of several but the coal crumbled from the balsam resulting in virtual destruction of the specimen. Some decay seems to have occurred before the scales were buried in the mud matrix and this had the partly useful effect that internal tissues, hypodermal fibres and sclereids were sometimes revealed.

Though no satisfactory isolated ovuliferous scale has yet been found there are several fragments which support statements based on the scales of the partly intact cones. The cones are presently two, one giving in effect a longitudinal view of the cone base and probably also of the leafy stem bearing it (though I am not certain that they are joined). The other gives a transverse section view of the cone (comparable transverse compressions are known in *H. muensteri* and *Araucarites phillipsii*). Both specimens had part and counterpart and all four blocks were ultimately made into balsam transfers, with results that unfortunately were only partly useful because much of the coal fell away as dust.

Most of the information was given by the longitudinal cone compression. This originally showed its bract scales with just the edges of ovuliferous scales projecting above them (Fig. 21 a). Since it was impossible to remove a whole scale for maceration, particles as large as possible were taken, 1 mm long or less. The position of each was recorded on a large drawing and they were then macerated separately and the cuticles mounted on numbered slides. This was done for two scales. Thus the kinds of cuticle present at each point were known though not their orientation, and, despite efforts, I failed to fit together (mentally) the little pieces of cuticle in the different slides. Most of the bract scale could be dissected away separately because there was a little rock between it and the ovuliferous scale, but below they were either in contact or continuous and separation was impossible. However, towards the base, the coaly substance was about 1 mm thick and sometimes upper and lower layers of it could be chipped off separately. The results of analysis of what was seen and deduced from 45 crumbs are shown diagrammatically restored in Fig. 21 c and also, more objectively, in Fig. 22 c, e.

Each of the two macerated cone scales yielded two seed megaspores but their position was irregular and all four were shrivelled. I feel sure that all represent abortive seeds and possibly the whole cone is one which failed to mature properly.

The lower part of the ovuliferous scale yields delicate internal cuticles, the total extent of which is indicated in Figs 21 c, 22 c, e. It seems likely that these form two sacs, one partly overlapping the other and each sac enclosing one seed megaspore. The cuticles of these sacs are double, the two layers having cells of very different character. The layers were pressed together during compression and are impossible to separate.

Over most of its extent this double membrane is so delicate as to be difficult to handle with needles but towards the basal end of the scale it becomes thicker and pale brown in colour. Little of this part remained for study but presumably the micropyle is in that region. Two features noted were some occasional brown spindles looking like resin, lying parallel with the outer layer, and also pollen grains probably between the two layers. In one group of pollen grains, 13 were *Classopolis*, with two different miospores.

Where the sacs formed by the inner cuticles overlap, a single macerated fragment gave (a)
both cuticles of the bract scale separated by a little coal, (b) the abaxial cuticle of the ovuliferous scale and under it much coal, then (c) the top sac, with four cuticles in all and all adherent or possibly the upper pair separable from the lower pair. Then a very little coal and (d) the four cuticles of the lower sac; then much coal and finally (e) the adaxial cuticle of the ovuliferous scale. Thus there are twelve cutinized membranes in addition to the megaspores.

The best of the megaspore membranes was not one dissected out of the cone scales but was isolated by maceration of a crumb of coal which fell off when the cone was collected. This was a sac 3 mm long (but broken at one end) and 0.75 mm wide. Both dissected cone scales yielded two megaspores each but these four were all in a very poor state, greatly shrivelled, and only about 1 mm wide. The megaspores occur in the region of the cone scale with the double membranes and were presumably enclosed by them as in a bag, but they were separated from it by soluble coal. The best megaspore membrane, which is also a flattened bag, seems to consist of an outer compact layer 2 μm thick and an inner very spongy and indefinite layer 1 μm thick. The membrane in surface view looks granular and also pitted, both granules and pits being 1 μm wide. One part showed faint imprints of elongated cells on its outer side.
Comparison. *Hirmerella kendalliae* is distinguished from all other species of the genus by its very broad ovuliferous scales with numerous marginal lobes, but we do not know its range of form. The cuticle in the outer parts of both bract and ovuliferous scales also distinguishes it from all other species, *Pagiophyllum maculosum* alone having similar stomata and epidermal cells.

Classification. Three Yorkshire conifer shoots now linked with reproductive organs have a strong claim to be included in the Hirmerellaceae. These are *Pagiophyllum maculosum*, with *Classopollis* pollen and the female cone *Hirmerella kendalliae* just described, *Pagiophyllum kurrii* with *Hirmerella estonianensis* female cone scales and an unnamed male cone, and *Brachyphyllum crucis* also with an unnamed male cone. In addition there are four species without described reproductive organs but resembling these three in cuticle which I regard as possible members of the same family, two of *Pagiophyllum*, one *Brachyphyllum* and one *Geinitzia*. Should these also prove to have similar cones the Hirmerellaceae would become the largest family of Yorkshire conifers.

Hirmer & Hörhammer (1934) instituted this family under the name Cheirolepidaceae, primarily for the shoots and cones long known as *Cheirolepis muensteri* (Schenk) Schimper. With it they included the associated conifer *Hirmeriella rhaetoliassica* Hörhammer (1933) and two Indian cones, *Indostrobus* and *Takliostrobus*, both of Sahni (1931). Later authors have removed the last two and *Cheirolepis* and *Hirmeriella* have undergone changes in both name and concept.

The name *Cheirolepis* Schimper proved to be a homonym of a Recent plant and Takhtadzhyan *et al.* (1963) substituted *Cheirolepidium*. Jung (1967), however, showed that *Hirmeriella* was not a complete cone as had been thought, but merely the persistent bract scales from which the ovuliferous scales called *Cheirolepis* had fallen. He named the whole plant *Hirmeriella muensteri* (Schenk), using the oldest distinctive generic and specific names available. Later he altered the spelling to the shorter and more euphonious *Hirmerella*, as is permissible, and in this has been widely followed.

If all *Classopollis* pollen was produced by members of the Hirmerellaceae we must accept that the family was widespread and abundant from the Upper Trias to the Lower Cretaceous, and was even present in the Upper Permian (Pocock & Jansonius 1961). Apart from *Classopollis*, the most characteristic organ is the female cone scale, now better understood through the work of Jung (1967) and Archangelsky (1968).

I now summarize the characters of the Hirmerellaceae, mainly to invite correction. Some of the statements are based on disputed observations or on a single species.

Conifers with persistent 1-veined leaves borne on caducous shoots. Leaves thickly cutinized, shape varied, including long tapering needles (*Geinitzia* form), broad and spreading (*Pagiophyllum* form) and either fairly thin or thick and succulent; including also small scale-like leaves surmounting an extensive stoma-bearing basal cushion (*Brachyphyllum* form). Leaves borne singly in a simple helix or in some members in opposite pairs. Stomata widespread on abaxial surface of lamina and often also on adaxial surface, either scattered or arranged in longitudinal files but not concentrated into bands. Guard cells variably orientated, sunken in a round pit formed by a ring of subsidiary cells which may bear strongly developed papillae. Hypodermis present and often cutinized.

Male cones borne singly on leafy shoots; microsporophylls with a stalk and expanded head, bearing 2–8 microsporangia below stalk. Pollen of *Classopollis* form, tending to remain in tetrads.
Female cones large and comprising many crowded scales, bract scale separate from ovuliferous scale; both scales robust and both ultimately falling from cone axis and normally separating. Bract scale simple, lanceolate. Ovuliferous scale with several terminal lobes which may overlap, lower part enclosing two seeds in epidermis-lined cavities.

Secondary xylem of Protocupressinoxylon type (Harris 1957, Vogellehner 1965).

As mentioned earlier the organization of the microsporophyll is disputed, and despite advances we do not yet understand the morphology of the seeds and their cavities in the scale. Until these points are settled it is difficult to discuss the relation of the Hirmerellaceae to the Voltziineae of Némejc (1968).

Where a name is needed for the whole plant, whether based on parts found connected or when the connection is merely inferred, I propose that the generic name be Hirmerella and the specific the one first given to any organ. Thus the Yorkshire examples would be:

\[ Hirmerella maculosa \text{m} (\text{Kendall}) \]
\[ Hirmerella kurrii \text{m} (\text{Schimper}) \]
\[ Hirmerella crucis \text{m} (\text{Kendall}) \]

**Pagophyllum fragilis** (Bose) comb. nov.

Figs 24, 25

1955 *Farndalea fragilis* Bose: 111, text-figs 1, 2.
1958 *Farndalea fragilis* Bose; Florin: 308; pl. 28, figs 3–6; pl. 29, fig. 1.
1966 *Farndalea fragilis* Bose; Harris & Rest: 104. (Middle Jurassic of Brora, eastern Scotland)
1970 *Farndalea fragilis* Bose; Vigran: 198; pl. 1, figs 5, 6; pl. 2, figs 1–3. (Middle Jurassic, Norway)

**Diagnosis.** (Slightly modified from Bose and from Florin.) Leaves probably borne helically (but stem scarcely known). Leaf commonly triangular, large ones 3.5 mm × 2.5 mm, smaller ones 2.0 mm × 1.0 mm, smallest leaves minute scales under 1 mm long produced on special zones of stem. Leaves of more oblong shape, about 3 mm × 1 mm, also produced. Vertical thickness of leaf about half its width. Leaf apex acute or obtuse, often curved slightly towards stem and thus bent underneath in dorsiventral compression (and apex accordingly appearing rounded). Adaxial surface originally flat in transverse direction, abaxial surface strongly convex but rounded and not keeled. Junction of adaxial surface with stem strongly arched and at sides adaxial surface extending as narrow strips to base of leaf cushion. Leaf margins sharp and commonly extended as a denticulate frill formed by a single layer of cells pointing obliquely forwards. Marginal frill often becoming broader towards leaf base and then contracting at extreme base to form slight auricle, auricle often bent over adaxial surface in dorsiventrally compressed leaf. Abaxial surface probably marked off by a furrow from stem surface. Stem surface (only known from small fragments) showing rather broad longitudinal tracts having evenly distributed stomata alternating with tracts without stomata.

Leaves with two well-marked adaxial stomatal bands. Bands starting just above the base of the adaxial surface and extending almost to the leaf apex where they approach but do not unite. More than half of the leaves entirely without abaxial stomata but some leaves (especially larger ones) with a few stomata on abaxial side, these being limited to lower half of leaf and occurring scattered in two regions, between the midline and margins, but scarcely forming definite bands. Adaxial stomatal bands not depressed, typically 0.2 mm (3–5 stomata) wide. Leaf cuticle up to 6 μm thick but brittle, commonly dark in colour.

Ordinary epidermal cells between stomatal bands and also cells outside the bands mostly rectangular, often about twice as long as broad; range from isodiamic to ten times as long as
Fig. 24. Pagiophyllum fragilis (Bose)

A–L, leaf fragments, all × 10, in some cases partially reconstructed and all more or less diagrammatic; M, N, drawings × 20. Stomata shown as black dots or ovals, margin and teeth by short oblique lines. A, nearly complete leaf, V.58945. B, upper part of oblong leaf; tip and right margin incurved (no abaxial stomata present), V.31361. C, broad leaf showing basal end of right stomatal band, V.30689. D, nearly complete leaf with incurved auricle at bottom right, V.30690. E, narrow, pointed leaf (stomata obscure); V.30742. F, showing auricle, V.31367. G, oblong leaf, tip incurved, no abaxial stomata, V.30693. H, I, two views of bent and incurved leaf with no abaxial stomata, V.58946. J, leaf apex, V.30694. K, leaf apex, V.30718. L, margin near base of leaf, V.31356. M, stem fragment with two minute scale leaves. Broken lines indicate end of adaxial cuticle and also the edge of the scale leaf at left. Cell files are suggested by light stippling, folds by dense stippling. At the right is an imaginary longitudinal section through the right-hand scale. V.58946. N, holotype, V.30692. Specimens in C, G, J, N originally figured by Bose (1955); here redrawn.
Fig. 25. *Pagiophyllum fragilis* (Bose)

A. lower cuticle of holotype, V.30692, ×200. B. obliquely compressed stoma with raised subsidiary cells, V.30696, ×400. C. marginal cells with teeth on the right, V.30690, ×200. D. a stoma and parts of three others, V.30695, ×400. E. cells of upper cuticle of holotype, showing crystal cavities, ×400. F. stomatal band from upper cuticle of holotype, ×200. All figures are from Bose (1955).
broad, forming short longitudinal files but these seldom conspicuous. Longitudinal and transverse anticlinal walls straight, thick, strongly marked; somewhat interrupted by cavities. Surface wall flat, not papilllose, nearly always strongly marked by angular cavities (? calcium oxalate crystals); cavities varying in different leaves from 5 μm wide and only 2–5 per cell surface down to 2 μm wide and more numerous, showing a thickened border. Towards margins, cells pointing obliquely outwards and cavities in wall smaller. Where cavities in surface wall are feebly developed or absent, surface wall often showing a longitudinal thin strip. Abaxial cuticle with similar ordinary epidermal cells but in some leaves cells in middle line narrower and suggesting an ill-defined midrib. On stem, cells usually broader and often forming isodiametric polygons not in files. Markings of cells similar but occasionally cell surface slightly thickened in middle though scarcely forming a papilla.

In stomatal bands of adaxial surface, ordinary cells mostly isodiametric or broader than long, appearing darker and thicker-walled than rest of epidermis; anticlinal walls extending considerable distance inwards, surface wall slightly bulging, often with smaller cavities than epidermal cells outside stomatal bands.

Stomata of adaxial bands monocyclic, crowded, subsidiary cells of adjacent stomata commonly in contact, occasionally subsidiary cells shared. Stomata mostly orientated transversely but some oblique, a few longitudinal. Subsidiary cells 4–8 forming a fairly regular ring and surrounding a round, oval, rectangular or dumb-bell shaped pit. Surface wall bulging, often thicker (darker) than that of other cells; crystal cavities small or absent; sides of pit more or less overhanging and usually appearing very thick, wall where subsidiary cells of adjacent stomata are in contact also often thick and extending deeply. Guard cells thinly cutinized, aperture about 20 μm long. Stomata of abaxial surface more widely spaced, variously orientated and apparatus often rounded. Encircling cells occasionally present. (Trichomes, apart from marginal teeth, absent. Hypodermal cells not apparent.)

**Holotype.** V.30692.

**Discussion.** The specific name *fragilis* refers to the fragility of the cuticle, which is surprising in view of its thickness. The generic name *Farndalea* was from Farndale in Yorkshire where many specimens were collected.

Though *Pagiophyllum fragilis* is based on material from an unusually large number of localities, every specimen is a small fragment. Only rarely have we a nearly complete leaf and this causes uncertainty of interpretation. It is necessary to visualize a form of leaf and shoot which serves as a frame into which all the fragments can be fitted. This imaginary shoot seems to be a typical *Pagiophyllum* in the sense that the genus is here defined.

The stem fragment shown in Fig. 24 bears two minute scale leaves without recognizable stomata. Such scale leaves are otherwise unknown, and all the leaves and leaf fragments picked out of macerations show well-formed stomata. I imagine that the shoot had well-marked growth zones, most of it producing foliage leaves but at times producing minute scale leaves. Since one of these scales is at a slightly different level from the other, and they are less than 180° apart, I suppose that the leaf arrangement was a helix rather than whorled.

Many fragments of *P. fragilis* have been obtained from bulk macerations since Bose (1955) originally described the species. Some of these were described and figured by Florin (1958) and still others are now available. These later fragments have led to one main change in the diagnosis. Bose, while openly uncertain, assumed for description that the two main stomatal bands were on the lower (abaxial) side, but Florin who compared them with other conifers having overlapping leaves considered that they were probably on the protected upper side. New
specimens confirm the latter view. A few leaf bases show the two stomatal bands ending abruptly at the bottom of the free leaf and such specimens as the one shown in Fig. 24 H, I support the idea that they are adaxial.

*P. fragilis* is remarkable in several ways. Although its cuticle is thick, it is strangely fragile. When lightly macerated it is black and brittle enough to shatter into small angular fragments when manipulated. When it is more macerated it never goes through the pliant but tough stage of most cuticles but turns from black, usually through greyish yellow to yellow and at the same time becomes weak and flimsy. It has some chemical peculiarity, rather like *Brachyphyllum mamillare*.

Bose commented on the large number of localities of this species, recording it from 104 Yorkshire localities. Florin (1958) had it from an additional 8 and since then it has been found in another 38, about 150 localities in all. All these are from bulk macerations. No other Yorkshire conifer with the possible exception of *Brachyphyllum mamillare* has so many records, but the high number is partly due to the ease with which very small pieces can be recognized among the cuticles from a bulk maceration.

**Occurrence.**

<table>
<thead>
<tr>
<th>Horizon</th>
<th>No. of locs</th>
<th>% of productive locs</th>
</tr>
</thead>
<tbody>
<tr>
<td>Upper Deltaic</td>
<td>20</td>
<td>17%</td>
</tr>
<tr>
<td>Middle Deltaic Gristhorpe Series</td>
<td>56</td>
<td>44%</td>
</tr>
<tr>
<td>Middle Deltaic Sycarham Series</td>
<td>19</td>
<td>26%</td>
</tr>
<tr>
<td>Eller Beck Bed</td>
<td>3</td>
<td>(nearly all)</td>
</tr>
<tr>
<td>Lower Deltaic</td>
<td>54</td>
<td>22%</td>
</tr>
</tbody>
</table>

Outside Yorkshire, *P. fragilis* occurs in the coal of Brora in eastern Scotland, of approximately equivalent age to the Upper Deltaic of Yorkshire (Harris & Rest 1966). It has also been recorded from the Middle Jurassic of Norway, by Vigran (1970).

*P. fragilis* is found in every kind of sediment and no other plant species seems particularly often associated with it. It ranks with *B. mamillare, Coniopteris hymenophylloides* (Brongniart) Seward and *Equisetum columnare* Brongniart in its wide distribution, but unlike those species it never occurs in local abundance. A typical maceration of a kilogram of coal or shale yields only 1–12 small fragments, none more than 1 mm long. Also, unlike other conifers widely represented by cuticle fragments, it is not yet represented by a single intact shoot. I am not willing to suggest an explanation but believe it was not a tree that overhung the delta river channels, since the fragments reaching them were of dust size.

**Classification.** *Pagiophyllum fragilis* has striking resemblances in various details of its cuticle to certain Taxodiaceae, as pointed out by Bose (1955) and Florin (1958), genera mentioned being *Sequoia, Cryptomeria, Glyptostrobus* and the fossil *Elatides*. Another is *Athrotaxis cupressoides* Don in which the structure varies but sometimes looks very similar. Several of these Taxodiaceae have the same inward prolongation of anticlinal walls among the stomata. It is unlikely however that even when fully known it will be possible to place it in any living genus.

I emphasize that by including *P. fragilis* in the form-genus *Pagiophyllum* I do not imply affinity with *P. maculosum* or *P. kurriti*; they are very different in everything except probably the aspect of the shoot.
'Pagiophyllum cf. peregrinum' of Black

1934 Pagiophyllum cf. peregrinum; Black: 269, 271.

The only available specimen is a shoot in the Sedgwick Museum about 10 mm wide (including its leaves), in which, though it looks like a Pagiophyllum, the leaves are appressed close to the stem. It has two small lateral branches only 3 or 4 mm wide. The leaves of the main stem are 7–8 mm long (which may include the basal cushion), and 2.5 mm wide at the base. The leaf tapers to an acute point. The side shoots have similar leaves but they are only half as long and half as wide.

Although this fossil is preserved in a black shale and comes from a locality where cuticles are well preserved, and although the substance of the shoot is fairly thick and coaly, it is crumbly and I was unsuccessful in preparing any cuticle at all, even the tiniest fragment. I am convinced that this is because it never had any substantial cuticle. It is certainly different from the five Pagiophyllum species described here (all with thick cuticles) and from P. peregrinum of the Lower Lias (Kendall 1948) which also has a thick cuticle. I suspect that it may not be a conifer at all, but perhaps might be a lycopod.

Black (1934) states that the shoots were locally abundant in a bed at Boulby Alum Quarry. I searched that extensive Lower Deltaic exposure but failed to find the bed, and until we can learn more about this shoot it appears to have little interest.

It is to be noted that apart from this one shoot and the five species of Pagiophyllum named and described above, which altogether are represented in several hundred localities, there is not a single specimen known to me which convincingly represents another species. Thus unless fresh ones are to be distinguished by taxonomic splitting of the species here described, the Yorkshire Pagiophyllum species may be considered well known.

Form-genus GEINITZIA Endlicher 1847

Emended diagnosis. Shoot, bearing leaves helically. Free part of leaf falcate or spreading, needle-like, equally thick in vertical and horizontal directions, merging into basal cushion on stem without contracting.

Endlicher (1847: 280–1) gives the following diagnosis. 'Folia quinquefuriam inserta cylindrica subdecurrentia. Strobili (amenta staminigera?) terminales ovato cylindrici, squamis rhachi crassiusculae spiraliter insertis, apice lanceolato-acutis squarrosos patulis.' For G. cretacea he gives 'foliis falcato-incurvis, acuminatis'.

First described species. Araucarites reichenbachii Geinitz 1842.

Discussion. The conifers which Endlicher placed in Geinitzia had earlier been in Sedites, Araucarites and Cryptomeria, and he instituted the genus to avoid suggesting particular affinities. If we omit the sentence referring to the cones he was making a form-genus. In 1868 Heer described more impressive specimens of shoots and cones under the name Sequoia reichenbachii and subsequently this name was used many times and Geinitzia was dropped. However, Seward (1919: 357) revived it as a form-genus. He considered that Heer’s specimens were not convincingly identified with Araucarites reichenbachii and also he was not satisfied that Heer’s cones were those of a Sequoia. But he agreed that certain later-described specimens called S. reichenbachii were rightly placed in Sequoia. Bunbury’s form-genus Cryptomerites (1851) is a junior synonym of Geinitzia.
As used here, *Geinitzia* has a wider scope than Endlicher proposed and includes Mesozoic shoots that have been described under the names *Araucaria*, *Araucarites*, *Pagiophyllum*, *Cryptomeria*, *Cryptomerites*, *Sequoia*, *Sequoiites*, *Elatides* and others. It merges into other form-genera, particularly *Pagiophyllum*, but that is distinguished by its somewhat dorsiventrally flattened leaf, a leaf looking broad when on top of a stem but narrow at its side. In a compressed shoot of *Geinitzia*, on the other hand, a leaf lying on top of the stem and another at the side of the stem look equally broad. This observation is one which I feel has not been sufficiently used in describing fossil conifer shoots. Thus certain figured species, for instance *Pagiophyllum revolutum* Wesley (1956) and *P. rewaensis* Bose & Sukh-Dev (1972), appear to have leaves as thick vertically as they are broad horizontally, and they would fit the present definition of *Geinitzia* better than that of *Pagiophyllum*. The elongated juvenile leaves of *Brachyphyllum crucis* too have the *Geinitzia* form.

*Cyparissidium* differs from *Geinitzia* in its appressed and somewhat flattened leaves.

Of the species here placed in *Geinitzia* two are known as shoots only but two others, with their male and female cones, are separated as species of *Elatides*. The form-genus *Geinitzia* probably includes conifers of diverse families.

*Geinitzia rigida* (Phillips) comb. nov.
Figs 26–29; Pl. 3, fig. 3

1875 *Cryptomerites rigida* Phillips: 231, lign. 63. (Rough sketch of holotype)
1900 *Cryptomerites divaricatus* Bunbury; Seward: 287–288 (in part). (Reference to Phillips’ specimen only)
1951 *Pagiophyllum gracillimum* Adams: 1132, text-figs 1, 2 $A$–$I$, 3 $A$–$C$. (Figures repeated here)
1952 *Pagiophyllum rigidum* (Phillips) Harris: 379, text-figs 9 b, c, 10 $A$–$F$. Invalid homonym. (Figures repeated here)

As mentioned below there are certain other Jurassic shoots which are at present imperfectly distinguished from *G. rigida*.

**EMENDED DIAGNOSIS.** Caducous shoot systems branching at first monopodially, then irregularly in three dimensions. Largest axes 5 mm thick, smallest under 1 mm, all bearing persistent leaves in a helix with 3 + 5 parastichies. (No resting buds or regions bearing scale leaves occurring.) Surface of shoot formed by leaf base cushions up to 5 mm long on main stems but short on small ones.

Free leaf commonly about 3·0 mm $\times$ 0·6 mm but up to 4·5 mm $\times$ 1·25 mm on largest stems and 1·5 mm $\times$ 0·25 mm on smallest; width and thickness often uniform to near apex and then contracting to an obtuse point usually with a mucro 100 $\mu$m long. Leaf in lateral view straight, at about 45° to axis, or bending forwards, shape in section somewhat convex adaxially but strongly convex abaxially, both surfaces rounded. Lateral margins sharply angular and projecting as ridges, normally bearing minute stiff hairs but hairs sometimes few, marginal ridges with hairs continuing onto basal cushion.

Cuticles thick (3–10 $\mu$m in folds) but brittle. Stomata frequent on abaxial surface but on adaxial surface many, few or none. Stomata of abaxial surface mostly in longitudinal files, files evenly spaced; stomata few near leaf margins, leaf apex and lower extremity of cushion. On adaxial surface stomata in files if numerous but scattered if few. Stomata in files separated by 1–7 files of ordinary cells, unevenly spaced in their files but always separated by ordinary cells. Ordinary cells mostly elongated and about 50 $\mu$m $\times$ 15 $\mu$m but sometimes shorter, particularly near leaf apex. Outlines marked by broad straight walls not interrupted by pits but occasionally somewhat moniliform. Cell surface on cushion and in lower parts of leaf flat, towards leaf apex bulging though scarcely papilllose, surface often obscurely mottled or striate. In stomatal files cells similar but often transversely elongated, near marginal angles cells elongated and surface
heavily cutinized. (Hypodermis not preserved.) Marginal trichomes typically conical, unicellular, about 40 \( \mu m \) long \( \times \) 20 \( \mu m \) wide at base but sometimes 100 \( \mu m \) long, arising from middle of a small and often raised cell. Free part tapering evenly to apex, usually solid. (No trichomes present on leaf surfaces.)

Stomata variously orientated, guard cells thinly cutinized, aperture typically 17 \( \mu m \) long. Subsidiary cells 4–6, uniform, forming a regular ring, outer margins of the cells often thickened and raised above general epidermal level, surface walls flat, becoming thinner and sloping inwards towards pit. Inner margins forming small round or irregular pit, guard cells being up to 40 \( \mu m \) below general surface, edge of pit more thickly cutinized than radial walls between subsidiary cells. Encircling cells absent or occasional and unspecialized.
Fig. 27. Geinitzia rigida (Phillips)

A–G, stem fragments and leaves, all × 10; marginal trichomes drawn only where they project at the edges. In A the gap at the base of the top leaf is short, in B long. In C–F marginal frills are seen on the upper surface but in G, an unusually small leaf, the frills are at the edges. H–K, leaf fragments, × 20. H, I, two sides of a laterally compressed hypostomatic leaf, leaf later destroyed by further preparation. J, K, lower (abaxial) and upper sides of a hypostomatic dorsiventrally compressed leaf. Figs A, B, V.57493; C–G, V.57494; J, K, V.57492.


Discussion. Phillips’ holotype is certainly the original of his sketches but has suffered somewhat and the leaves are less regularly placed than he drew them. Adams’ (1951) figures of old Museum specimens bear the manuscript name ‘gracillima’ and she described them as Pagiophyllum gracillimum. In 1952 I redescribed the holotype as Pagiophyllum rigidum (Phillips). This is a different plant from Moreauia rigidia Pomel (1849), from the Corallian of France, renamed Pachyphyllum rigidum (Pomel) Schimper 1872.

Adams (1951) and Harris (1952) stated a number of differences which were supposed to distinguish the species gracillimum and rigidum but specimens found later showed intergradation of these characters. Where G. rigida is found in local abundance all forms occur together. For
instance some leaves have many adaxial stomata, some few, some none; cell length varies and the marginal hairs may be numerous and prominent or few and obscure.

The change of name from Pagophyllum to Geinitzia results from the generic definitions here used. Most leaves of G. rigida are just as thick as broad though a few are slightly less thick and thus approach Pagophyllum.

The classification of G. rigida is open but its cuticle resembles Hirmerella. Its reproductive organs are unknown and nothing unusual was seen among the pollen in the matrix.

Comparison. The only Yorkshire conifers with shoots like G. rigida are G. divaricata and Elatides thomasii. Both have far thinner cuticles and neither has marginal hairs. Their leaves are seldom of just the same shape. Mesozoic shoots rather like G. rigida have sometimes been
described as species of *Widdringtonites*, though unlike *Widdringtonia* their phyllotaxis is helical. The figures suggest leaves that are appressed and probably dorsiventrally flattened, so they might fit *Cyparissidium* rather than *Geinitzia*. Two of the best known are *Widdringtonites liasinus* Kurr (see Salfeld 1907, Kräusel 1923 for stoma) and *W. keuperianus* Heer (see Kräusel 1955). Both have shorter leaves and papillate stomata. The specimens of Corallian age described by Saporta (1884: 652; pl. 223 (95), figs. 4, 5a, 5) under the names *Brachyphyllum assimile* and *B. orbignianum* look like *G. rigida*. We have no microscopic details.

**Occurrence.** Hand specimens of *G. rigida* are rare. The holotype is from the Gristhorpe Bed but *G. rigida* has not been recorded from there since and the other old specimens have no recorded localities. In more recent years *G. rigida* has been found as single specimens at Haiburn and also in fallen blocks from Beast Cliff and Hawsker cliffs. At a few points in the Cloughton Wyke cliffs it is locally common, but only seen in fallen blocks. Cuticle fragments

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**Fig. 29. Geinitzia rigida** (Phillips)

from bulk macerations are distributed throughout the Deltaic Series and sometimes are locally abundant. The localities are as follows:

<table>
<thead>
<tr>
<th>Series</th>
<th>Number</th>
</tr>
</thead>
<tbody>
<tr>
<td>Upper Deltaic</td>
<td>1</td>
</tr>
<tr>
<td>Middle Deltaic Gristhorpe Series</td>
<td>5*</td>
</tr>
<tr>
<td>Millepore Bed</td>
<td>1</td>
</tr>
<tr>
<td>Middle Deltaic Sycarham Series</td>
<td>8</td>
</tr>
<tr>
<td>Eller Beck Bed (Hydraulic Limestone)</td>
<td>1</td>
</tr>
<tr>
<td>Lower Deltaic</td>
<td>7</td>
</tr>
</tbody>
</table>

*Some of these are from fallen blocks and may represent parts of a single bed.

The frequency of *G. rigida* in the rather barren Sycarham Series is noteworthy. It is mostly found in shales rather than in sandstones with drifted material and this, together with the preservation of occasional large shoot systems, suggests that it was a species of the delta itself. I imagine that it grew on river banks but clearly it was not a common species.

**Geinitzia divaricata** (Bunbury) comb. nov.
Figs 30, 31; Pl. 2, fig. 14; Pl. 3, figs 1, 2

1851 *Cryptomerites divaricatus* Bunbury: 190; pl. 13, fig. 4. (Shoot, refigured here)
1875 *Cryptomerites divaricatus* Bunbury; Phillips: 230; lgn. 62. (Sketch of shoot)
1877 *Cryptomerites divaricatus* Bunbury; Lebour: pl. 57. (Shoot)
1900 *Cryptomerites divaricatus* Bunbury; Seward: 287 in part, excluding *C. rigidus* Phillips and *C. divaricatus* of Feistmantel 1876. (Discussion)
1929 *Cryptomerites divaricatus* Bunbury; Edwards: 391; pl. 4, fig. 9. (Middle Jurassic; Sardinia)
1951 *Elatides divaricatus* (Bunbury) Harris: 931, text-figs 4 A, B, D, 5. (Shoot and cuticle, figures repeated here)

**Emended diagnosis.** Shoot systems dropped intact; main shoot branching in one plane, smaller shoots branched less regularly but also in one plane, smallest very slender and often only 0.5 mm wide. Leaves on main shoots distant, tending to become closer on smaller twigs but never crowded, borne in a loose helix but those of lateral branches bent at their bases so as to lie in a horizontal plane; tapering evenly from a broad base to acute apex. Length of leaf 3–6 mm, leaves of larger twigs at least 1 mm wide near base but leaves of small twigs only 0.6 mm wide. Leaves nearly square in section with rounded angles facing upwards, downwards and laterally; basal angle decurrent on stem, though probably not the lateral ones. Leaves of larger twigs arising perpendicularly, leaves of smaller twigs arising at 70°–80° to the stem; typically straight, frequently slightly recurved, rarely incurved. Surface of leaf showing 6–8 (possibly fibrous) ridges converging from broad base to apex. Scattered fibres also occurring. In certain small twigs leaves only 1.5–2.0 mm long, borne at an angle less than 70°, such leaves often incurved and probably not flattened into the horizontal plane.

Cuticle very delicate (imperfectly known from small fragments, diagnosis supplemented by observations on surface markings of leaves); differentiated into eight longitudinal regions, four angles without stomata and four flatter sides with stomata. Leaf angles showing square or elongated rectangular cells, outlines finely marked but distinct, straight; cell surface flat, not papillose but sometimes showing one or more faint striations. Stomatal regions of flatter sides with polygonal, often transversely extended cells. Anticlinal walls straight, marked by a very fine ridge, surface of cell flat, often showing striations parallel with long axis of cell. Stomatal arrangement not known, but stomata commonly separated from one another by ordinary cells; most stomata transverse to leaf axis, guard cells only slightly sunken in wide shallow pit.
Fig. 30. *Geinitzia divaricata* (Bunbury)

Subsidiary cells very little specialized, often two large lateral and two small terminal ones, not markedly thickened nor papillose, nearly as large as other cells. (Encircling cells not seen. Trichomes absent, even from leaf angles.)

**Holotype.** Specimen figured by Bunbury 1851: pl. 13, fig. 4; Sedgwick Museum no. K.303.

**Discussion.** I earlier included *G. divaricata* in *Elatides* but now restrict *Elatides* to species having female cones like those of *E. williamsonii*. The present species is unlikely to be closely related to *Elatides* as the cuticle is different. The largest shoot has a main axis with radially pointing leaves but all the smaller axes have leaves bent into the horizontal plane, none lying directly over or under the axis. The coaly substance of the leaves is thin (much thinner than in *Elatides*) and suggests an originally delicate leaf. Probably the surface ribs sketched by Phillips represent the fibre bundles of the leaf angles and perhaps other fibre bundles also. One naturally rotted specimen, V.57370, shows brown streaks rather than ridges, and a thicker brown streak may be a single vascular bundle.

**Comparison.** No other Yorkshire conifer resembles a typical straight-leaved specimen of *G. divaricata* though *G. rigida* and *Elatides thomasi* have shoots of similar dimensions. Two Jurassic conifers from SE Asia resemble *G. divaricata* in form but nothing is known about their cuticles. One, called *Pagiophyllum* sp. cf. *P. divaricatum* (Bunbury) Sahni (1928: pl. 2, figs 30, 31), from the Lower Cretaceous of Kach, India, was earlier figured by Feistmantel (1876) under the name *Pachyphyllum (?) divaricatum*. As Sahni points out its leaves are less spreading than in typical Yorkshire *divaricata* and they are not longitudinally striated. They may not be bent into the horizontal plane as they are in most Yorkshire shoots. The other species, *Pagiophyllum*
*burmense* Sahni (1928: pl. 4, figs 48–51) from the Jurassic of Burma usually has branches arising almost at right angles, and its leaves though equally divergent are usually shorter. But one fragment (Sahni 1928: pl. 4, fig. 51) certainly looks, as he pointed out, like Yorkshire *divaricata*. He describes the lamina as vertically flattened, probably meaning thicker vertically than from side to side, and this is unlike *G. divaricata*.

**Occurrence.** The holotype was from an iron-impregnated part of the Gristhorpe Bed, whilst the specimens collected more recently are from spoil heaps of the Middle Deltaic moorland coal pits and from scattered points in the Lower Deltaic. The largest specimens as well as the smaller shoots occur in sideritic clay-ironstone blocks fallen from a bed having a peculiar flora which outcrops just above the Eller Beck Bed in Beast Cliff. *G. divaricata* is too delicate to be recognized in drifted material or in cuticle fragments from bulk macerations.

**Genus ELATIDES** Heer 1876

**Diagnosis** (emended from Harris 1943). Tree bearing caducous shoots, branching of shoots distichous or irregular. Leaves persistent, borne helically and diverging radially, arising from decurrent cushion; free part falcate and isodiametric, rhomboidal in section, with single vascular bundle and abaxial resin canal. Hypodermis uncutinized or absent. Stomata crowded in bands on the flat sides, orientated transversely or irregularly. Guard cells sunken in shallow pit formed either by more or less uniform subsidiary cells or by wide lateral ones and narrower terminal ones. Subsidiary cells with papillae. Cutinization of anticlinal walls of subsidiary cells and of adjacent epidermal cells of stomatal band extending deeply inwards. Neighbouring stomata occasionally sharing subsidiary cells. Encircling cells occasional, unspecialized. Epidermal cells outside stomatal bands elongated, walls straight, surface sometimes thickened to form a longitudinal ridge.

Resin canals present in stem cortex. Wood of *Cupressinoxylon* type, much xylem parenchyma present, field pits taxodioid.

Female cone terminal, oval, 2–6 cm long, composed of persistent helically-arranged scales. Scale flattened, not very woody, composed of a stalk which expands as it reaches outer surface and then tapers to a sharp, upward point. Upper surface bearing broad rather membranous ligule (free part of ovuliferous scale), ligule more or less lobed. Placentae of 3–5 seeds proximal to ligule and close to it. Seeds flattened, orthotropous, micropyle facing cone axis. Integument free from nucellus, archegonial group apical, pollen received in micropyle.

Male cones borne in terminal cluster, cylindrical. Microsporophylls in a crowded helix, the slender horizontal stalk ending in a vertical rhomboidal expansion. Pollen sacs three, somewhat elongated, fused to stalk and also to one another. pollen grains round, wall composed of a fairly thick nexine loosely enclosed in a thin sexine, nexine forming an inconspicuous pore possibly on a low papilla.

**Type species.** *Elatides ovalis* Heer (1876: 77; pl. 14, fig. 2).

**Discussion.** In this diagnosis the information about the male cone, the pollen and the interior of the seed is provided by *E. williamsonii*, whilst *E. bommeri* Harris 1953 provides the internal anatomy of the leaf, stem and female cone scale. The other characters are supported by both of these species and by others as well, particularly the Siberian material described by Krasilov (1967).

Nathorst (1897) revised Heer's *Elatides ovalis* and also several other Upper Jurassic or Lower
Cretaceous conifers, identifying them all with Dunker's *Lycopodites curvifolia* which he renamed *Elatides curvifolia* (Dunker). At the same time he described good material from Spitzbergen. Many authors have accepted Nathorst's identification but Krasilov (1971) considered *E. ovalis* distinct from *E. curvifolia*.

*Elatides* was abundant from the Middle Jurassic to the Lower Cretaceous and its points of resemblance to particular genera have been summarized by Harris (1953). Every character of the genus matches that of one or more living genera of the Taxodiaceae, *Cunninghamia* being the nearest though very different in leaf. Several of its characters are also known in other families but the form of the female cone scale, the organ to which most taxonomic weight is assigned, is exclusive to the Taxodiaceae.

*Elatides williamsonii* (Lindley & Hutton) Nathorst

Figs 32–34, 35 H–J; Pl. 2, figs 1–7

The following references are principally to shoots and leaves but include some to cones. References specifically to the male and female cones are listed separately below.

1828 'Plant allied to *Equisetum*', Murray: pl. 5, fig. 4. (Shoot and female cone)
1828 *Lycopodites Williamisonis* Brongniart: 83. (Name only)
1829 *Lycopodites uncifolius* Phillips: 147; pl. 8, fig. 3. (Sketch of shoot)
1829 'Spike of *Lycopodites*', Phillips: pl. 8, fig. 1. (Detached male cone)
1833 *Lycopodites Williamisonis* Brongniart; Lindley & Hutton: pl. 93. Brongniart's *nomen nudum*. (Good shoot and female cone)
1870 *Pachyphyllum Williamisoni* (Brongn.) Schimper: 251. (Attributed to conifers)
1875 *Walchia Williamisoni* (Brongn.) Phillips: 230, lignon. 61 (Sketch of shoot). Pl. 8, fig. 3. (As 1829 but male cone identified)
1884 *Pachyphyllum (?) Williamii* (Brongn.); Saporta: 306; pl. 162, figs 1, 2. (Shoot and female cone)
1897 *Elatides Williamii* (Brongn.) Nathorst: 34. (Name)
1900 *Pagiophyllum Williamii* (Brongn.) Seward: 291; pl. 10, figs 2, 3; text-fig. 52. (Shoots, male and female cones)
1919 *Elatides Williamii* (Brongn.); Seward: 271. (Discussion, text-fig. 742 redrawn from Seward 1900)
1943 *Elatides williamsonii* (Brongn.); Harris: 325, text-figs 1–3; pl. 8. (Leaf cuticle, details of cones, discussion)
1958 *Elatides williamsonii* (Brongn.); Florin: 307; pl. 28, figs 1, 2. (Cuticle, discussion)

**Diagnosis** (shoot and leaf). Caducous shoot systems shed intact. Main axis commonly 6 mm thick, branching monopodially, smaller shoots about 2 mm thick branching irregularly, angle of branching 45° or less. Leaves borne in helix showing 2 + 3 parastichies, those at apex and base of shoot small (but no bud scales produced); leaf base cushion on stem about 2 mm long, bearing leaf at its end. (Axes of unlimited growth unknown.)

Free leaf usually 6–10 mm long, occasionally 12 mm; falcate, middle part at 45° to axis, upper part parallel or converging. Width and thickness even over most of leaf but tapering in upper third and finally narrowing strongly to obtusely pointed apex. Section in middle region square with upper, lower and lateral angles, upper angle ending at stem, lateral ones continuing as edges of cushion and lower angle continuing as keel of cushion. Width and vertical thickness of a large leaf up to 1.75 mm, but of small leaves less. Near base of leaf adaxial surface reduced and abaxial expanding. Substance of leaf dense.

Cuticle of leaf delicate and very fragile, thicker at angles but even there only 1 μm thick (in folds). Flat sides of leaf showing epidermal cells about 40 μm × 30 μm, in longitudinal files; anticlinal walls finely marked, surface walls flat and unmarked or with one or two faint ridges. Stomata forming bands on the two abaxial sides and bands continuing onto basal cushion, probably absent from adaxial sides. Stomatal bands occupying nearly half of each abaxial side. Stomata irregularly placed and variously orientated but often transverse, subsidiary cells alike.
or lateral ones somewhat elongated, scarcely overhanging stomatal pit; surface of subsidiary cells with a thin strip parallel with pit. Hypodermal cells absent except possibly at angles (mesophyll cell contents often adhering to cuticle). Resin bodies absent from leaf but small round ones present in stem tissues.

Holotype. Specimen figured by Lindley & Hutton (1833: pl. 93).

Discussion. Brongniart (1828: 83) gave the nomen nudum Lycopodites Williamsonis and Lindley & Hutton validated the name with a good figure in 1833, quoting Brongniart as author of the species as have later writers. Earlier, however, Phillips (1829) gave a sketch of a shoot he called Lycopodites uncifolius and I suppose this really is E. williamsonii, but rather because it is from Gristhorpe than because of any diagnostic features in the figure. Phillips later dropped the name uncifolius in favour of Williamsoni. No one has subsequently used it and I do not revive it here.

Shoots from the Gristhorpe Bed look beautifully preserved but the cuticle is extremely weak and difficult to study. Even before it is collected the coaly substance is commonly crossed by
cracks dividing it into rectangles 0.3 mm × 0.1 mm or even smaller. These limit the size of cuticle preparations and even then the preparations may be obscured by mesophyll cell contents which resist maceration better than the cuticle. In favourably preserved leaves the stomatal bands on the two lower sides can be seen by surface observation, but none has been seen on the two upper sides. Florin (1958: 308) had doubted whether this unusual distribution was fact but I can now confirm it. I examined the leaf surface of five exceptionally well preserved shoots and saw none above, though they were clear below. I then took pieces from the adaxial and abaxial surfaces of laterally compressed leaves at the sides of a shoot and macerated them separately on slides under coverslips. Plenty of the tiny abaxial pieces showed stomata but not one in 20 macerations of adaxial ones. I conclude that stomata are normally absent above in E. williamsonii, though the Cretaceous E. bommeri certainly does have adaxial stomata.

The delicacy of the cuticle of E. williamsonii suggests that the shoots were dropped at the end of their first summer, like those of Taxodium, and were not retained for several years like the caducous shoots of Sequoia sempervirens (D. Don) Endlicher, but if so the thick coaly substance of the fossil leaf needs to be explained. Its branching also suggests that the shoot was deciduous, for the lateral branches like those of Taxodium merely have small basal foliage leaves. This is unlike Sequoia, which has specialized winter bud scales at the branch bases.

Male Cone and Pollen
Fig. 33 A–D, F–I, K; Pl. 2, figs 1–7

1829 'Spike of Lycopodites', Phillips: pl. 8, fig. 1.
1875 Walchia Williamisonis Phillips: pl. 8, fig. 1. (Same figure)
1900 Pagiophyllum Williamisoni, male cone, Seward: 291; pl. 10, fig. 2a, b.
1943 Elatides williamsoni, male cone, Harris: 327; pl. 8, figs 1–9; text-fig. 2.
1958 Elatides williamsoni, pollen, Couper: 129; pl. 27, figs 7, 8.
1958 Perinopollenites elatoides Couper: 129, 152; pl. 27, figs 9–11. (Similar dispersed pollen widespread in British Liias to Lower Cretaceous, not all attributed to this species)
1970 Elatides williamsoni, pollen, van Konijnenburg-van Cittert: 58; pl. 13, figs 3, 4; pl. 14, fig. 2.
1971 Masocolostrobus harrisii van Konijnenburg-van Cittert: 66; pl. 16, fig. 5 (pollen); text-fig. 10 (cone). See below.
1972 Masocolostrobus harrisii van Konijnenburg-van Cittert: 97; pl. 2, fig. 3. (Photograph of same cone)
1973 Elatides williamsoni, pollen, Harris: 2. (Discussion of abnormal pollen)

**Diagnosis.** Male cones borne in groups of 3–6 at end of leafy shoot. Immature cones up to 16 mm long × 5–7 mm broad, then expanding to about 28 mm long but occasionally shorter, width remaining at 5–7 mm; falling after shedding pollen. Pedicel short, bearing small sterile scales. Cone axis about 1 mm thick, marked with ridges recurrent from sporophyll bases. Sporophylls in a crowded helix showing 5 + 8 parastichies but irregularity frequent and sometimes in alternating whorls of about eight. Sporophyll stalk slender, horizontal, about 2 mm long; heads expanded, overlapping and almost parallel with cone axis. Head inversely kite-shaped, attached to stalk just above basal angle; lateral and basal angles rounded, edges delicate, surface showing narrow cells running to apex; middle region thicker and enclosing an oval resin body 200 μm long or occasionally a second behind the first. Pollen sacs three, attached along the stalk and to the head and also to one another, length typically 1.3 mm, width at outer end 0.4 mm, tapering inwards. Wall delicate, cells showing transverse bands of thickening, dehiscence longitudinal.

Cuticle of head delicate, showing elongated, straight-walled cells; pollen sac lined by delicate granular tapetal cuticle.

Pollen grains round, not remaining in tetrads. Diameter about 45–50 μm (grains smaller than
45 μm presumed to be immature). Exine double, sexine separated from nexine by a gap of 5 μm. Sexine very delicate, finely granular (often torn and missing or found separately; usually absent from small pollen grains). Nexine about 1 μm thick, almost smooth. Pore possibly on a slight elevation and appearing as a ring when compressed vertically (but not often seen). (Walls, especially sexine, forming small irregular folds in compression.)

Discussion. Phillips (1829) recognized the detached male cone as belonging to his *Lycopodites uncifolius* whilst Seward (1900), who figured detached male cones accurately, attributed it to *Pagiophyllum williamsonii* and stated that attached cones were also known. No one has doubted this attribution though the first figures of attached cones were those of Harris (1943). We know the male cones at all stages, from small budlike bodies to almost mature ones with ripe pollen and then detached expanded and nearly empty cones. A few of the immature cones are only slightly compressed because the gaps between the microsporophylls were filled with some mineral and these, after impregnation with synthetic resin, have been sectioned serially by grinding. Each microsporophyll clearly shows three sacs full of pollen, confirming the impression given by macerations.

The pollen of *E. williamsonii* has been described three times and each time the sizes given were different, so a fresh study was made to explain these and other discrepancies. Most of the male cones are either fully expanded and empty of pollen or have just a few grains, not all of them belonging to *E. williamsonii*. The rock matrix also contains a good many grains resembling those of *E. williamsonii* but not safely attributed to it. So the further studies were made on somewhat immature male cones, mostly detached though some were still on shoots. Such immature male cones have not fulfilled their normal development and are suspect as abnormal. From a study of the pollen in prematurely dropped *Pinus radiata* cone-bearing shoots, Harris (1973) had concluded that their pollen ranged from mature, through slightly immature to totally abnormal. The shoots died slowly on the damp ground and perverted development of pollen occurred. Thus some pollen sacs have rather small grains with defective contents, e.g. a foursaccate grain; or a grain with an annular sac, such grains being larger than normal and perhaps resulting from an undivided pollen mother cell. This is a hazard to be borne in mind when studying fossil pollen from unopened pollen sacs.

Many of the immature *E. williamsonii* male cones studied were found together on a single slab. Their size varied and it proved impossible to predict the state of the pollen though the smallest (5 mm long) did give very small and thin-walled grains 22–29 μm wide. Another cone 10 mm long gave almost similar grains but another, also 10 mm long, gave grains only slightly larger (about 30 μm) though with a well-developed nexine (but no sexine). Still another, 10 mm long, gave varied grains 25–49 μm wide, some with a well-developed nexine closely enveloped in a sexine. Certain larger cones gave grains that appeared perfectly developed but still others gave pollen that was poorly developed. I suspect that all the small grains in these unexpanded cones are abnormal rather than strictly immature stages since I would not expect normal pollen to have resistant sporopollenin in the walls when only half grown. Thus I accept the larger grains of van Konijnenburg-van Cittert (1971) which have a separate sexine as normal and mature, and also those of Couper (1958), though they are somewhat smaller. They agree with much of the pollen in the rock matrix. The small and featureless single-walled grains I obtained (Harris 1943) from a small cone, and which match many obtained in this study, are I think by no means mature, and neither do I imagine they are the same as would have been shown by a cytologically fixed half grown cone.

I suspect that *Mascolostrobus harrisii* van Konijnenburg-van Cittert (1971, 1972) from the
Fig. 33. *Elatides*, male cone and pollen

A–D, F–I, K, *E. williamsonii*; E, J, *E. thomasii*. A–C, sections through sporophylls seen also in K but at different levels, ×40. D, pollen sac wall in celloidin pull, V.21375, ×200. E, portion of expanded male cone in transfer, V.57006, ×20. F, immature pollen grain, showing neither separate sexine nor pore but with a strong fold, V.21401, ×800. G–I, nearly mature pollen grains, V.56718a, b, ×1000 (position on slides not recorded). J, pollen grain at edge of intact sac, V.56729, ×1000. K, oblique section revealed by grinding through a nearly ripe cone embedded in bakelite. Coaly matter black, pollen sacs stippled and labelled a, b, c; resin bodies shaded with oblique lines. V.26844, ×40. Figs A–D, F, K are from Harris (1943).
Gristhorpe Bed is an expanded and detached *E. williamsonii* male cone which has lost its pollen and was then heavily contaminated with foreign pollen of a single sort, possibly *Brachyphyllum mamillare*. The grain diameter, 59–70 μm, is well outside the range of that of *E. williamsonii* and the wall details are different. The discovery of a similar but somewhat immature cone providing intact sacs with these large pollen grains inside would confirm that *M. harrisii* is distinct, but at present there is only one specimen known.

Female cone and seed
Fig. 34

1833  *Lycopodites Williamonis* (Brongn.) Lindley & Hutton: pl. 93.
1900  *Pagiophyllum Williamonis* (Brongn.) Seward: 291; pl. 10, fig. 3; text-fig. 52.
1943  *Elatides williamsoni* (Brongn.); Harris: pl. 8, figs 10, 15, 17, 18; text-fig. 3. (Cone and seed)

**Description.** Cone borne terminally on a shoot with either normal or rather short leaves, surface covered with upward-pointing, tapering scale apices (but upper part often broken). Mature cone oval, 4–6 cm long × 2·0–2·5 cm wide. Cone scales in a crowded helix showing 5 + 8 parastichies, each scale with a robust stalk 1 cm long at 45° to cone axis, stalk broadening to about 5 mm and bearing up to five seeds in a curved row. Scale then bending upwards to form the exposed head, main part of head rhomboidal and about 5 mm broad, upper 3 mm tapering to a fine point. Total length of cone scale about 17 mm. Seeds borne separately, each on a small placental projection on upper surface; at about 1 mm distal to seeds a delicate ligular up-growth with a lobed margin, probably one lobe opposite each seed. Cone scale enclosing oval resin bodies about 0·5 mm long.

Seeds oval, typically 2·0 mm × 1·0–1·4 mm, originally flattened, margins thin but not winged or scariosus. Micropylar end often slightly pointed; hilum minute. Epidermis and cuticle of integument similar on the two surfaces of the seed; cuticle thin but coherent, showing straight-walled cells, elongated over most of seed but shorter near micropyle. Stone and other tissues outside megasporae only 0·1 mm thick at compressed margin. Micropyle lined by a thin cuticle, cell outlines conspicuous and surfaces bulging, in mature seed micropylar canal blocked by ingrowths from cells at sides. Cuticle lining integument very delicate, continuing to base of seed (but owing to compression inseparably adherent to cuticle of nucellus). Nucellus free to its base, in micropylar part forming a robust cap, but becoming very delicate below. Megaspore membrane robust, densely granular contents of outer cells of endosperm 40 μm wide usually preserved. Archegonia forming an apical group of about six.

**Discussion.** The female cones in the Gristhorpe Bed never disintegrated before preservation but they have lost nearly all their seeds and the dispersed seeds are common. No cone as ordinarily seen shows the placenta or ligule but in one where there is a layer of matrix between the cone scales they can be exposed by degaging the substance of the fossil until the upper surface of a cone scale is reached. Seeds found both in cones and dispersed were studied by ordinary maceration. Most showed the cells regarded as the outer layer of the endosperm but only a few showed the archegonial eggs as cavities in the endosperm. Immersion of blocks from the Gristhorpe Bed and the Cloughton Wyke *Solenites* Bed in water gave intact seeds, but other rocks required treatment with acid and alkali and then the megaspore membranes lose the integument. Such denuded megaspores obtained by macerations of blocks from Middle Deltaic localities are identified as *E. williamsonii* whilst similar or smaller megaspores from Lower Deltaic rocks are identified as *E. thomasii*. 
Comparison. *E. thomasii* of the Yorkshire Lower Deltaic has smaller shoots, leaves, male and female cones and seeds. Though the ranges of size overlap the difference is striking where material is abundant. The contrast in shoots is strongest between large shoots of the two species. The leaves of *E. thomasii* on large shoots are commonly 5 mm long and 0.75 mm thick, those of *E. williamsonii* 10–12 mm long and fully 1.0 mm thick. The leaf of *E. thomasii* tapers evenly from base to apex but of *E. williamsonii* is nearly uniformly wide to the upper third. But small shoots of *E. williamsonii* are certainly like *E. thomasii*. Their cuticles (less known in *E. thomasii*) are not yet distinguishable.

The expanded and empty male cone of *E. thomasii* is 15–17 mm long and 3–4 mm wide, and its sporophyll heads up to 1.3 mm long. That of *E. williamsonii* is 15–28 mm long, often about 23 mm long and 5 mm wide. Its microsporophyll heads are up to 2.0 mm long.

The detached female cone of *E. williamsonii* is typically 40–60 mm long and 20–25 mm wide, that of *E. thomasii* 15–20 mm long and about 12 mm wide. Individual cone scales of *E. thomasii* are about half as large and its seed megaspores (few measured) are two-thirds as large. These differences in cones are considerable but a few abnormally small cones (abortive) are found in each species. The intact seed of *E. williamsonii* is commonly 2.0 mm long, that of *E. thomasii* about 1.0–1.5 mm long, but small, perhaps abortive seeds are known in *E. williamsonii*.

*Elatides asiatica* Krasilov 1967 (the new name for *E. manchurica* Yokoyama 1906, *Elatocladus manchurica* and *Elatocladus subzamioides* of various Japanese and Russian authors) is represented by good material from the Lower Cretaceous of eastern Asia. It differs from *E. williamsonii* in its straight leaves with normally longitudinal stomata and its cone scales have a narrower apex.

*E. curvifolia*, see Nathorst (1897), from the Lower Cretaceous of Spitzbergen, has similar shoots and female cones, but its leaves are straighter and its cones occur more often at the ends of long shoots. The cone surface looks smoother and the outer surface of each scale has a keel with a groove.

A cone from north-east Scotland described by Seward (1911) as *E. curvifolia* apparently has a single median seed. This is thus quite different, though it is associated with some similar-looking shoots.

*E. falcifolia* Teixeira (1948: 24) from the Lower Cretaceous of Portugal has shorter leaves and a smaller cone than *E. williamsonii*.

*E. bommeri* of the Lower Cretaceous (Harris 1953) has small shoots and small cones, more like those of *E. thomasii*. Its seeds are like those of *E. williamsonii* in size, shape and in having no marginal wing.

*E. ovalis* Heer, redescribed by Krasilov (1971), is a smaller cone and well distinguished by its broadly winged seeds.

Occurrence. Fine specimens of *E. williamsonii* are abundant in the Gristhorpe Bed and frequent at Cloughton Wyke in the *Solenites* Bed. I imagine the trees must have grown near where these beds, thought to represent lagoons, were deposited. Seed megaspores occur widely in the Middle Deltaic and the comparable dispersed pollen *Perinopollenites elatoides* Couper 1958 (equally like pollen of *E. thomasii*) occurs widely in the British Jurassic and Lower Cretaceous.
Fig. 34. *Elatides williamsonii* (Lindley & Hutton), female cone and seed

A, portion of inner membranes of macerated seed, showing obscurely marked, elongated nucellar cells and cells of endosperm with clear margins; V.26849, ×400. B–G, inner membranes of seeds, ×5. The archegonial depression at the apex is shown black; fragments of the integument are present in D. B, C, V.26850; D, V.26846; E, F, V.26847; G, V.26851. H, cells of integument, V.26846, ×400. I, adherent cuticles of inside of integument and outside of nucellus, V.24674, ×200. J, upper surface of cone scale showing part of the ovuliferous scale as a ridge, and below it one seed and two seed impressions; V.25860, ×5 approx. K, upper surface of cone scale showing curved row of six placentae below and three of the ligular processes from the ovuliferous scale above, ×8. L, lower surface of cone scales exposed by the removal of several others, showing expansion at top of ovule-bearing part. A full-sized seed is exposed by the removal of one of the scales; ×4. J–L, from V.25860, a specimen subsequently made into a transfer. All figures are from Harris (1943).

**Elatides thomasii** sp. nov.

Figs 33 e, j; 35 a–g, k, l; Pl. 2, figs 8–13

1913 *Pagiophyllum williamsoni* cf. *Elatides setosa*; Thomas: 224. (Name in list)
1913 *Elatides* sp. cf. *E. setosa* (Phillips); Thomas: 224, 226. (Name in list, brief discussion of specimens from Marske Quarry)
1913a *Coniferous twigs (Elatides), with male and female cones*; Thomas: 199. (List for Roseberry Topping)
**SYSTEMATIC DESCRIPTIONS**

**Diagnosis.** Caducous shoot systems richly branched, monopodially or irregularly. Axis of large shoots typically 3 mm thick, rarely up to 10 mm, smallest 1 mm.

Leaf of a large shoot up to 5 mm long, 0.75 mm wide in middle and 1.0 mm wide basally, tapering to acute apex; shape strongly falcate, in section square, angles without projecting cells. Leaves at ends of shoot shorter, leaves of small shoots shorter and narrower.

Leaf cuticle thin (ill-known and no distinguishing differences from *E. williamsonii* recognized). Male cone (only known detached and fully extended) about 15–17 mm long, 3–4 mm wide. Axis slender, about 0.5 mm thick, bearing microsporophylls in a crowded helix; stalk of sporo-phyll slender, 1.5 mm long, attached just above base of expanded head. Head square, often 1.0 mm long and broad but up to 1.3 mm × 1.2 mm; angles rounded, middle region thick but edges delicate. Pollen sacs 0.8 mm × 0.4 mm, containing rounded pollen grains 45–55 µm wide, pollen probably with delicate sexine round the nexine. (Microscopic details of male cone and of pollen imperfectly known.)

Female cone borne terminally on a shoot 1.5 mm thick, leaves of cone-bearing shoot small and short; fertile shoots grouped in a cluster (but cones mostly preserved separately). Cone round or oval, about 15 mm × 12 mm (range 13 mm × 10 mm to 20 mm × 15 mm), surface covered by upturned distal ends of cone scales. Cone scales arranged in a helix showing 5 + 8 parastichies, exposed part of scale 4 mm × 2 mm, its apex acute; basal limb up to 5 mm long broadening from base to 3 mm, borne at about 60° to cone axis. (Other details unknown.)

Seed enclosing a megaspore slightly over 1 mm long, 1.0 mm broad, membrane showing faint marks of elongated cells on surface and containing cellular endosperm with hardened cell contents.

**Holotype.** V.56730; Pl. 2, fig. 8.

**Name.** After H. H. Thomas, who collected the original material.

**Discussion.** Thomas collected good material of this species in about 1912 and recognized it as distinct from *E. williamsonii* but he did not describe it. Wherever the shoots are common there are associated but detached fully-expanded male cones and also female cones, some of them still attached to leafy shoots; such cones have never been found without the shoots.

The cuticle is just as delicate as that of *E. williamsonii* but in none of the *E. thomasii* localities is preservation as good as in the Gristhorpe Bed. It is thus less well known. A few of the expanded male cones have an occasional pollen sac still full of pollen but it proved impossible to separate the grains undamaged.

**Comparison.** *E. thomasii* has been compared with *E. williamsonii* on p. 73. The two species have not yet been found together. *E. falcifolia* Teixeira (1948: 24) has rather stouter and straighter leaves and a longer cone of similar width. *E. bommeri* Harris 1953 (Lower Cretaceous of Belgium) has very similar twigs but the leaves arise from the middle instead of the top of the cushion. Its stomata are adaxial (their distribution in *E. thomasii* is not yet known). Its cone is of similar size but the cone scale has a shorter apical point.

*Elatides muensteri*, described by Genkina (1963: 88), has equally short but much thicker leaves. It is from the Middle Jurassic of the Urals.

*Elatocladus setosus* (Phillips) has shoots of similar size but the leaves are flat, bifacial and narrowed below. It's cuticle is also different.

**Occurrence.** *E. thomasii* is abundant in several localities at the very base of the Lower Deltaic, some of them with marine microfossils. Where it occurs commonly the specimens
Fig. 35. A–G, K, L, Elatides thomasii sp. nov.; H–J, Elatides williamsonii (Lindley & Hutton)
include intact branch systems and the cones also occur, strongly associated with the shoots, so I have no doubt that it grew near to where it was preserved. The cuticle of the leaf is too delicate to recover by bulk maceration although seed megaspores like *E. thomasii* have been found repeatedly.


Upper Deltaic occurrence: Scalby—one small shoot, Sedgwick Museum no. 164.

**Form-genus CYPARISSIDIUM Heer 1874**

**Diagnosis.** (From Harris 1969: 249.) Shoot, bearing leaves helically. Free part of leaf contracting gradually from basal cushion, somewhat flattened, appressed to stem, elongated; its length exceeding width of basal cushion.

**First described species. Widdringtonites gracilis** Heer (1868: 83).

Though species of fossil conifer shoots having appressed needle leaves are few, they are sufficiently distinct to merit a generic name, and *Cyparisidium* Heer (1874: 74) seems appropriate. But possibly Heer’s holotype (1868: pl. 43, figs 1e, 3c), from the L. Cretaceous of Kome, Greenland, did not have the characters he attributed to it. Heer (1874) later added further specimens to this species and renamed it *Cyparisidium gracile*, giving a revised diagnosis to fit this material. In my opinion the additions, which are mostly from the Upper Cretaceous (Senonian) of Patorfik and Kuk, are specifically distinct from the holotype. Their relevance is merely that their identification raises doubt about Heer’s interpretation of the holotype.

Heer’s (1868) diagnosis of *Widdringtonites gracilis* is: ‘*W. ramis erectis fastigiatis, ramulis filiformibus confertis, foliis adpressis alternis, obtusiusculis.*’ (W. with erect fastigate branches, close filiform branchlets, leaves alternate, rather obtuse, appressed.) The part referring to the leaves is close to the diagnosis given here.

The holotype of *W. gracilis* (in Copenhagen) is indifferently preserved and may have deteriorated since Heer described it. I thought it had appressed free leaves but could not be certain. I was on the other hand certain that some of the later specimens do not have appressed leaves but have decurrent cushions surmounted by short free leaves, the *Brachyphyllum* form. I cannot tell what Heer had in mind in 1868 when he described *W. gracilis* with the words *foliis adpressis*, but in 1874, when he used them again, he certainly confused a decurrent ridge on a stem with a free, appressed leaf. Others too have done this.

However, shoots with appressed free leaves certainly do occur in the Cretaceous of West Greenland for Seward (1926: 111, text-fig. 20) shows one and his photos (pl. 11, fig. 167) may include others. He named these specimens as *Cyparisidium gracile* but also accepted those of Heer (1874) even though recognizing that some had *Brachyphyllum* form. Thus until there is positive evidence that he was mistaken, I prefer to suppose Heer’s interpretation and description of his holotype was correct, but doubt will remain until fresh material from Kome is studied. Various Cretaceous conifer shoots and cones from Europe, Asia and America have been identified with *C. gracile* (Heer), but these identifications are with the later (1874) material rather
than the holotype. It is often impossible to tell from the figure how much of the adaxial surface of the leaf is free from the stem, for in some specimens from France (Carpentier 1927), Central Asia (Sikstel' & Khudaiberdýev 1968) and the Kolyma River, Siberia (Samylina 1967) they look adnate as in a typical Brachyphyllum.

The living Dacrydium franklinii Hook. fil. has shoots of Cyparissidium form, and a number of dimorphic conifers, e.g. Glyptostrobus, also have certain shoots of this form.

Cyparissidium blackii, which is represented by abundant specimens, has appressed leaves on all its shoots. With species represented by only a few specimens, however, we cannot say whether or not this is merely one form of variable foliage. Where two forms certainly occur, as in Elatocladus heterophylla, I arbitrarily take the spreading form to decide on the form-genus.

**Cyparissidium rudlandicum** sp. nov.

*Fig. 36; Pl. 4, fig. 9*

**Diagnosis.** (Based on two caducous ultimate shoots.) Shoots unbranched, about 2 mm wide; leaves borne helically with 1 + 2 or 2 + 3 parastichies (shoot not originally flattened).

![Diagram of Cyparissidium rudlandicum sp. nov.](image-url)
Leaves mostly close to stem but free from it to near their base, occasional leaves diverging. Leaf in abaxial view nearly rhomboidal, length up to 4 mm, width in middle 1.0–1.5 mm; tapering to obtusely pointed apex and also somewhat narrowed below, but attachment to basal cushion usually overlapped and concealed.

In lateral view, leaf near its base parallel with and close to stem, diverging slightly in middle region but becoming parallel or converging above. Thickness (adaxial to abaxial) about 1 mm near leaf base, diminishing to 0.6–0.8 mm in middle and thinning upwards to acute or acuminate point. Leaf in section probably semicircular in middle region, becoming flatter distally and more oval proximally (but still with lateral angles), near base becoming almost round. Lateral margins scariosus towards leaf apex. Abaxial surface rounded, without any keel or obvious midrib, surfaces showing epidermal cells but otherwise smooth (without ribs or obvious stomatal pits).

Cuticles about 1 μm thick (imperfectly known from fragments). Epidermis showing stomatal regions and regions without stomata, stomatal regions forming elongated bands. In regions without stomata, cells 2–3 times as long as broad, lateral and end walls marked by fine, straight, slightly nodular ridge. Cells not forming clear longitudinal files, ends mostly pointed, cell surface without a papilla but occasionally showing faint longitudinal striae.

In stomatal regions cells shorter and dimensions varied, some cells broader than long, outlines often obscure. Stomata frequent though not crowded in their bands, arrangement and orientation varied but often nearly transverse. Guard cells only slightly sunken in a rectangular pit and surface largely exposed. Subsidiary cell ring irregular, lateral cells often wide and polar ones smaller; (encircling cells absent). (Epidermis not cutinized, no trichomes seen.)

Holotype. V.57415, Fig. 36 b–d; Pl. 4, fig. 9.

Name. The specific name is from Rudland Rigg, where the specimens were found in the tip of an old Middle Deltaic coal pit at about 50° 20' 21" N, 0° 59' 3" W.

Discussion and Comparison. The two specimens were once well preserved but have become weathered and the leaf substance has cracked into minute rectangles which limit the size of cuticle preparations. The shoots look like certain forms of Brachyphyllum crucis but are distinguished by their much thinner cuticle and more extensive adaxial leaf surface. Cyparissidium blackii has smaller leaves in relation to the shoot width and therefore higher parastichy numbers. Its cuticle is thicker and different.

Certain imperfectly known specimens described from various regions as species of Cyparissidium, Brachyphyllum or Sphenolepidium cannot at present be distinguished from C. rudlandicum.

_Cyparissidium blackii_ (Harris) comb. nov. (shoot)
with _Pityanthus scalbiensis_ van Konijneng-van Cittert (male cone)
and _Scarbursia hillii_ (female cone and seed)

_Cyparissidium blackii_ (Harris) comb. nov.
Figs 37, 38; Pl. 4, figs 10–12, 14

1952 Haiburnia blacki Harris: 367, text-figs 3 d, 4, 5.
1958 Haiburnia blacki Harris; Florin: 318, 357. (Discussion)
1971 Haiburnia blacki Harris; van Konijneng-van Cittert: 68. (Discussion of association with _Pityanthus scalbiensis_)

Emended diagnosis. Axes of unlimited growth (rarely preserved) straight, richly branched, bearing caducous shoots at about 45° on all sides. Leaves larger than on caducous
shouts, less clearly appressed to stem and their decurrent bases better developed, borne in a rather loose helix with $3 + 5$ parastichies. Caducous shoots simple and straight but undeveloped buds frequent; if branched the branches arising irregularly and at $45^\circ$ from all sides, smallest branchlets very slender and often curved. In normal shoots surface covered with appressed leaves, borne in a crowded helix with $3 + 5$ parastichies, but smallest shoots with fewer ranks of relatively broader leaves.

Leaves of caducous shoots overlapping bases of leaves above, closely appressed, largest $5 \text{ mm} \times 1 \text{ mm}$ and widest at middle; smaller leaves widest near base, typically $2 \text{ mm} \times 0.7 \text{ mm}$; smallest $0.5-1 \text{ mm}$ long and nearly as broad. Free leaf merging basally into its cushion, in section semicircular or very slightly concave above, abaxially rounded (not keeled and midrib not externally apparent). Margins sharp in middle part, becoming scarious and microscopically denticulate towards apex; apex obtuse, acute or occasionally mucronate.

Abaxial cuticle 2–4 $\mu$m thick, adaxial thinner. Epidermal cells of both sides isodiametric or
slightly elongated, seldom forming well-marked files; anticlinal walls straight, uninterrupted, marked by broad ridges. Surface wall flat, smooth. Stomata occurring on both sides, often more numerous adaxially; widely spaced, scattered and not forming files. Apertures variably orientated but often longitudinal, guard cell surface thinly cutinized. Stomata sunken in small pits often of hemispherical shape, pit round, polygonal or slightly elongated in surface view; formed by 6–8 subsidiary cells. Subsidiary cells often all alike and forming a perfect ring, seldom an elongated group; terminal cells occasionally less thickened than lateral ones. Subsidiary cell surface flat, thickness similar to rest of epidermis or slightly thicker near pit and thinner in middle of cell; outer (anticlinal) wall often conspicuous. Encircling cells often present but unspecialized. (Trichomes apart from projecting marginal cells absent, hypodermal fibres probably absent.)

Fig. 38. *Cyparissidium blackii* (Harris)
A, apex of a leaf on the shoot shown in Fig. 37 E, F, showing marginal cells; V.29299, ×200. B, adaxial cuticle, V.29298, ×200. C, monocyclic stoma, epidermal cells mostly showing thin central areas; V.59021, ×500. D, two dicyclic stomata, V.29298, ×500. Figs A, B, D are from Harris (1952); C is new. All the specimens are from Black’s (1934) Channel C, at Horse Back Rock, Burniston Wyke.
Holotype. V.8973.

Discussion. When preserved in a sandy shale C. blackii forms an ordinary compressed fossil but in the clay of Black's level bedded series at Scalby the shoots are scarcely compressed and the leaves remain plump, probably through impregnation with oil. Internal tissues, particularly the mesophyll, are often preserved and they are troublesome to remove from the macerated cuticle. A few leaves show a central dark strand suggesting a small vascular bundle and others a central pale strand above or below the vein, suggesting a resin canal. The transverse bars seen in some leaves perhaps indicate transfusion mesophyll like that of some living conifers.

In compressed leaves from the sandstone their original form can be inferred from changes in apparent width of leaves on top of the stem compared with those at its sides. The fact that the margins are seldom bent over the surface or at most only bent at the extreme edge indicates that the upper surface was not normally concave or at most only slightly concave.

Although C. blackii is abundant at a classic locality and was occasionally collected long ago it was confused with Brachyphyllum mamillare and therefore often overlooked. But manuscript notes indicate that Seward and later Black were aware of its separate identity. It was first described and named in 1952.

Comparison. The most similar Yorkshire conifers are Cyparissidium rudlandicum which has flatter leaves in fewer parastrichies and Brachyphyllum mamillare also with fewer parastrichies on a shoot of similar size. B. mamillare has very short free leaves surmounting a keeled cushion and the cuticle differs in many ways. The constricted shoots of the Rhaetic conifer Stachyotaxis septentrionalis (Agardh) Nathorst look similar but differ in cuticle. A specimen named Cyparissidium gracile by Seward (1926: 111) from the Cretaceous of West Greenland also looks similar, but its stomata (which are scarcely sunken) are all adaxial. The Cretaceous shoot figured by Turutanova-Ketova (1963: pl. 25, fig. 8) as C. japonicum looks similar to C. blackii but according to Oishi (1940) the original specimen is a Brachyphyllum.

Occurrence. Most of the specimens of C. blackii are from the upper, mainly clay part of the Upper Deltaic where it has many localities within 10 km of Scarborough. It occurs also in sandy stream channel deposits which cut into the clay. It is rare further to the north and west, though there are about 20 available Upper Deltaic localities which might have provided it.

It is doubtful if C. blackii occurs below the Upper Deltaic. At Roseberry Topping there are a few similar-looking shoots but they gave no satisfactory cuticles. On the other hand a very few cuticle fragments resembling C. blackii have been obtained by bulk maceration of Lower and Middle Deltaic rocks but the form of their shoots is unknown.

C. blackii is well represented in collections at Cambridge and Utrecht as well as in the British Museum (Natural History). All the good specimens are from coast sections, mostly near Scalby Ness, though recently also from a block fallen from a new bed at Yons Nab, collected by C. R. Hill.

Form-genus PITYANTHUS (Nathorst) Seward 1919

Diagnosis. Male cone bearing small crowded microsporophylls; each microsporophyll having a slender stalk, an upturned and expanded end and bearing two pollen sacs below the stalk; pollen grains bisaccate.

First described species. Ophioglossum granulatum Heer 1883.
Discussion. Nathorst (1897) made the word Pityanthus and applied it to an unnamed fossil resembling a conifer male cone, but he made it clear that it was a descriptive term and not a generic name. Seward (1919: 395) was the first to use it in a binomial. Newberry (1895) referred a cone-bearing shoot apparently surmounting a three-leaved caducous dwarf shoot to the type species and Stopes (1911) showed that it had bisaccate pollen. She doubted if it was specifically identical with Heer’s specimen and renamed it Pinus granulatus (Heer). Barnard (1968: 168) treated Pityanthus as a valid name applicable to male cones with bisaccate pollen and van Konijnenburg-van Cittert used it in describing P. scalbiensis, though Pityanthus had never been defined.

The above diagnosis covers the male cones of many living Pinaceae and Podocarpaceae, but in each of those families some members have pollen grains of different structure and would thus be excluded. I know of no general way to tell whether bisaccate pollen is pinaceous or podocarpaceous, though it is true that pinaceous grains are commonly of shapes infrequent among podocarps and vice versa. Most pinaceous pollen grains are larger than most podocarp ones.

Since P. granulatus is thought to be pinaceous, and P. scalbiensis podocarpaceous, Pityanthus remains a form-genus.

The genus Podostrobus Rao & Bose (1971) overlaps Pityanthus Seward. It was erected for Masculostrobus rajmahalensis Rao (the type species) and M. sahni Vishnu Mittre, both from the Indian Mesozoic. P. rajmahalensis is distinguished specifically from P. scalbiensis by its narrower shape but its pollen is similar; P. sahni however has 3- or 4-saccate grains. The distinction of Podostrobus was its attribution to the Podocarpaceae (whilst Pityanthus was attributed to Pinaceae) and also its Gondwana rather than northern distribution. If P. scalbiensis and various Cretaceous fossils described by Krasilov (1967) are, as I believe, podocarpaceous, no distinction remains in distribution.

Pityanthus scalbiensis van Konijnenburg-van Cittert
Figs 39, 40; Pl. 5, figs 1–9

1952 ‘Male cone with holotype of Haiburnia blacki’; Harris: 373, text-fig. 4 e. (Ill-preserved specimen)
1971 Pityanthus scalbiensis van Konijnenburg-van Cittert: 67, text-fig. 11 (holotype); pl. 16, figs 4, 6 (pollen).
1972 Pityanthus scalbiensis van Konijnenburg-van Cittert: 98; pl. 2, fig. 4. (Photo of holotype)

Emended diagnosis. Male cone (known detached only), shed at maturity without stalk, shape long ovoid or cylindrical, length at maturity 8 mm (occasionally 10 mm), width 3–5 mm. Microsporophylls in a crowded helix with about 5 + 8 parastichies but often irregular, in ripe cone usually perpendicular to axis but lower ones sometimes strongly reflexed; upper ones sometimes pointing obliquely upwards, those at ends of cone short and at base a few small sterile scales also present. Microsporophyll consisting of stalk 1.5–2 mm long in middle of cone and a nearly vertical expanded head. Basal region of stalk slender and nearly round in section but becoming broader distally and also developing a downward keel. Near the head, width of stalk up to 0.5 mm, keel up to 0.4 mm deep. Head inversely kite-shaped, extending upwards for 0.7 mm and laterally for 0.5 mm from end of stalk; tissue thick where it joins stalk and keel, with slight upward midrib, but becoming delicate towards margins. Cuticles delicate. Pollen sacs attached to underside of stalk and to keel and also to lower part of head; in expanded cone length up to 1.5 mm, width and depth up to 0.4 mm but narrowing towards cone axis, each opening by a longitudinal split along side facing downwards and outwards; wall of pollen sac delicate.

Pollen grains (terminology of van Konijnenburg-van Cittert 1971 and of Couper 1958)
disaccate, sacci offset distally. In equatorial or lateral longitudinal view, corpus rounded and distinctly broader than high (but if contracted to form a sulcus height appearing reduced and sacci drawn together). Sacci nearly semicircular. Proximal surface of corpus thickened to form a cappus but thinning gradually towards equator and then thinning sharply to join distal surface (a fold commonly present near junction of two parts).

In polar view and in end or lateral transverse view of grain, corpus thickness (depth) nearly same as its height, but saccus length much increased and sacci showing angular roots, inner margins of sacci bounding the corpus.

Wall of corpus just over 1.0 μm thick in cappus, composed of thin sexine, then short columnellae and at outside rounded capita 1 μm wide which make the outer surface rough and form a

Fig. 39. *Pityanthus scalbiensis* van Konijnenburg-van Cittert

Drawings of selected sections of microsporophylls from cone V.58839, illustrated also in Pl. 5, figs 2–5; all ×10. The drawings show the plant substance exposed by grinding, the figures being depths in μm below the starting level. The top three rows show tangential sections of three sporophylls. At 100 μm there is some of the tissue of the heads, by 190 μm the lowest shows its keel, and by 340 μm all three show keels and walls of the pollen sacs. By 620 μm the stalk has narrowed and the pollen sacs have ended; at 850 μm and at 900 μm the stalks (picked out by arrows) are merging with the ridges on the cone axis. The bottom row shows a series of approximately radial sections through a single sporophyll; at 750–800 μm most of the stalk is included whilst at 830 μm the section is nearly median through the head. The pollen sacs are not seen well.
reticulum enclosing lumina 1 \(\mu\)m wide. Wall of distal part much thinner and only faintly granular, no definite aperture apparent. Wall of saccus just over 1 \(\mu\)m thick, reticulate, muri formed by rows of granules 1 \(\mu\)m wide enclosing lumina up to 2 \(\mu\)m wide, but at root of saccus meshes wider and considerably elongated.

**Dimensions** of pollen. In equatorial view breadth of grain with expanded corpus 64–75 \(\mu\)m, with sulcate corpus 60–69 \(\mu\)m. Breadth of expanded corpus 45 \(\mu\)m, of sulcate corpus 35 \(\mu\)m. Saccus length (from edge of corpus) 22–30 \(\mu\)m, breadth 18–28 \(\mu\)m. In polar or in end view corpus thickness (front to back) 42–50 \(\mu\)m. Saccus from end to end 40–50 \(\mu\)m.

**Holotype.** No. 2966, University of Utrecht.

**Discussion** of pollen dimensions. The measurements just given refer to selected grains isolated from cones and also to others dispersed in the matrix of the shoots and cones (where they may be the commonest miospore). No average is given because a great many grains seem to have had a dimension reduced in preservation and any average would depend on which grains were accepted for measurement. An average would be near the lower figure of the pairs given above.

Dimensions seem to have been diminished in the following three ways; I have no evidence that compression ever increases a dimension.

1. Compression in the rock matrix. Compression is complete, reducing the compressed interior dimension to nil. Grains lie (and are thus compressed) in all orientations, equatorial, polar, end to end without obvious preference, but the equatorial view is the easiest to recognize and the end view the hardest. Nearly all grains are in mixed orientations and this causes moderate loss in one or another dimension.
2. Crumpling. Many grains have crumpled folds and these may be anywhere on the wall though particularly on the sacci. The cause of these folds is unknown but their effect is to diminish the dimension across a fold (Harris 1974).
3. Collapse of the distal pole from strongly convex, through flat, to strongly concave forming a deep sulcus. This may have happened before preservation and more than half the grains are sulcate. With a deep sulcus, the sacci are drawn together and may touch, and the width of the whole grain is reduced; the height of the corpus is also much reduced. At the same time a fold commonly develops in the distal hemisphere near where it joins the proximal hemisphere and this too diminishes corpus length.

I believe that apart from the effects of distortion, the dimensions would be rather uniform. The figures given by van Konijnenburg-van Cittert (1971) are remarkably similar considering that she had only nine grains, some awkwardly orientated. However, her figures are smaller for total breadth and for corpus breadth.

**General discussion.** *Pityanthus scalbiensis* was originally known from three specimens. The first seen was crudely sketched by me but neither named nor described and its only apparent interest was that it occurred on the same block as the holotype of *C. blackii* (Harris 1952: text-fig. 4 e). Van Konijnenburg-van Cittert had two specimens, her holotype from the Scalby Ness *Ginkgo* Bed associated with *C. blackii* and the second from Black’s level bedded series, also with *C. blackii*. Both cones yielded a few of their characteristic pollen grains. Various collectors have since found *P. scalbiensis* at different points at Scalby Ness, sometimes in abundance and often associated with *C. blackii*. The Scalby Ness plant bed (*Ginkgo huttoni* Bed) was a river channel
Fig. 40. *Pityanthus scalbiensis* van Konijnenburg-van Cittert

A, restoration of cone axis and two microsporophylls, ×20. B, pollen masses representing pollen sacs macerated out of the immature cone shown in G; V.59061a–c, coordinates not recorded, ×10. C–F, pollen grains from this cone, V.59061c, ×400. G, immature male cone, isolated and partly macerated; only the clearer sporophyll heads are drawn; ×8. H, I, delicate cuticle probably from sporophyll heads, I has a possible stoma; V.59062, ×400. J–Q, dispersed pollen grains associated with *C. blackii* in Black’s (1934) Level Bedded Series, preserved in various planes of compression; V.59042–51, exact slides and coordinates not recorded; all ×400.
providing many layers with different assemblages of plants and in only a few of these is C. blackii abundant or even present at all.

Many of the Scalby cones are empty or have only stray pollen but some, although of almost full size, still have intact pollen sacs containing compressed masses of pollen. The grains were hard to separate undamaged but at the edges of the masses they showed their form clearly enough and served to identify the more satisfactorily seen grains which either adhere separately to the cones or occur in the matrix.

The morphology of the cone scales was worked out from certain empty cones in which silt had penetrated between the microsporophylls and also into the open pollen sacs. On compression the plant tissue formed a very thin film of coal whilst the silt compressed only moderately. The rock was embedded and permeated with araldite and the structure displayed in serial sections by grinding.

In Cayton Bay some small immature male cones were found with C. blackii shoots and seeds. Their main value is in their association, but they also gave pollen grains, ranging from normal ones down to oval bodies about 25 μm wide with folds that doubtfully represent sacs. As their walls are about 1 μm thick I suppose they are grains that have developed abnormally after the detachment of the cone rather than being strictly immature, an idea discussed by Harris (1973).

P. scalbiensis is discussed in relation to the whole plant, Scarburgia blackii, on p. 92. We do not know the shoots that bore these male cones but if they are preserved it should be possible to recognize them by the scars of the fallen cones, about as large as a foliage leaf. I presume the fertile shoots were thicker than many C. blackii twigs.

Comparison. The Indian cone Masulostrubus rajmahalensis Rao has similar pollen but is narrower. It was redescribed by Rao & Bose (1971) as Podostrobus rajmahalensis.

Genus SCARBURGIA nov.

Diagnosis. Elongated seed-bearing cone, axis slender. Fertile appendages borne sparsely and singly on all sides, each composed of a short stalk expanding into a pointed triangular scale. A single rounded seed borne on upper surface of scale and partly covered by scale tissue, its obtusely pointed micropylar part free and pointing towards the axis, integument including a stone surrounded by a thin fleshy. Five cuticles present: outermost (cover cuticle) covering the scale and overlapping the seed, outer cuticle of integument, integument inner cuticle lining micropyle and extending to base of seed, nucellus forming a beak under the micropyle where pollen (Pityanthus) is received, and megaspore membrane. Stone of seed composed of small cells, intercellular spaces between cells occupied by a maceration-resistant resin which forms a three-dimensional network of fine threads.

Type species. Scarburgia hillii, the only species.

Name. From Scarborough, a town near to the localities where this cone was found.

I have termed the outer layer of cuticle which partly overlaps the integument the ‘cover cuticle’ and I believe it corresponds to the epimatium of Recent podocarps (where it is widely held to represent the ovuliferous scale). However, since the word ‘epimatium’ is used for podocarps alone its use in describing Scarburgia would prejudge its taxonomic position.
Fig. 41. Scarburgia hillii sp. nov.

A, cone transfer shown in Pl. 5, figs 10, 12, showing axis and cone scales; V.58963, ×4. B–D, three half-seeds in sandstone which occupies the interior, fragments of coal still remaining shown darker. To the right and below each drawing are imaginary longitudinal and transverse sections to show the contour; sandstone shaded, coal black, dotted line showing where coal is presumed to have been originally but has crumbled away. V.58841, ×20. E, outline of compressed seed subsequently macerated; on maceration it broke into five fragments a–e of which d was lost; V.59065a–e, ×10. F, interior membranes from seed in E; V.59065c, d, ×10 approx. G, megaspore and base of nucellar beak; V.59063, ×20. H, complete megaspore and nucellus, V.59067b, ×20. I, seed megaspore and nucellus, V.59064, ×20. J, top fragment of F; V.59065c, ×50; pollen grains outlined. K, top of L showing elongated nucellar cells and broad cells of integument lining, V.59064, ×400. L, top of I showing nucellus overlapped by integument lining, V.59064, ×50. In F–L the megaspore is coarsely stippled. Figs A–D, Scalby Ness Ginkgo Bed; E–L, Cayton Bay, Upper Deltaic fallen block. See also Plate 6.
**Scarburia hillii** sp. nov.
Figs 41, 42; Pl. 5, figs 10–17; Pl. 6

**Diagnosis.** Mature cone exceeding 5 cm in length, axis 2 mm thick below but tapering to under 1 mm. Substance of axis rather delicate, cuticle rather thin, cells rectangular, surface longitudinally striated. Appendages at mature stage imperfectly known, in immature cone comprising a stalk about 2 mm long and 0·5 mm thick, expanding into scale 2 mm long and 2 mm broad at its base. Margins and apex of scale thin but substance about 0·5 mm thick in middle region around the seed. Point of scale about 1 mm long.

At mature stage seed-stone rounded, about 2 mm wide. Cavity in seed-stone rounded below but becoming pointed towards micropyle, in section probably round below but flatter towards micropyle. Cover ending transversely to long axis of its cells, cuticle thick, cells about 40 μm × 20 μm, their anticlinal walls very unevenly thickened. Outer cuticle of integument thick, cells either isodiametric or elongated to 30 μm × 15 μm; anticlinal walls projecting strongly inwards but on surface bordered by broad and often ill-defined thickenings; surface wall flat, vaguely mottled. Resin spindles 80 μm × 10 μm present between this cuticle and stone. Inner cuticle of integument very thin indeed except in micropylar region, its cells often isodiametric with finely marked continuous walls. Nucellus thin except in beak, its cuticle becoming very delicate below; surface cells elongated, anticlinal walls finely marked, moniliform. Megaspore membrane nearly 4 μm thick but thinner near micropyle, composed of thin continuous outer layer and inner layer of inwardly pointing rods.

**Holotype.** V.58842. Pl. 5, fig. 17.

**Name.** After Dr Christopher R. Hill, who found the Yons Nab material.

**Discussion.** The material is from beds of Upper Deltaic age at Yons Nab and Scalby Ness.

1. A fallen block of sandstone at Yons Nab in Cayton Bay, representing a previously unknown bed, was found and collected by C. R. Hill in the winter of 1972 and subsequently by me. Plant fragments occurred in thin silts between thicker sandstone layers and the total fossiliferous surface examined may have been 2 m². The richest surfaces were strewn with *Cyparisidium blackii* and along with these a few immature *Pityanthus scalbiensis* cones and *Scarburia* seeds. About six ill-preserved seeds occurred scattered and there was a close group of eight suggesting an elongated cone though there was no visible connection between them. All the seeds had suffered in contact with the matrix but the interior cuticles of some were good. In the end all these seeds were macerated. Apart from these fossils, held to belong to one plant, there were many fragments of fusain, not studied, but little else; merely a leaf fragment of *Baiera furcata* (Lindley & Hutton) Braun and one megaspore, *Trileites murrayi* (Harris) Marcinkiewicz. Both *B. furcata* and *T. murrayi* are widespread in Yorkshire.

2. At Scalby Ness, where I had previously collected a few scattered seeds, a fresh cliff fall collected by K. Allen gave many remarkably rich layers of the Scalby Ness flora. As usual the assemblages on different bedding planes were different and only some gave material of *C. blackii* and its reproductive organs. The significant bedding planes either gave numerous specimens of *C. blackii* with many empty *P. scalbiensis* cones or else many specimens of *C. blackii* with seeds of *Scarburia*. Only one block showed all three. All the fossils are poorly preserved in fine detail, as though considerable oxidative decay had occurred after deposition and also some recent weathering which had caused the coaly substance to shrink and crack. Two of the blocks, for example, show the seeds arranged merely in elongated groups. Block V.58842 (Pl. 5, fig. 17) has
Fig. 42. Scarburgia hillii sp. nov.

A, details of seed cuticles shown in Fig. 41 F, J, to show pollen grains (stippled) in relation to cuticles; V.59065c, × 300. Many cell outlines are too obscure to follow and those of the upper layer are merely sketched. B, imaginary section in plane x-x of A; i, lining cuticle of integument forming base of micropyle at top; p, pollen grains; n, cuticles of nucellar beak. C, sketch of megaspore membrane at a folded edge, showing inward pointing rods, V.59064, × 1000. D, network released by maceration of stone; V.59065e, × 400. E, surface of cover cuticle, showing uneven anticlinal walls, V.59072c, × 400. F, margin of cover cuticle continued inwards as a delicate membrane; V.59072c, × 400. G, cover cuticle from another seed, anticlinal walls obscure; V.59067a, × 400. H, cells of nucellar beak (one layer drawn only), from seed shown in Fig. 41 G; V.59063, × 400. I, integument outer cuticle, V.59067a, × 400. J, pollen grains in micropyle shown in A, overlying and underlying cells omitted by focusing; V.59065e, × 400. K, top of integument showing bent and shrivelled micropylar papilla, V.59064, × 20. L, cover cuticle with possible stomata, V.59066, × 200. See also Plate 6.
the holotype, a group of about 30 seeds, and also groups of 12, 10, 7 and 5 (though some of these smaller groups may belong to a larger group). Apart from these there are just two seeds not in any group. The holotype group has an axis along its middle suggesting a cone, but the smaller groups have no axis. The other block, V.58843, also has a central axis but the group is less convincingly a cone because the block has many scattered seeds. Other blocks merely show scattered seeds or half seed stones. I presume the holotype was deposited as an intact cone but underwent oxidative decay, so that scarcely anything remains except robust seed stones and a trace of the axis. Associated fern fragments are barely discernible.

Two other smaller cones from Scalby, however, are rather better preserved, showing the seed scales undoubtedly connected to the cone axis (Fig. 41 a; Pl. 5, figs 10–14). They were collected some years ago but only reached me very recently, having been examined and studied by others. I saw them as balsam transfers prepared by Miss Diana Lacey working with Dr K. Allen. Later they were examined by Dr van Konijnenburg-van Cittert who prepared fragments of the scale and megaspore cuticles and forwarded the transfers and preparations to me. I made no further preparations.

In all the specimens the outer cuticles of the seed, particularly the cover cuticle, have suffered damage from contact with the matrix; they deserve study from better specimens. Neither the seed base nor apex has been recognized.

The seed stone forms a thick mass of coal even in ill-preserved seeds and when well-preserved yields a network of threads representing intercellular spaces between isodiametric stone cells. This network is like that of *Allicospermum retemirum* Harris (1944), known also from Poland (Reymanówna 1968), and is less resistant than cuticle. Experiments suggest that it may represent oil which has escaped from the endosperm and entered and then hardened in the intercellular spaces of the stone. I succeeded in producing such a net by baking a walnut at about 350°C and then macerating the charred shell, but separate shells of this and other nuts yielded no net. When poorly preserved the net breaks up in ammonia into minute separate threads connected to a node, looking like little nails. (I do not of course suggest that the Jurassic plants were heated, at any stage in their preservation.)

Some of the Yons Nab seeds gave well-preserved inner cuticles though mostly in small pieces. The nucellar beak has a truncate end where its cuticle ceases and bends inwards, and this is where two pollen grains were found (i.e. not in any deep pollen chamber). Although seen through a number of layers of cuticle these grains were remarkably plain. The upper grain has its sacci spread out but each is somewhat crumpled, the lower having one sacculus over the other so that the corpus is scarcely seen. Both grains agree in their fine details with *Pityanthus scalbiensis* pollen and similarly distorted dispersed grains are frequent in the Upper Deltaic black shales.

**Classification.** The shoot, the male cone and the female cone taken separately are classifiable only with doubt, but taken together there is a strong case for assigning them to the Podocarpaceae. I name the whole plant *Scarburgia blackii* but emphasize that it is essentially a hypothesis, for no specimen shows continuity. I emphasize also that there is additional uncertainty about how the female cone is organized and the discussion below depends both on taking the organs together and on the essential accuracy of the description of the cone.

The shoot, *Cyparisidium blackii*, has remarkably small leaves, and it seems true that small-leaved conifers in general show taxonomic characters in their foliage less strongly than do their larger-leaved allies. I can see no resemblance with any living families except certain Podocarpaceae and Taxodiaceae with exceptionally small leaves. The shoot of *Dacrydium franklinii*
Hook. fil. is similar in aspect except that the fossil is on a smaller scale, whilst the cuticle of the minute leaves of Dacrydium colensoi Hook. agrees in its scattered stomata with rounded subsidiary cell groups. Normal podocarps have files of stomata with elongated cell groups. No taxodiaceous shoot known to me is quite as similar. I see no agreement with any other family, particularly not with the Pinaceae.

The male cone and pollen, Pityanthus scalbiensis, fits both the Podocarpaceae and the Pinaceae. The morphology of the cone is the same in these two families and about half of each family have bisaccate pollen grains. In no living conifer family other than these two do bisaccate grains occur, though they are of course well known in other Mesozoic gymnosperms. On the whole the Pinaceae have larger grains but I can find no general difference, Podocarpus andinus Poepp. for example producing grains over 100 $\mu$m wide. The pollen of Pityanthus scalbiensis is of a size frequent in both families. Although Tertiary bisaccate grains resembling particular living species are placed in one or other family with confidence, I feel no confidence in such identification of a bisaccate Jurassic grain.

Certain other kinds of pollen grains are exclusive to one or other family, for instance trisaccate grains to the podocarps. One of the original obscurely-seen grains of P. scalbiensis was interpreted as possibly trisaccate by van Konijnenburg-van Cittert (1971: 68) but I have seen no definitely trisaccate grain amongst a very large number in the present material, either from cones or dispersed.

The female cone and seed, Scarburgia hillii, is taxonomically the most important organ even though the morphology of the scale is incompletely known. It is a long and lax cone composed of stalked cone scales, each forming a cover round a single ovule. In this it agrees with podocarp cones but with nothing else living. It differs however from any modern podocarp cone in being longer and in having more numerous scales. Cephalotaxus and the Taxaceae agree in producing exposed ovules, but in no other character, whilst the Upper Triassic conifer Stachyotaxus has a similar lax cone, though the scales differ in bearing two ovules, and it has round pollen grains without sacci.

Today the Podocarpaceae is almost limited to the southern hemisphere and Florin (1940, 1963), who considered that it had always been a southern hemisphere family, dismissed the northern hemisphere records. But since then many dispersed Podocarp-like grains have been reported in the Mesozoic and Tertiary, particularly from the USSR. Krasilov (1967) described convincing podocarp shoots and ovules from the Lower Cretaceous of eastern Siberia and in 1974 reviewed the occurrence of the family in the Cretaceous and Tertiary of the northern hemisphere. The present plant may thus be a member of a well-represented family in the north. It is of special interest in being of Middle Jurassic (Bathonian) age. Its fairly large cone is better developed than in any living podocarp and this perhaps suggests that the modern cones, which often comprise just one or two cone scales, may be reduced.

**Genus PITYOCLADUS** Seward (shoot and leaf)  
with **SCHIZOLEPIS** C. F. W. Braun (female cone)

**Introduction.** *Pityocladus* is a genus of coniferous shoots. Its woody long shoots bear foliage leaves sparsely and short shoots which are crowded with leaves. The leaves (*Pityophyllum*) attributed to the shoots are flat, linear and single-veined and they readily fell off from both the long shoots and the short ones. As explained below the genus was poorly based and the foliage leaves had not been seen in continuity with typical shoots. Their attachment in the Yorkshire material is merely an inference based on impressive association and also on points
of structural agreement, particularly with the bud scales that remain attached to the dwarf shoots. However, a specimen of *Pityocladus ferganensis* Turutanova-Ketova from the USSR (1963: 276; pl. 18, fig. 1) retains the leaves on its dwarf shoots. It looks much as I imagine the holotype of *P. scarburgensis* must have looked before it dropped its leaves.

**Genus PITYOCLADUS** Seward 1919

**Diagnosis.** Long shoots slender and woody, bearing caducous foliage leaves and persistent short shoots, short shoots bearing bud scales and foliage leaves in a crowded helix. Foliage leaves simple, linear, single-veined; bud scales small, persistent.

**First described species.** *P. longifolius* (Nathorst) Seward 1919: 377, fig. 775, selected by Andrews 1970; previously *Cycadites longifolius* Nathorst 1876, then *Taxites longifolius* (Nathorst) Nathorst 1878.

**Discussion.** *Pityocladus* is an unsatisfactorily-based genus. Nathorst (1897: 62, 65) put it forward not as a generic name but as a designation of part of *Pinites* Endlicher. Seward (1919: 377) was the first to treat it as a generic name, attributing it to Nathorst, though Andrews (1955) rightly names Seward as the author. Seward gave no diagnosis and named no type species and indeed thought it would prove heterogeneous. At the same time he instituted *Pityites* for specimens which in his judgement showed more evidence of affinity with the Pinaceae. Andrews selected *Pityocladus longifolius* (Nathorst) Seward as the type species and this species too is unsatisfactorily based. The original leaf fragments from Pälslö in Sweden which Nathorst (1876: 47; pl. 13, figs 1–3) described as *Cycadites longifolius* have a single vein, are 4–5 mm wide in the middle and taper to the apex and probably also to the base. Later Nathorst (1878) described rather similar leaves from Höganäs as *Taxites longifolius* and Möller (1903) described others from Bornholm as *Pityophyllum longifolius*. The name *longifolius* Nathorst has often been used for elongated simple leaves.

The situation was complicated by Seward's description of another Swedish specimen as *Pityocladus longifolius* (Nathorst) (Seward 1919: 378, text-fig. 775). This is a detached dwarf shoot bearing the lower parts of linear leaves which differ from Nathorst's original *Cycadites longifolius* in having parallel sides. The specimen suggests to me the detached dwarf shoots with persistent leaves of one of the Czekanowskiales. Not one of these specimens provides any microscopic details which might unify the series.

Seward dealt also with *Pityocladus schenkii*, the shoot and leaves that Schenk attributed to *Schizolepis braunii*, and with *P. nathorstii*, the shoot and leaves that Nathorst attributed to *S. follinii*. Solms-Laublich (1891: 70) questioned this attribution and Nathorst (1897: 38) accepted his objection. I discuss these species below. *Pityocladus kobukensis* Seward (1911) is based on material comparable with that described here, a long woody shoot bearing short shoots, both kinds of shoot denuded but associated with detached, linear single-veined leaves.

**Pityocladus scarburgensis** sp. nov.

Figs 43, 44; Pl. 4, fig. 13

1880 *Schizolepis* sp.; Nathorst: 28. (Reference to present leaves and stem)
1897 *Schizolepis* sp.; Nathorst: 38.

**Diagnosis.** Long shoot slender, bearing occasional long shoots and more numerous short shoots. Main shoot (in part known) about 2 mm wide, showing a woody core flanked by a rind
about 0.3 mm wide. Surface of long shoot glabrous but with scattered, slightly raised, leaf scars and also with more numerous lenticels. Leaf scars rounded, 0.3–0.4 mm wide, each with one central vascular print. Most scars distant and each subtending short shoot but in regions of slow growth more crowded and without short shoots. (No scale leaves or scale leaf scars observed on long shoot.)

Cuticles of long shoot moderately thick but fragile, showing isodiametric cells about 50 μm

Fig. 43. *Pityocladus scarburgensis* sp. nov.
A, B, two portions of a single leaf fragment from block no. 2. × 20. A, at 2 cm above the base, the coal at the top having partly flaked off to reveal the imprint. B, the leaf base. C, portion of leaf with rock imprint beneath, block no. 270. × 20. The imaginary section shows the contour of the two surfaces, vertical scale exaggerated. D, twisted leaf in which twisting has scarcely altered the apparent width; imprint at top, block no. 270. × 20. E, leaf from same block, × 20. F, portion of *holotype* where leaf scars are crowded and there are no dwarf shoots. The small lumps are lenticels. Block no. 278. × 10. G, side shoot with a dwarf shoot, from *holotype*, × 10. H, J, top and bottom of leaf shown in I, × 20. I, leaf from block no. 1, × 2. K, leaf apex, lower part merely outlined; block no. 1, × 20. All specimens are in the Section for Palaeobotany, Riksmuseum, Stockholm.
wide (stomata and hair bases not observed). Dwarf shoot covered with small triangular bud scales about 0.7 mm long and 0.5 mm broad in part exposed. Bud scales robust and thick, with raised keel; cuticles delicate, about 1 μm thick on one side and thinner on the other. On thicker side cells mostly elongated, often 50 μm × 20 μm, anticlinal walls straight, marked by a fine ridge which may be continuous or interrupted or moniliform. Surface wall finely mottled or with longitudinal striations. Stomata few, orientated longitudinally, elongated; usually with single elongated subsidiary cell on each side, polar subsidiary cells unspecialized. Stomatal pit long and narrow, poles of guard cells exposed, thinly cutinized. Aperture region often slightly thicker and marked off from poles. (Trichomes absent.)

Length of foliage leaf probably much exceeding 50 mm, width about 1.0 mm in middle and distal parts (0.6–1.1 mm); towards base tapering gradually to 0.6 or 0.3 mm; towards apex narrowing slightly, obtusely pointed, not mucronate. Leaf apparently stiff, probably round in section near base but becoming flatter above; margins rounded (neither angular nor scarios). Leaf substance thick, especially near base. Midrib scarcely visible near leaf base but becoming better defined distally, appearing as a ridge on presumed lower surface; on upper surface flat though bordered by fine ridges. Margins most often flat but sometimes slightly depressed towards lower surface.

Cuticle of leaf about 1 μm thick; very fragile (and imperfectly known from minute fragments). In some leaves structure apparently uniform over whole surface; stomata sparsely scattered but always longitudinal, not forming files or bands. Epidermal cells elongated, uniform, typically 50–70 μm long × 10–15 μm wide; lateral and end walls straight, very finely marked and often indistinct; interrupted. End walls mostly oblique but sometimes transverse when cells form files. In occasional preparations (near apex ?) stomata mainly on one surface, rather frequent between midrib and margins but sparse elsewhere.

**Holotype.** Specimen no. 278, Section for Palaeobotany, Riksmuseum, Stockholm; Fig. 43 f, g; Pl. 4, fig. 13.

**Name.** From the town of Scarborough.

**Discussion.** All the material is in Stockholm and comes from a locality on the beach between Scarborough and White Nab. Almost all of it was collected by Nathorst but a little also by Halle a few years later. We do not know the exact position of this ‘New Layer’ but from its location it must be in the upper part of the Upper Deltaic. The rock agrees with Black’s ‘Level Bedded Series’.

The material consists of a branched shoot and a large number of leaves both associated with the shoot and also on other pieces of rock. There is also a detached short shoot. The block bearing the branched shoot, about 50 cm² in area, has 33 fragments of detached leaves and just four minute scraps of indeterminable plant material, nothing else. The fairly large collection from this ‘New Layer’ provided good leaves of *Baiera furcata* (mentioned in Harris, Millington & Miller 1974: 34) and in addition the five cone scales of *Schizolepis* described below. Relative abundance is illustrated by the small blocks bearing *Schizolepis* which together have an area of about 100 cm² and show parts of 74 *Pityophyllum* leaves but in addition only irrelevant plant scraps, one fern pinnule and one twig of *Cyparissidium blackii*. *Pityocladus*, *Pityophyllum* and *Schizolepis* are peculiar to this one bed in Yorkshire, but the associated species are relatively widespread. There seems nothing in the bed which could be confused with specimens of these three.

The matrix, a black oil-rich shale, was evidently difficult to collect in large pieces, and
breakage during collection rather than before deposition explains why there is no complete leaf. I estimate the length at over 10 cm, possibly 20 cm, from the small number of extremities in relation to the total length of fragments. The leaves are unusual in having apparently undergone no oxidative decay and their cuticles, considering their extreme delicacy, are well preserved. The leaves show none of the downward collapse into the underlying matrix of the kind observed by Walton (1936), I presume because they were in an organic slime which compressed more than the plant tissues. I consider the fossil leaves show their original shape in section apart from a general reduction in the vertical direction and that the midrib projected downwards when first buried, as it does in the fossil. Occasional leaves which were twisted during deposition, the twist being shown by the files of epidermal cells, indicate that most of the leaf was flat though it was nearly as thick as broad near its base where the midrib becomes inconspicuous. At the leaf margins numerous files of crushed cells (in cuticle preparations) indicate an originally rounded
edge rather than a sharply angular one. The surface often shows transverse bars due to tissues beneath the epidermis which may therefore have been transversely elongated transfusion mesophyll.

The long shoot shows two zones of crowded scars without short shoots (? regions of slow growth) and then zones of distant leaf scars and axillary short shoots. The stem is just over 2 mm wide before the first zone of slow growth, then just under 2 mm wide and at the tip about 1.5 mm. Bits of dwarf shoots detached when they were degaged from matrix gave bud scale cuticles which served to identify the detached dwarf shoot. This in turn gave rather better preparations of bud scales which provided some evidence for linking the detached foliage leaves with the _Pityoclados_ stem.

The prime reason why I attribute the detached Yorkshire leaf fragments to this denuded shoot is their association, and no doubt Nathorst used the same evidence. As mentioned below, there is some evidence too of association elsewhere. There is also supporting evidence from agreement in structure. The base of the leaf matches the leaf scar on the long shoot and the scar has a single vascular print. Bud scales on the dwarf shoot gave cuticle preparations which agree in their extreme delicacy, similar epidermal cells and in their similar and unusual stomata. The guard cells are almost fully exposed, their poles being on the surface. This is unlike the stomata of any conifer foliage leaf known to me but more like the stoma of the cycad _Stangeria_ and of some pteridosperms. I have, however, seen a few similar stomata on _Pinus sylvestris_ cotyledons. The bud scale stomata are nearly twice as large as those of the foliage leaf, a difference comparable to that which occurs in _Larix_. The stomata of the foliage leaf are small, those of the ovuliferous scale and bract scale rather similar but larger whilst the minute bud scales have a very few much larger stomata.

**Comparison.** The resemblance to Schenk's (1867: pl. 44, fig. 4) figure of a leafy shoot which he named _Schizolepis braunii_ is striking but superficial. His attribution was widely accepted and Seward (1919) renamed the shoot _Pityoclados schenki_. However, although Schenk's specimen shown in this figure has been lost, Kräusel (1958) recognized it as the counterpart of the specimen that Ettingshausen had described as _Halochloris baruthina_. It is poorly preserved, but Kräusel found that some of its leaves fork and renamed it _Sphenobaea baruthina_. It is thus most unlikely that it has anything to do with _Schizolepis_ and this cuts out Schenk's other figures of shoots and leaves from consideration as evidence, precluding identification of the Yorkshire specimens as _Pityoclados schenki_.

The three stems which Nathorst (1876) attributed to _Schizolepis follinii_ seem to be heterogeneous and I doubt if any of them really belongs to it. The one shown in his pl. 14, fig. 7 (determined with doubt) is a fragment of a large, denuded branch of an unknown plant. That in pl. 14, fig. 8 is a shoot covered and concealed by leaves about 5 cm long. They taper evenly from near the base to the apex and I suspect it is just an unusually large shoot of what Florin (1958) named _Camptophyllum schimperi_. The third (pl. 15, fig. 12) is a denuded axis with marks which may be leaf scars in whorls.

Yet although Nathorst's three stems have no link with _Schizolepis_, I suspect that the separate but associated leaves do belong to it. The material is from Pålssjö, an exposure no longer available. The best slab (1876: pl. 14, fig. 9) shows many linear leaves and this slab was redrawn, better, I think, by Saporta (1884: pl. 195, figs 1, 2) but unfortunately the original specimen is missing from the Stockholm collection. However, Professor Lundblad sent me some unfigured leaf fragments and these agree fully with the Yorkshire leaves in texture and in their extremely delicate cuticle. They probably had similar epidermal cells and stomata.
Authors figuring *Schizolepis* do not as a rule figure associated leaves and these particular leaves are not of a kind that seems interesting. However, Corsin (1973: 64), in a small Liassic flora from northern France, had two typical *Schizolepis* cone scales and with them noted linear needle leaves like *Pityophyllum* (perhaps included in his 1973: pl. 1, fig. A). Many floras described from Russia, Siberia, China and Japan include figured specimens of a *Schizolepis* species and references either figure leaves of a *Pityophyllum* or mention the occurrence of such leaves, but there is no statement that they occur together and I do not use these records as evidence (particularly because 'Pityophyllum' without details is an uncertain determination).

Schenk’s error discourages speculation about what kind of leaves may be associated with *Schizolepis* cones in Franconia but it would be interesting if leaves like those of *P. scarburgensis* should prove to occur on the same slabs. Roselt (1958) mentioned linear leaves 15 cm long but may have had ‘*Halochloris baruthina*’ in mind. Gothan-Berlin (1914: 160; pl. 26, fig. 4) described similar leaves as *Schizolepis brauni* but mentions no associated cone.

**Genus SCHIZOLEPIS** C. F. W. Braun 1847

**Diagnosis** (translated from Roselt 1958: 389 for *S. liasokeuperianus*). Female cones, cylindrical when mature, 1-0-2.5 cm broad, covered with helically arranged seed scale complexes. These are about 10-15 mm long, narrowed into a stalk below; in the upper third divided into two rounded or pointed lobes. Bract scale probably small, rounded and united with the seed scale complex. Seeds two, one on the surface near base of each rounded or triangular lobe. Leaves of twigs attributed to *Schizolepis* needle-shaped, up to 15 cm long, helically arranged, distantly attached on the long shoot but crowded on the short shoots. (Roselt points out that there was uncertainty about the ovules, the bract scale and also the attribution of the foliage.)

**Type species.** *Schizolepis liasokeuperianus* C. F. W. Braun 1847.

**Discussion.** The type species was first called *Voltzia schizolepis* Braun (1846: 1258), renamed *Schizolepis liasokeuperianus* by Braun (1847: 86), in erecting the genus, with a brief diagnosis. It was further renamed *Schizolepis brauni* by Schenk (1867), with full description and figures. This is the name that has been most used until recently. Little has been learnt about the morphology of *Schizolepis* since Schenk’s work, though we now have numerous records of similar cones or detached scales from the Mesozoic of Europe and northern Asia. We can now add the following few points to the diagnosis.

Bract scale delicate, free to its base but closely pressed to ovuliferous scale. Whole seed scale complex (ovuliferous scale with bract scale and seeds) readily falling as one unit from cone; ovules with micropyles pointing towards cone axis, chalazal region embedded in scale tissue, upper surface of scale not becoming detached to form a wing to each seed. Outer part of ovuliferous scale rather thin but including strands of longitudinal fibres, slightly concave on upper side. Stomata of leaves, scale leaves of dwarf shoot and ovuliferous scale monocyclic, with long very shallow pit, poles of guard cells reaching surface.

The taxonomic affinity of *Schizolepis* is open, even with the present conclusion that certain leafy stems belong to the same plant as the cones. Many authors have thought of relationship with the Pinaceae, and both Nathorst (1897: 38) and Seward (1919: 377) mention *Larix*. The resemblance of *Larix* shoots to *Pityocladus* is striking and the present work somewhat extends this though also demonstrating differences. The leaf differs from that of any living pineaceous conifer in its scattered stomata and it is unusual also in its very long stomatal pits with the guard cell poles exposed.
The female cone scales (seed-scale complex) agree with those of the Pinaceae in their separate delicate scales and the pair of ovules which point towards the axis. The forking of the ovuliferous scale however is different and a more serious difference is that there is no membranous wing above the seed. The pinaceous wing consists of the epidermal and hypodermal tissues of the ovuliferous scale, and, although it is not abscissed from the scale until late in development, its outline is easily recognizable when the scales are immature. Nothing of the sort could be discerned in the Yorkshire Schizolepis scales nor has it been figured in Schizolepis scales from other regions. Some pinaceous cones like Cedrus and Abies do drop their whole cone scales but each winged seed falls separately. So far as we know the two-seeded Schizolepis cone scale was dispersed as a unit.

Kräusel (1959) compares S. liasokeuperianus with various older genera—Voltzia (in which it was originally placed), Glyptolepis, Ulmannia and with Heer’s (1876) Schizolepis permensis.

We do not know the male cone of Schizolepis. Schenk (1867) thought that Stachypteris preslei belonged to it but nearly everyone has preferred to suppose that it belongs to Baiera, because of its morphology; see for example Kräusel (1959: 110).

**Schizolepis liasokeuperianus** C. F. W. Braun
Figs 45–47; Pl. 4, figs 1–8

The following are references to cones or cone scales identified as *S. liasokeuperianus* and as *S. follinitii*, together with a few similar ones under other names, but not necessarily identical with the Yorkshire specimens.

1846 Volztia schizolepis Braun: 1258. (Name)
1847 Schizolepis liasokeuperianus Braun: 86. (Name and diagnosis)
1867 Schizolepis Braunii Schenk: 179; pl. 44, figs 5–8 (figs 1–4 are stems and leaves discussed above on p. 97)
1876 Schizolepis Folliniti Nathorst (in part): 57–62; pl. 15, figs 3, 4, 9. (Excluding the leaves and stems in pl. 14, figs 7, 8 and the cones in pl. 15, figs 5, 8, 10, 12; see p. 103 below.) According to Nathorst (1908: 5) the cone figured by him in 1876; pl. 14, fig. 1 as Palysia braunii should be included.
1880 Schizolepis sp.; Nathorst: 28. (Reference to the present Yorkshire specimens)
1884 Schizolepis Braunii Schenk; Saporta: 505; pl. 194, figs 1–4. (Schenk’s figures of cones repeated but figures of shoots are excluded)
1884 Schizolepis Folliniti Nathorst; Saporta: 507; pl. 194, figs 5–7, 7a. (Fig. 5 is a copy from Nathorst; figs 6, 7, 7a are new. Other figures are of leaves)
1890 Schizolepis Braunii Schenk; Schimper & Schenk: 306; pl. 212a–c.
1891 Schizolepis Braunii Schenk and S. Folliniti Nathorst; Solms-Laubach: 70. (Names limited to cones and cone scales)
1892 Schizolepis Folliniti Nathorst; Raciborski: 355; pl. 2, figs 1, 20a. (Cone scale, Lower Jurassic of Poland)
1897 Schizolepis sp.; Nathorst: 38. (Reference to the present Yorkshire specimens)
1928 Schizolepis Braunii Schenk; Makarewiczówna: 30; pl. 2 (11), fig. 8. (Cone scale, Lias of Poland)
1944 Schizolepis folliniti Nathorst; Florin: 495; pl. 181–2, fig. 18. (Bract scale demonstrated)
1950 Schizolepis spp. Turutanova-Ketova: 53–68; pl. 8, figs 113, 114. (See Krishtofovich 1957)
1957 Schizolepis sp. (of Turutanova-Ketova); Krishtofovich: 359, fig. 354, 2. (Specimens redrawn)
1958 Schizolepis liasokeuperianus Braun and S. folliniti Nathorst; Roselt: 389. (Discussion)
1959 Schizolepis liasokeuperiana Braun; Kräusel: 109; pl. 5, figs 22–25; text-fig. 5a, b. (Cone scales). Possibly cone on p. 112; pl. 4, figs 18, 19; text-fig. 6.
1962 Schizolepis folliniti Nathorst; Prinada: 258, 260; pl. 18, fig. 1; text-fig. 68. (Cone, eastern Siberia)
1973 Schizolepis liasokeuperiana Braun; Corsin: 63, text-fig. 3 A, B; pl. 1, fig. F, G. (Cone scales, northern France; associated leaves noted)

**Description** (Yorkshire specimens only). Detached cone scales about 9 mm long, 5–8 mm wide; comprising three regions, the basal stalk, the fertile region above the stalk and the distal blade. Blade divided into two lobes, the division extending almost to the fertile region (when the lobes diverge and the whole blade is broad) or shallow and blade relatively narrow. Substance of lobes rather thin but as thick as substance of associated Pityocladus leaves),
margins entire or with slight and uneven lobing; edge composed of more than one cell layer. Both surfaces of blade marked with longitudinal ribs (probably due to internal fibres), ribs beginning and ending blindly; surfaces of scale also showing small bulging cells in longitudinal files. Upper surface of blade nearly flat or with a slight concavity both in longitudinal and transverse directions, where strongly lobed each lobe transversely concave; lower surface correspondingly convex. Upper surface where lobes join sometimes showing a slight ridge in distal part; towards the fertile region this becoming a groove continuing onto top of stalk. Lower surface with a groove passing down from point of union of lobes to where it is covered by bract scale.

Fertile region considerably thickened; on upper surface bearing two nearly round ovules about 1 mm wide, micropyle facing the cone axis, basal part of ovule overlapped by cone scale.

Fig. 45. *Schizolepis liasokeuperianus* Braun
Female cone scales, all ×4. Next to each are imaginary sections at the levels marked, vertical scale exaggerated four times. A, scale labelled 'C', lower surface, bract scale missing. B, lower surface of scale 274 showing bract. C, upper surface of scale 277a showing ovules. D, scale 277b, mainly from above but at its base the coal has flaked off to reveal the underside and bract. E, scale 271, originally seen from below but coal flaked off to expose imprints of the seeds. See also Pl. 4, figs 1–8. All specimens are in the Section for Palaeobotany, Riksmuseum, Stockholm.
and forming a bulge in its upper side. Surface of ovule showing small, uniform, nearly flat and obscurely marked cells. On lower surface of fertile region a bract scale present; bract scale broadly fan-shaped, almost 5 mm wide at its rounded top. Most of bract very delicate and close to ovuliferous scale but middle part robust and separate from it, middle part extending down onto the stalk as a ridge, probably free to near base of stalk. Cone scale stalk 0.5 to nearly 1 mm wide, becoming broader above where it merges with fertile region; upper surface showing two strong ridges (? vascular strands) which diverge just below the seeds; surfaces showing elongated cells. Substance of stalk dense.

Cuticles (only known from distal edge of ovuliferous scale) thin (about 1 µm thick in folds), fragile; presumed upper or adaxial surface slightly thinner but other details of the two surfaces similar so far as is known. Epidermal cells polygonal, often twice as long as broad, often forming longitudinal files. Surface wall either smooth or showing mottled marks or a few obscure longitudinal striations; lateral walls straight, finely marked, often interrupted and with minute waves. Stomata occasional on both surfaces, orientated longitudinally but not arranged in obvious longitudinal files. Guard cells only slightly sunken in a shallow elongated rectangular pit, poles of guard cells exposed on surface. Subsidiary cells often about six, two terminal and four lateral; little specialized but surface of lateral ones may show a ridge parallel with pit margin. (Encircling cells not observed, trichomes not observed.) Fibrous ribs of cone scale sometimes shown by lines of crushed cuticle. (Internal tissues partly preserved and tending to obscure cuticles but no resin bodies recognized.)

**Lectotype**, here selected. Schenk 1867: pl. 44, fig. 6.

**Discussion.** *Schizolepis liasokeuperianus* is represented in the Riksmuseum, Stockholm, by five Yorkshire specimens which Nathorst collected in 1879 from his 'Scarborough New Layer' between Scarborough and White Nab. It has been found nowhere else in Yorkshire. The rock and its flora have been described above (p. 95) and the striking association of the cone scales with *Pityoclados* leaves has also been noted above.

The five specimens differ in their lobing but in other respects agree well with one another and I identify them all as one species confidently. The seeds in the only scale showing them clearly are small: the largest (Fig. 45 c) is only 1 mm long, but in Kräusel's figures of *S. liasokeuperianus* they are twice as large. This may be a real difference but I think it more likely that the scale shown in Fig. 45 c is defective, with diminutive seeds. Many Recent conifers produce numerous diminutive seeds along with good ones. Krishtofovich (1957) illustrates variability in seed size of *Schizolepis*, presumably of one species.

The Yorkshire specimens, though younger (Bathonian), are identified specifically with the original German species *S. liasokeuperianus* Braun because they agree with the isolated scale figured by Schenk (1867) and the later specimens of Kräusel. No single specimen is precisely like Schenk's isolated scale (1867: pl. 44, fig. 8, 8a) but the different specimens overlap it and I could not state a diagnostic difference for the five. The early figures (Schenk 1867, Nathorst 1876) show cones with scales of varied size. Krishtofovich (1957) accepted variability in the shape of the scale in a single species whilst other authors have distinguished new species on the basis of just one or two scales of a particular size and shape. Many of these scales look fairly like one or another of the present five specimens. At least 27 species have been named but of these about 20 seem unsatisfactory and there is a need for monographic revision. For references see Vachrameev (1964) and also Vachrameev, Dobruskina, Zaklinskaja & Meyen (1970).

The most used specific names are *S. braunii* Schenk (synonym of *S. liasokeuperianus*), *S. moelleri* Seward (1907) for rather broad scales lacking a stalk (but stalks are liable to break off),
Fig. 46. *Schizolepis liasokeuperianus* Braun

Drawings of cone scales with lighting from top left; A, C, D, ×20, B, ×100. The main features are drawn accurately but the cellular texture is merely a sketch of the appearance. In general the matrix is left blank but the imprint on the matrix in A is shown at bottom right. A, basal region of scale 274, shown also in Fig. 45 B. B, portion of same scale at about 1-2 mm from left, showing change in cellular texture marking edge of bract. C, portion of scale 277a, shown also in Fig. 45 C. D, portion of scale 277b, shown also in Fig. 45 D, here placed upside down to illuminate the middle part. Preparations are in the Section for Palaeobotany, Riksmuseum, Stockholm.
and *S. follinii* Nathorst (1876) for specimens from the Lower Lias of Pålsjö, Sweden. Nathorst assigned 10 cones to *S. follinii*. To these must be added another Swedish cone figured by Saporta (1884: pl. 194, figs 6–8) and yet another figured by Florin (1944: 495; pl. 181–2, fig. 8). Nathorst's cones are bewildering and the easiest interpretation is that they represent two or possibly three different genera. I regard the cones on his pl. 15, figs 3, 4, 9 and perhaps also pl. 14, fig. 1 as true *Schizolepis*, together with those of Saporta and of Florin, all of which have forked scales. But the cones on Nathorst's pl. 15, figs 5–8 seem to have strongly fluted fan-shaped scales subtending two large seeds and I suppose these are generically distinct. His fig. 10 shows simple oval bodies like those of 'Carpolithus' or *Schizolepis* of his figs 14–16 and these seem different again. I am indebted to Professor Lundblad for notes on these specimens, some of which are obscure and ill-preserved.

Even if *S. follinii* is restricted to the specimens with forked scales, its distinction from *S. liasokeuperianus* is uncertain. A difference given by Nathorst and restated by Florin is that *S. follinii* scales are sessile. This may be correct but the evidence is not clear. In intact *Schizolepis* cones the scales overlap and conceal the bases of the scales above, so that the stalk is not seen. Thus as all the Swedish specimens known to me are intact cones the scales are clearly in no position to show any stalk. Prinada however (1962: pl. 18, fig. 1; text-fig. 68) has figured a partly disintegrated cone as *S. follinii* in which some of the scales do show their bases, and these have stalks which resemble those of *S. liasokeuperianus*.

**Fig. 47. Schizolepis liasokeuperianus** Braun
Cuticle fragments from near top edge of scale 277a, × 500. A, C, from surface with thicker cuticle. B, from other surface with thin cuticle; stomata shown in C partly obscured by mesophyll substance. Preparations are in the Section for Palaeobotany, Riksmuseum, Stockholm.
Form-genus *ELATOCLADUS* Halle 1913

Halle (1913: 84) defined *Elatocladus* as follows: ‘sterile conifer branches of the radial or the dorsiventral type which do not show any characters that permit them to be included in one of the genera initiated for more peculiar forms’. The first species he placed in it was *E. heterophylla*. Halle clearly intended the genus for a conifer shoot of any appearance but it has never been used so widely. Some have treated *E. heterophylla* as the type species and restricted *Elatocladus* to specimens like it, whilst others, for instance Seward (1919), have used the genus for shoots with spreading needles of varied shape. Harris (1969) gave a modified definition: ‘shoot bearing leaves spirally (rarely opposite). Leaf elongated, dorsiventrally flattened, diverging from stem; at base strongly contracted and forming a short petiole attaching it to basal cushion. Lamina with a single vein.’ However, this is too narrow, for it would exclude *E. heterophylla* itself which has no definite petiole and there was also too much emphasis on the spiral attachment of the leaves. I now give the following emended definition.

Fossil conifer shoot bearing elongated, dorsiventrally flattened leaves with a single vein. Leaves divergent from stem.

This excludes *Cyparissidium* with its consistently appressed leaves, *Geinitzia* with spreading but not flattened leaves and *Cupressino cladus* with short opposite or whorled leaves.

As here redefined, *Elatocladus* covers 9 Yorkshire species known from leafy shoots and 10 or 11 others which are named leaf fragments, all previously described by Florin (1958). Apart from *Pagiophyllum fragilis* (Bose), described earlier, I have no additional morphological facts to contribute to the species based on cuticle fragments. I have, however, redescribed all Florin’s leafy shoots with the help of fresh material. Of these I consider two securely linked with a fructification and have described them under ordinary generic names, as I do also Florin’s *Torreya* species. But the remainder, all sterile shoots to which Florin gave generic names, are described here as species of *Elatocladus*. I discuss the family assignment of each species at the end of the description.

Florin’s species based on cuticle fragments are: *Elatocladus areolatus*, *E. coriaceus*, *E. costatus*, *E. depauperatus*, *E. foveolatus*, *E. kendalliae*, *E. kilburnensis*, *E. speciosus*, *E. striatus* and ‘*E. spec.’* (1958: 330). This last is based on fragments resembling *Sciadopitys* too small for determination. Apart from ‘*E. spec.’* the affinities of all the above species are open.

In addition there is the better-known *Bartholinodendron punctulatum* Florin, based on whole but separate leaves from Bornholm and cuticle fragments from Yorkshire. For this I give the new combination *Elatocladus punctulatus* (Florin) Harris. The holotype, preserved in the Riksmuseum, Stockholm, is described by Florin (1958: 338; pl. 48, figs 1–3; pl. 49, figs 2, 8). Florin emphasizes its points of agreement with *Taxus* and *Marskea*.

As well as these named fragments, there are several others in the Yorkshire flora which are certainly distinct but have not been described at all.

Field key to Yorkshire species of *Elatocladus* shoots

It is not possible to key out every specimen, even with a ×10 hand lens, and all determinations should be confirmed by the leaf cuticle. Though the form of the leaf base is liable to be altered in compression it may be disclosed by comparison of leaves on top of the stem with ones at the side.

1. Leaves not or only slightly contracted at their bases... 
   Leaves contracted basally to one-third or less of their full width...
E. ramosus often has large leaves, 3–4 mm wide, and has marginal teeth (visible with a lens). Torreya gracilis often has a very slender stem. Some specimens of Marskea jurassica have leaves under 1.5 mm wide.

Genus Marskea Florin 1958

Emended diagnosis. Plant woody (main stems unknown), lateral branch systems bearing nearly opposite horizontal branches. Leaves opposite and pairs decussating, spreading horizontally through bending and twisting at their bases, persisting over several seasons but ultimately abscissed. Leaf base strongly narrowed but scarcely forming a petiole, scar of detachment at extremity of cushion, broad and not projecting, the two opposite cushions quickly expanding to cover internode surface apart from deep grooves separating them. Leaf blade flat, margins entire, stomata limited to band on either side of midrib on abaxial surface. Shoot apex protected by minute bud scales.

Cuticles well developed. Cells on adaxial surface square or moderately elongated, anticlinal walls straight or undulating especially in region above stomatal bands; surface wall in some leaves flat and evenly thick, in others showing a more or less conspicuous longitudinal ridge. On abaxial cuticle, cells outside stomatal band often elongated, anticlinal walls often undulating, surface wall usually thickened to form prominent longitudinal ridge.

In stomatal bands, stomata mainly in ill-defined longitudinal files, unevenly spaced, mostly longitudinal. Stomata monocyclic, subsidiary cells 5–8 forming a ring. Each subsidiary cell with strong solid papilla next to stomatal pit, papillae united to form round or oval rampart with bulges representing separate papillae, papillae of terminal cells like lateral ones. Subsidiary cell surface commonly with thin strip just outside papilla, outer part of subsidiary cell often bearing second papilla. Stomatal pit round or oval. Each ordinary cell of stomatal zone bearing papilla.

Ovules borne singly at ends of female dwarf shoots, dwarf shoots arising singly on leafy shoots. Axis of dwarf shoot slender when young, mainly smooth but bearing decussately overlapping scales round base of ovule. Ovules developing over two seasons, micropyyle of young ovule at apex of a beak but later apex rounded. Aril thin, arising early and extending close to micropyyle, probably free for only a short distance but largely adnate to integument, its outer epidermis thickly cutinized.

Male cones borne singly on leafy shoots, microsporophylls probably with upturned distal points and bearing two or possibly three round pollen sacs below. Pollen grains round and smooth, wall thin but with single thinner area.

Type species. Taxus jurassica Florin (1944: 516).
Fig. 48. Marskea jurassica (Florin)

A–E, selected leaves, F, group of leaf fragments; all on block V.34698, figured by Florin (1958: text-fig. 4). G, main shoot of V.34702, specimen figured in Fig. 50 F and in Pl. 7, figs 8, 10; and also by Florin (1958: pl. 9, fig. 7). K, side branch of the same shoot. Figs G, K are drawn to show the decurrent leaf cushions. H, L, diagrammatic analyses; the thickness of the axis in these diagrams is exaggerated and the leaves represented as diverging radially. At bottom right of each diagram are imaginary transverse sections of the two lowest internodes. I, small detached leaf, base twisted through nearly 90° and thus looking very narrow; V.57622. J, denuded stem showing leaf scars, V.57623. M, shoot with small leaves, V.57622. Figs A–H, K, L, Beast Cliff Otozamites Bed; I, J, M, Whitby Plant Bed. All ×3.
Marskea jurassica (Florin) comb. nov.
Figs 48–51; Pl. 7, figs 3–6, 8, 10

1910 Taxites zamioides (Leckenby); Lane & Saunders: 16. (Listed for Marske Quarry. Not Cycadites zamioides Leckenby)
1913 Taxites zamioides (Leckenby); Thomas: 245. (Brief notes on Marske specimens. Not Cycadites zamioides Leckenby)
1944 Taxus jurassica Florin: 516; pl. 135/6, figs 7–18. (Shoot, cuticle, ovule)
1958 Taxus jurassica Florin; Florin: 286; pl. 9, figs 1–9; pl. 10, figs 1–7; text-fig. 3. (Shoot, cuticle, ovule)
1958 Taxus harrisii Florin: 290; pl. 11, figs 1–6. (Cuticle, see p. 112)
1958 Marskea thomasiana Florin: 301; pl. 22, figs 1–6. (Shoot, cuticle, see p. 109)

Emended diagnosis. Leaves straight or curved slightly backwards, spreading from shoot at about 45°. Leaf pairs varying from crowded to widely spaced. Leaf widest in its basal third, narrowing rapidly to a quarter of its width at attachment to cushion, upper part tapering gradually, apex usually acute, occasionally obtuse. Midrib prominent on lower side in proximal half of leaf, narrower on adaxial side. Lamina typically 2:0 cm long (longest 2:5 cm), width typically 2:0 mm (widest 2:5 mm) but slender stems bear small leaves down to 1 cm × 1 mm. Leaf margins mainly thick and entire. (No marginal teeth present.)

Cuticles 2–4 μm thick, upper showing elongated cells over midrib and extreme margins but cells otherwise broad, usually in well-marked longitudinal files. Cells isodiametric in some leaves, elongated in others, rectangular tending to become hexagonal. Anticlinal walls marked by sharp inward-projecting ridge, nearly straight over midrib and near margins, sometimes straight between, but more often undulating and in some leaves strongly undulating. Surface of cells more or less distinctly mottled, often uniformly thick and flat but in some leaves a distinct, thick and raised longitudinal ridge present.

Lower cuticle with elongated, usually straight-walled cells on midrib, surface wall often thickened as a ridge. Stomatal bands typically 200 μm wide (up to 300 μm), but narrow in small leaves and at extremities; each band with 3–6 ill-marked files of stomata. Ordinary cells isodiametric but outlines often ill-marked, surface forming large strongly thickened solid papilla, papillae not divided into lobes. Subsidiary cell papillae strongly developed and united to form lobed rampart 70–100 μm wide (but in occasional leaves these and other papillae weakly developed). Cells of lateral zones forming longitudinal files, varying from isodiametric in some leaves to elongated in others, longitudinal wall straight or undulating, surface wall thickened to form strong longitudinal ridge but towards leaf margins ridges weaker and sometimes broken into file of small papillae or in some leaves absent.

Leaf margins several cells thick over most of leaf; near leaf apex only one or two cells thick and cells spreading outwards at 30° to form a scarios edge.

Ovuliferous dwarf shoot at immature stage comprising a stalk 4 mm long, 0:5 mm wide below but slightly wider above and marked by ridges decurrent from lowest scales. Scales rounded, about 2:0 mm long and broad, lowest slightly keeled in middle; all scales thinning to scarios margins. Micropylar part of seed extending for 0:5 mm beyond edge of aril, cuticle extending back for another 0:5 mm under aril, thick in exposed part but thinning below, cells elongated except at top of micropylar beak. Substance of aril thin, but its outer surface thickly cutinized especially near free edge; anticlinal walls broad and projecting inwards deeply, especially at cell corners. Ovule when mature oval, aril edge shown by change of texture near micropyle; dwarf shoot axis 1 mm thick, still bearing scales. (No other details known.)

Male cones probably in axil of foliage leaf. Dimensions (when nearly mature) 5 mm × 3 mm, microsporophyll points 0:6 mm × 0:3 mm, pollen sacs about 0:3 mm wide. Pollen grains
Fig. 49. Marskea jurassica (Florin)
20 μm wide, showing thin area up to 8 μm wide. Wall thin, in surface view showing minute granules and gaps, in optical section showing probable columellae. Plaques 2 μm wide frequent on tapetal membrane.

**Holotype.** Specimen figured by Florin (1944: pl. 135/6, figs 7–18).

**Discussion.** Much of the information in the above diagnosis agrees with that of Florin but the male cone is new and his *Marskea thomasiana* is identified with his *Taxus jurassica* in a new combination. Differences of interpretation lead me to conclude that though the plant is taxaceous it cannot be placed in *Taxus.*

**Vegetative characters.** Florin noted that the leaves twist at their bases so that the blades spread uniformly in the horizontal plane. This causes lateral compression of the base of an attached leaf, making it look narrower. Detached leaves, however, show that there is no distinct petiole, merely contraction to the rather broad midrib. The scar on the stem after leaf fall is much broader than high.

Many shoots show their phyllotaxis if only after degement of their leaf bases. Every leaf is one of an opposite pair and in shoots which show several successive pairs they alternate in strict decussation. One shoot showing six nodes has the uppermost leaf base cushions above the lowest. Florin (1944: 516) originally described *T. jurassica* as having spirally placed leaves, but the specimen to which he referred (which has lost its leaves along one side through damage) gives no evidence to my eye. Later (1958: 287) he gave ‘spirally arranged’ and ‘alternate or subopposite’ for *T. jurassica,* whilst for *M. thomasiana* (1958: 302) he gave ‘opposite or subopposite’, suggesting that subopposite leaves might indicate a bijugate spiral (= double helix) as seen in *Torreya.*

In the stomatal bands the anticlinal walls are often ill-marked and it is then impossible to say if any epidermal cell is precisely opposite a subsidiary cell and thus to be taken as an encircling cell. In some leaves, however, particularly feebly papillose ones, the anticlinal walls are shown clearly and I can state that encircling cells are then absent. I saw no cell in any leaf that I was convinced was an encircling cell. (This interpretation differs from that of Florin, who reported lateral encircling cells in both *T. jurassica* and *M. thomasiana.*) The living *Taxus* has conspicuous encircling cells. A less important difference from *Taxus* is that the papillae appear to be solid and simple, not hollow and lobed.

**The identity of *Taxus jurassica* and *Marskea thomasiana.** The evidence is that the two forms intergrade, intermediates being common, and also that wherever one form occurs the other does too.

Florin (1958: 303), after describing both species in detail, compares them thus: ‘Besides the main diverging character (i.e. the undulating longitudinal walls of the lateral zones of upper and lower surfaces), the differences between *M. thomasiana* and *Taxus jurassica* are but few. Incidentally both occur in the same bed at Beast Cliff and Marske Quarry. In contradistinction to the latter species [*T. jurassica*] the upper leaf epidermis of the former [*M. thomasiana*] is usually rather mottled and has more or less distinct median cuticular ridges in the cells of the lateral zones on not only the under, but also the upper sides of the leaves.’ He gives no macroscopic differences, and I cannot detect any in his figures: the distinction is in the cuticle. He pointed out the wide variability in the cuticles of different leaves of both his taxa and the present study not only confirmed this but also showed that the variability extends sufficiently to obliterate the distinction. I can state that every well-preserved cuticle of the two forms is mottled, finely or
Fig. 50. *Marskea jurassica* (Florin)

A, front view of ovule surrounded by scales; brown scarious edges shown lightly striated, stippled representing shadows; V.34698, ×10, shown also in Pl. 7, figs 5, 6. B, as A but with scales numbered; f, front, b, back, l, left, r, right. Possible edge of aril shown by broken line round the micropyle. C, back of same ovule. D, as C but scales labelled and axis tissue shown black. E, specimen drawn under oil; previously figured dry by Florin (1958: pl. 9, figs 3, 4) as showing an aril round the seed; V.34863, ×5. F, ovule in axil of scale leaf; V.34702, ×5 (see also Fig. 48 G and Pl. 7, figs 8, 10). G, male cone in Pl. 7, figs 3, 4, showing pollen sacs (rounded) and possible microsporophyll apices (pointed); V.57623, ×5. H, I, two pollen masses from G, V.57623a, ×50. J, K, pollen grains at edge of a pollen mass, broken lines indicating thin area of the wall; V.57623a, ×1000.
coarsely, and I could find no relation between this character and the waviness of the longitudinal walls.

The ridges along the middle line of the cells of the lower and upper surfaces of the leaf vary greatly in development, but they are always stronger below and especially near the stomatal band. Leaves where ridges are only moderately developed near the stomata show scarcely any ridge further out and no visible ridge at all on the upper side. I could detect no correlation between ridge development and the waves of the longitudinal walls. There is, however, a marked relation between ridge development and papilla development in the stomatal bands.

Fig. 51. *Marskea jurassica* (Florin)

A, cuticle from apex of ovule, V.34698a, × 20. Form originally a cone but flattened and split on mounting; integument shaded by short lines, aril by dots. The vertical line represents plane of section, arrow marking position of cuticles drawn in B. B, part of A, × 200. At top right is the thick integument cuticle near the micropyle, at top left the thin integument cuticle is further from micropyle and folded under it; below is the cuticle of the aril. C, cuticle at edge of scale leaf below ovule, V.34698b, × 200. The cells above form the scarious margin; below is one epidermis with thin areas on the cells. D, cuticle of aril showing two possible stomata, V.34698a, × 400. E, cuticle of scale leaf surface, cells with thin areas; V.34698b, × 200. F, diagrams of possible organization of small and large ovules of holotype of *Taxus jurassica* Florin, × 4. a, aril, i, integument, the level at which they unite unknown. The stalk of each has two scale leaves, broken short in the old ovule.
The waves in the cell walls are at their strongest on the upper epidermis, midway between the midrib and margin. Wave height (crest to trough) was measured in this region in many leaves and for each cuticle preparation the highest wave was recorded. An unexpected observation was that several leaves with mainly wavy walls also show patches of straight-walled cells, the change being either abrupt or gradual over about 1 mm. (Where such a patch was met, the waves in the patch were recorded as though from a separate leaf.) I did not measure the waves in the holotype of *T. jurassica*, kept at Stockholm, but Florin’s photograph shows that the upper epidermal cells are moderately wavy. I have, however, examined many slides made by him from British Museum specimens in addition to my own preparations. About 130 shoots or separately preserved leaves gave good enough preparations and 10 of these had the patches of different cells referred to above, giving 140 measurements in all. The data are presented in a histogram which shows no clear division into straight and wavy; the slight dip around 9 µm is not statistically significant with this small number of measurements.

Though I feel sure the differences in cuticle between different *M. jurassica* leaves are not of taxonomic significance they are greater than I have observed in any Recent conifer. As an attempt to learn the effects of the environment on cuticles I subjected different buds of *Taxus* and of some other conifers to severe treatments: unseasonable heat or frost, drought at roots, intense shading and toxic spray. If the buds survived they were apt to produce small leaves with a feebly differentiated epidermis, thus approaching the embryonic condition. None of these ill-treatments caused a stronger development of any feature such as cell wall undulations or papillae. It seemed to me possible that the less thickly cutinized *Marskea* leaves with weak papillae might be shade leaves, but if so *Marskea* was very responsive. Patches of straighter-walled cells might be a response of the young leaf to local injury but there was no other evidence of this.

The field evidence that *T. jurassica* and *M. thomasiana* are one is now much stronger. Florin knew that they occurred together in two localities, but recorded them separately in several others. Now there are seven localities where *Marskea* is frequent enough to be represented by at least three determinable cuticle fragments (the others provide just one or two specimens). In all seven localities some specimens have nearly straight and others distinctly wavy walls. In some of these seven localities specimens are numerous and then there is the whole range of waviness, intermediate forms being the most frequent. Wavy and straight walls are not found separately in particular localities.

**Union of *Taxus harrisii* Florin with *Marskea jurassica***. The material of *T. harrisii* consists of two fragments of leaf cuticle each from a different Lower Deltaic locality. The distinguishing characters are said by Florin to be the longer epidermal cells (3–10 times their width as against 1–6 times their width) and a narrower rampart round the stoma. However I have seen occasional *Marskea* leaves, where the species is abundant, with even narrower ramparts than those of *T. harrisii*, and very narrow cells are also met with in some *Marskea* leaves, particularly at the basal end. I thus consider *T. harrisii* a form of *M. jurassica*.

**Male cone**. There is a single Whitby specimen, part and counterpart, which looks like a bud near the top of a partly defoliated *M. jurassica* shoot. A little coal has been lost but the imprint convinces me that the cone was attached. The cone surface shows pairs of round bulges which proved to be sacs full of pollen and it also shows upwardly-directed points which suggest microsporophyll apices. Nothing suggesting a ring of pollen sacs like *Taxus* was seen.

Cuticle preparations were unsuccessful but the pollen sacs yielded pollen grain masses. The grains could not be separated though individual grains could be observed at the edges of the mass.
Ovule. The five small ovules and one large one on the holotype have not been studied microscopically. The following discussion is based on three less valuable small ovules, only one of which was macerated.

Unlike Florin (1944, 1958) I regard the small ovules as immature, preserved when half grown, and I believe their stalks were not defoliated but are in their original state, bare below and scaly round the ovule. The aril extends to within 0.5 mm of the micropyle and was already thickly cutinized (and thus mature) at its free edge, but further back its cuticle and that of the integument are thin, as would be expected if basal growth occurred. The scales below the ovule are in three decussate pairs. Florin does not discuss the large ovule on his holotype specimen but I suppose that it was much older than the small ones and was more or less mature. The change of texture near the micropyle (Florin 1944: pl. 135/6, figs 9, 10) would mark the edge of the aril.

Florin interpreted the ovules of *Taxus jurassica* in terms of the living genus. He supposed that the whole axis of the female dwarf shoot was covered with scale leaves as it is in *Taxus* but that in the fossil most or all of the scales had fallen off, leaving a bare stalk. But this seems unlikely because in *Taxus* the scales remain firmly attached even after death and their forcible removal leaves scars whereas in the fossil the stalk is smooth. He also considered that certain specimens, apparently without any scales, showed a cup-like aril round the ovule. However, following re-examination, the most aril-like of these is here interpreted differently (V.34698, figured Florin 1958: text-fig. 4 (marked by arrow); this work Figs 50, 51; Pl. 7, figs 5, 6). The specimen certainly looks like Florin's photograph when dry but appears very different when under oil. The cup is no longer seen as a single structure but is plainly made up of overlapping scales, each thinning at its margin to a brown, scarious edge. There is a minute film of rock matrix between the scales. The round body above is not an ovule; it is another scale, also with a scarious edge. Between this scale and the others there is, however, a considerable amount of rock matrix. I presume the ovule is beneath it and had a pointed apex like the other young *Marskea* ovules.

**Comparison.** Every character of *Marskea* is shared by one or another genus of the Taxaceae but it differs from each in at least one important character.

The vegetative shoot for example agrees with *Amentotaxus* in phyllotaxis, a statement I base not on Yamamoto's accounts (1927, 1932), which are confusing, but on herbarium specimens at Kew which consistently have leaves attached in opposite decussating pairs. *Amentotaxus* differs, however, in its cuticle, and also in its feebly petiolate leaf which is even more narrowed at the base than in *Marskea*. The leaf cuticle of *Marskea* resembles *Taxus* in its stomatal ramparts and papilllose stomatal bands, and also in the ridges outside these bands, but differs in its monocyclic stomata. Its cell walls when wavy differ from the normal form of *Taxus* and are more like those of the Liassic fossil *Palaeotaxus rediviva* Nathorst (see Florin 1944), though in other respects the cuticle of *Palaeotaxus* is very different.

The ovule agrees with that of *Torreya* and *Amentotaxus* (and probably with *Palaeotaxus*) in having an aril that is formed early and extends almost to the micropyle. In the living genera it is largely adnate. The ovules are borne singly in leaf axils, as in *Amentotaxus* and *Torreya*, and not in pairs on special dwarf shoots as in *Taxus* (though Florin (1958: 289) states that they are occasionally borne directly). Like *Amentotaxus* and *Torreya* the scales below the ovule are in decussating pairs while in *Taxus* they are in a helix. Like *Amentotaxus* alone there is a bare stalk, formed early, below the ovule and its scales.

The imperfectly known male cone of *Marskea* may be like *Torreya* in the way it is borne and also in its sporophylls and pollen. The male cones are borne differently in *Amentotaxus* and the microsporophylls are different in *Taxus*. 
By combining in itself characters scattered among the rather diverse genera of the Taxaceae, Marskea unifies the family, but I see no reason to think that its particular combination of characters is primitive. Its position as a member of the Taxaceae is clear.

At the species level, Marskea jurassica is close to *M. laticosta* Reymanówka (1963) from the Middle Jurassic of Poland. The cuticles are very similar in detail but *M. laticosta* has short broad leaves and stomatal bands widely separated, well outside the range of *M. jurassica*.

*Elatocladus ramosus* (Florin) is compared with *M. jurassica* on p. 117. *Elatocladus* (*Bartholinodendron punctulatus* was compared by Florin (1958).

**Occurrence.** *M. jurassica* is limited to the Lower Deltaic where it occurs in about 15 widely scattered localities, often in local abundance. Intact shoots with attached ovules are known from the Whitby Plant Bed and at Beast Cliff, *Otozamites* Bed.

**Genus TORREYA** Arnott 1838

As the reproductive organs of the fossils *Torreya gracilis* and *T. valida* are unknown I would normally have described them as species of *Elatocladus*, but their resemblance in vegetative characters to the living species is so exceptionally close that I follow Florin in placing them in the living genus.

The present account is based on the material studied by Florin (1958) and agrees closely with his. New information is provided about phyllotaxis and there is also a small difference in interpretation of the subsidiary cells. He considered that both in the fossils and in living species these cells were apt to lose their cuticles at their exposed ends, as a result of destruction by the Schultz' mixture. But I believe there is no destruction and that the effect is purely optical. The form of these cells is rather like that of a square-ended specimen tube. Light passing up the open interior merely has to penetrate about 2 µm of cuticle at the end, but that passing up the side wall has to penetrate 50 µm of cuticle and the end wall appears blank by comparison, especially in a stained preparation. I experimented with *T. taxifolia* Arnott, macerating it for varying periods (including much too long) without causing more damage to the end than the side walls. This was particularly clear when vertical sections of the leaf were macerated but it can be demonstrated more easily by heavily crushing a macerated cuticle, when the vertically elongated cells become spread horizontally.

**Torreya gracilis** Florin 1958

**Fig. 52**

1958 *Torreya gracilis* Florin: 293; pl. 12, figs 1–12; pl. 13, figs 1, 2.

**Diagnosis** (slightly emended). Small shoots (only ones known) branching in horizontal plane at 45°. Axis slender, only about 1 mm thick below and less near apex, its surface marked with two narrow decurrent cushions ending at next node below and two broader and more prominent ones extending to second node below. Leaves borne in opposite pairs which form a double helix, blades spread horizontally by bending and twisting at their bases; typically diverging at 45° but less near stem apex. (No resting bud or scale leaves observed.)

Leaf straight or curved slightly outward, typically 2 cm × 1.5 mm, largest 3 cm × 2.2 mm, uppermost leaves short and narrow. Lamina of uniform width in middle region, tapering gradually to acute or acuminate apex, at base narrowing more rapidly to a short flat petiole. Adaxial surface flat, midrib obscure; abaxial surface nearly flat but midrib prominent and marked with a median groove; margins slightly prominent.
Fig. 52. Torreya gracilis Florin

A, small shoot, V.34932, \( \times 1 \). B, same shoot, \( \times 2 \); node 6 is approximately above node 1 and 7 above 2. C, stomatal band, V.44975c, \( \times 200 \); small papillae on adjacent cells unusual. D, margin of leaf, projecting cell unusual, V.44982a, \( \times 200 \). E, upper cuticle, V.34933, \( \times 200 \). F, two stomata, V.44975c, \( \times 400 \). G, surface of upper epidermal cell, showing pits; V.44975c, \( \times 800 \). H, detached leaves and leaf fragments; a, b, upper surface, c, d, lower surface; V.44988, \( \times 6 \). I, imaginary sections through leaves in H to show surface contour (exaggerated), \( \times 12 \). Note raised margins and stomatal bands in c and d. All specimens are from Whitby Plant Bed.
Cuticles rather fragile (estimated at 2 μm thick). Upper showing midrib feebly marked by broader and thicker-walled cells; cells of lateral regions very long and narrow (up to 1 mm × 25 μm), ends usually tapering but occasionally oblique and next cell then in the same file; longitudinal walls conspicuous but narrow, straight, frequently interrupted. Surface wall flat, without local thickening but with numerous small crystal (?) cavities. Marginal cells even narrower, thicker-walled, occasionally forming a bulge but not a definite tooth; edge of leaf formed by unpitted cuticle 2 μm broad.

Lower cuticle as thick as upper, ordinary cells like those of upper surface. Stomatal bands strongly marked by prominent subsidiary cells, often having also special marginal epidermal cells with median thick ridge or with file of about six papillae tilted towards stomata. Stomata all longitudinal, moderately frequent, subsidiary cells of adjacent stomata usually in contact but seldom shared. Guard cells in deep pits formed by subsidiary cells, sides of pit smooth but mouth narrowed by enlargement of subsidiary cells at their ends to form thick-walled papillae. Subsidiary cells forming a round or oval group of 5–8, all similar, almost isodiametric in end view. Occasional isodiametric vertically elongated cells out of contact with any stoma also occurring in stomatal band, their free end bearing one or more solid papillae.

Holotype. Specimen figured by Florin (1958: pl. 12, fig. 1). Section for Palaeobotany, Riksmuseum, Stockholm.

Discussion. Although T. gracilis has a cuticle of very characteristic appearance the available preparations leave some points uncertain. No original fold was seen, which would give a measure of the original thickness, and no obliquely compressed leaf is known which might have shown the depth of the stomatal pit. The vertical walls of the subsidiary cells, though strongly marked, give a confused picture and the number of them per stoma was often uncertain. Even in cuticles of the living T. grandis Fort. it may be difficult to see the anticlinal walls of the subsidiary cells, particularly at the level of the guard cells. T. gracilis certainly shared with some leaves, at least those of the living species, occasional bulging cells on the leaf margins and at the sides of the stomatal band, and a few moderately papillose cells intermediate between the ordinary cells and the subsidiary cells.

Comparison. The Yorkshire T. valida is compared below. T. moelleri Florin (1958) from Bornholm has much longer leaves than T. gracilis and other differences pointed out by Florin. T. nicanica Krasilov (1967) from the Lower Cretaceous of eastern Siberia has similarly opposite leaves but they are short and broad. The subsidiary cell group stands out as a dark ring in the stomatal band. T. longifolia Gomolitzky (1964) from the Jurassic of central Asia agrees in its elongated epidermal cells but has fewer and less prominent subsidiary cells.

Occurrence. T. gracilis is known only from two Lower Deltaic localities, the Whitby Plant Bed and a fallen block not far from Whitby.

**Torreya valida** Florin 1958

1958 *Torreya valida* Florin: 294; pl. 13, figs 3–5; pl. 14, figs 1–5; pl. 15, figs 1, 2.

Florin’s diagnosis gives all that can be learned from the available fragments of cuticle. I am satisfied that *T. valida* is distinct from *T. gracilis* but less sure that the two sets of specimens on which it was based belong to a single species. *T. valida* has broader leaves than *T. gracilis* (2–5 mm), shorter epidermal cells (their length not more than 20 times their width), broader stomatal bands and more numerous subsidiary cells. Its cuticle is more robust.
Occurrence. Middle Deltaic, Collier Gill coal pit; Upper Deltaic, Lockwood Gill Head.

Elatocladus ramosus (Florin) comb. nov.

Fig. 53

1958 Tomharrisia ramosa Florin: 297; pl. 16, figs 1–7; pl. 18, figs 1–6; pl. 19, figs 1–6.

Emended diagnosis. Lateral branch systems spreading horizontally; ultimate branches borne at about 50°, their axes up to 4 mm thick at their bases but tapering to under 1 mm, bearing leaves in opposite pairs (sequence of pairs unknown); separation between leaf pairs typically as wide as lamina. Stem surface covered with moderately prominent decurrent leaf cushions, each internode showing two broad and two narrow cushions. Leaves persisting for more than one growing season. Apical and basal leaves of shoot small and narrow (no definite resting buds recognized).

Foliage leaves spreading regularly in horizontal plane by bending and twisting of their bases, typically diverging at 45° to stem; straight or curving slightly towards stem apex. Dimensions typically 25 mm × 3 mm, largest 38 mm × 4 mm; small and narrow leaves also produced. Leaf linear lanceolate, widest in basal third, at extreme base narrowing to midrib (about one-fifth of full width) and attached to basal cushion probably without forming distinct petiole. Lamina tapering distally to acute or occasionally acuminate apex, margins not scarious but sharply angular.

Midrib broad and conspicuous towards leaf base, projecting abaxially; tapering distally but then enlarging just below apical point. Stomatal bands inconspicuous.

Cuticles fairly tough, thickness estimated at 2–3 μm; the adaxial slightly thicker, divided into a well-marked midrib, broad lateral zones and narrow marginal regions. Midrib cells elongated, walls straight or with minute jagged extensions, seldom slightly wavy, surface coarsely pitted. Cells of lateral regions elongated, forming ill-marked files, lateral walls well marked, forming rounded waves, wave height (crest to trough) nearly equal to cell width. Cell surface flat, marked with small pits. Edge of leaf formed by single cell layer, marginal cuticle 6 μm thick. Marginal cells narrow, straight-walled, occasionally projecting as a short tooth or forming the base of a tooth composed of two or three cells; length of tooth up to 100 μm.

Stomatal bands narrow, situated close to midrib. Ordinary cells resembling those of upper surface but in region outside stomatal bands shape often less regular. Cells in stomatal band mostly isodiametric, walls straight but often obscurely marked, surface bulging and often thickened to form an ill-defined papilla. Stomata numerous, longitudinal, seldom forming files, guard cells sunken in oval or rectangular pits. Subsidiary cells 4–6, lateral one or two cells strongly thickened next to pit to form an undivided rampart (outside which is a thin strip and then a region at least as thick as general surface). Terminal subsidiary cells often little specialized and scarcely thickened at ends of pit, but sometimes thickened and rest of surface unspecialized. (Encircling cells absent.) Guard cells well cutinized, their cuticles extending under pit margins.

Additional material is needed to establish the precise phyllostaxis and the number of seasons a leaf remains attached. There is not even a well-preserved detached leaf to show the form of the base.

Holotype. V.34865, V.34866 (part and counterpart).

Comparison. E. ramosus closely resembles Marskea jurassica and the only distinguishing character which is absolute is the presence of marginal teeth; Marskea has none. But there are
Fig. 53. Elatocladus ramosus (Florin)

differences that distinguish nearly all specimens. Its leaves are often longer and broader than the widest Marskea leaf and the ordinary epidermal cells are elongated and with sinuous walls in all available specimens, like a fraction only of Marskea leaves. In the stomatal bands the cells are at best feebly papillose and outside the band the cells lack a median ridge, whilst in almost every Marskea leaf the papillae and ridges are strong and conspicuous. The stomata themselves often have a lateral rampart on each side of the pit, and only slight or no thickening at the ends of the pit connecting these ramparts, but in Marskea the rampart is complete, round and strongly lobed.

Tomharrisia florinii Krasilov (1967), from the Lower Cretaceous of eastern Siberia, is distinguished by its short, broad leaves. Its epidermal cells are similar but the stomatal pit is surrounded by a ring of separate papillae.

Tomharrisia kurbatovii Gomolitzky (1964) from the Jurassic of central Asia has short crowded leaves and almost straight-walled cells. The subsidiary cell papillae are close to one another but are not united into a rampart along the sides of the pit.

Florin (1958) compares E. ramosus with other species.

**Occurrence.** Good material of E. ramosus is known from the Lower Deltaic Whitby Plant Bed and there is a fragment of cuticle macerated out of the clay of Marske Quarry. A shoot preserved without cuticle was found in a fallen block of sideritic ironstone from the Beast Cliff Neocalamites Bed, probably Middle Deltaic, Sycarham Series.

**Genus POTERIDION** nov.

**Diagnosis.** Ovuliferous dwarf shoot; axis short and slender, covered with scale leaves. Lower scale leaves minute, lanceolate; upper ones longer and broad above, overlapping and forming a conical cup. Substance of scale leaves thin but cuticles robust. Ovule terminal, rounded; possessing cutinized integument, stone layer, and thinly cutinized megaspore membrane.

**Type species.** Poteridion hallei, the only species.

**Name.** From Greek ὑπηρίδιον, a small drinking cup.

Poteridion is regarded as a detached taxaceous dwarf shoot, resembling that of Recent Taxus.

**Poteridion hallei** sp. nov.

Fig. 54; Pl. 7, figs 1, 2

**Diagnosis.** Length of dwarf shoot including scales nearly 1 cm, width at top about 5 mm; axis (exposed at base only) 0-5 mm wide. Upper scales thinning upwards into membranous margin, uppermost about 2 mm wide and forming an open cup. (Arrangement of scales not determined.)

Cuticles of scales showing elongated cells with strongly-marked lateral walls, sometimes with jagged extensions. Stomata few (not recognized with certainty but possibly represented by rectangular pits bordered by unspecialized cells). (No papillae or trichomes present.)

Ovule concealed under scale leaves; integument cuticle delicate, showing isodiametric hexagonal cells with broad lateral walls. Traces of thinly cutinized megaspore membrane and of stone cell layer present.

**Holotype.** In the Riksmuseum, Stockholm; the only known specimen.

**Name.** After T. G. Halle, who collected the specimen from the Whitby Plant Bed in 1910.
Discussion. The interest of *Poteridion* was only realized after it had been degaged and then made into a transfer. Much remains to be learnt, for example the ovule concealed among the scales is particularly ill-known and I suspect abortive; when mature I would expect it to project as in *Taxus*. When the Whitby Plant Bed is again satisfactorily exposed, this is one of the species that should be looked for.

Apart from an unknown ill-preserved seed and *Poteridion* the block showed nothing determinable on its surface, but there were leaf fragments in the residue from the transfer: the Bennettitalean *Otozamites gramineus* (Phillips) and *Ptilophyllum pectinoides* (Phillips), *Marskea jurassica* (Florin) and *Elatocladus ramosus* (Florin).

As the female dwarf shoot of *Marskea jurassica*, though comparable, is distinct, the association with *E. ramosus* suggests that *Poteridion* might have been borne on that plant; to call

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Fig. 54. *Poteridion hallei* sp. nov.
A, cells considered to be of seed integument, ×200. B, cells of upper scale leaf (no. 8 of D), with a possible stoma; ×200. C, transfer (original shown in Pl. 7, figs 1, 2), ×10. D, diagram of C, individual scales numbered, ×5. E, cells of lower scale leaf (no. 2 of D), ×200. All specimens represent the holotype and are in the Section for Palaeobotany, Riksmuseum, Stockholm.
attention to this possibility I describe it next to *E. ramosus*, but without implying that I am convinced. There is no supporting evidence from structure and a study of *Taxus* gave no hope that there would be because I can find no point of specific agreement between a *Taxus* foliage leaf and a scale on its dwarf shoot.

**Comparison.** *Poteridion hallei* is distinguished from the female dwarf shoot of *Marskea jurassica* by having no bare region on the stalk and by its narrow, minute basal scales. Its conical and rather elongated shape distinguishes it from that of *Taxus*. It seems perhaps more like that of *Torreya* or the fossil *Palaeotaxus rediviva* (refigured by Florin 1944).

**Elatocladus laxus** (Phillips) comb. nov.  
Figs 55, 56

1829 'Leaf’, Phillips: pl. 7, fig. 24. (As 1875 below)  
1875 *Taxites laxus* Phillips: 231; pl. 7, fig. 24; lign. 64.  
1958 *Sewardiodendron laxum* (Phillips) Florin: 303; pl. 25, figs 1–8; pl. 26, figs 1–15; pl. 27, figs 1–8. (Not p. 332, pl. 45, figs 1–4)

**Diagnosis** (slightly emended from Florin). Lateral shoots shed with their branchlets and leaves intact (no other shoots known); branching occasional, angle varied. Axis up to 4 mm thick, commonly 2–3 mm; narrowing to 1 mm near apex. Leaves spreading in the horizontal plane by bending and twisting at their bases except at shoot apex where they overlap to form a bud. Leaves usually close but seldom overlapping, occasionally distant; blade commonly straight; usually at 90° to stem but sometimes at 60° and at a smaller angle near shoot apex; widest at its base and tapering to acute or acuminate apex (in smallest leaves an obtuse apex); length uniform over most of shoot but diminished near shoot base and apex. Bud scales occurring at base of main shoots (but not of side shoots), small, triangular, strongly keeled (transition to foliage leaves gradual or abrupt).

Foliage leaves commonly 12 mm × 2 mm; largest 30 mm × 2.5 mm, smallest 4 mm × 0.8 mm. Lamina flat but midrib prominent below and sunken above; margins flat, entire, apex simple (not scarious). Upper surface of lamina showing uniform cell striations, lower showing two well-marked stomatal bands which continue onto cushions; substance of lamina thin, interior of cushions and of lamina outside stomatal bands containing scattered longitudinal fibres.

Cuticles delicate, about 1 μm thick (in folds). Upper, and non-stomatal parts of lower, showing nearly uniform rectangular cells often 80 μm × 15 μm, but narrower and more thickly cutinized at leaf margins and over midrib. Cell surface showing faintly marked darker areas which may unite to form a median darker line; lateral walls fairly distinct, straight or very slightly sinuous, sometimes obscurely moniliform. Cells forming short and inconspicuous longitudinal files. Stomatal bands well defined, up to 0.2 mm wide but narrowing near leaf apex. Stomata scattered in middle of leaf, forming up to four ill-marked files (near apex a single file); if in file spacing uneven but two stomata only rarely sharing a subsidiary cell. Orientation of stomata varied, mainly transverse in some leaves, mainly longitudinal in others.

Epidermal cells of stomatal band nearly isodiametric, smaller than other epidermal cells; anticlinal walls often projecting inwards more than those of cells outside stomatal band and their surface wall often darker, probably flat (not papillose). Subsidiary cells resembling other cells of stomatal band and forming an ill-marked ring around a wide, shallow pit; edge of pit vertical and not overhanging guard cells. Guard cells thinly cutinized but aperture well marked.
Fig. 55. *Elatocladus laxus* (Phillips)

A, transfer of small shoot with nearly decussate leaf pairs, numbers placed opposite points of attachment. Odd numbers refer to leaves above the stem and even numbers to leaves at the sides; V.58521, × 3. B, shoot with leaves mostly in decussate pairs; V.28509A, × 1. C, shoot with branch and long leaves, phyllotaxis obscure; V.34774, × 1. D, small shoot with successive leaf pairs mostly at about 70°; V.28509B, × 1. E, typical shoot; V.28507, × 1. F, lower region of E, showing partly decussate phyllotaxis, × 2. G, details from base of F, × 4. H, small shoot with successive leaves or leaf bases numbered; V.58515, × 3. I, diagram to show approximate planes of successive leaf pairs in H. The divergence varies but the average is about 60°. J, shoot base, V.58846, × 2. K, shoot base, V.58847, × 2. The phyllotaxis in J and K is obscure but the leaves may be in opposite pairs. All specimens are from the Gristhorpe Bed except H, J, K which are from Hasty Bank.
**Holotype.** Specimen figured by Phillips (1829: pl. 7, fig. 24). Yorkshire Museum.

**Discussion.** Phillips' (1875) sketch of *E. laxus* showed the broad bases of the leaves, but Seward (1900) merged the species with *E. zamioides* which has narrow leaf bases. *E. laxus* was only revived in 1958 by Florin, who gave the first detailed description. The present description agrees closely with his though details of phyllotaxis are added.

*E. laxus* is fairly common but the substance of the fossil is fragile and often falls to dust. The cuticle is very delicate and most attempts to prepare it fail. One specimen (39302) is preserved as a delicate brown film showing only the cuticles and lignified walls of tracheids, fibres and guard cells. There is no sign of a thick-walled hypodermis.

The lateral branches as a rule have rather small foliage leaves at their bases, not bud scales, but V.28509C (Florin 1958: pl. 26, fig. 12) shows them at the base of a main shoot. Two other shoots with basal scales are shown in Fig. 55 i, k.

Unsatisfactory preservation makes the phyllotaxis of many specimens obscure. Phillips' sketch showed opposite leaves but Florin described them as spirally arranged although several of the specimens he figured show some of the leaves as opposite. His photographs seem to have been taken under oil since the same specimens when dry show further leaves as imprints and many more opposite pairs are then visible; for instance his pl. 26, fig. 11 specimen (V.28509B, redrawn here) shows successive pairs which seem to be inclined at 65°–70°, whilst that shown in his pl. 26, fig. 7 (V.28509A) shows them at about 90° in the part of the shoot where they are seen best. Internodes of slender shoots show just two decurrent cushions, but the broader shoots, my Fig. 55 b and Florin's pl. 26, fig. 7, show two broad cushions separated by wedges narrowing downwards. The broadest shoots (Florin 1958: pl. 27, figs 4, 5) show two wide and two narrow cushions at all levels.

Various authors have noted that shoots of *E. laxus* tend to have shorter leaves in Lower Deltaic localities than they do in the Middle Deltaic Gristhorpe Bed, and Nathorst, who thought they might be distinct, gave the name *Taxites brevifolius*, a nomen nudum. Florin (1958: 305) discussed this point and decided that there were no grounds for making a specific distinction. Since then long-leaved shoots have been found associated with short-leaved ones at Hasty Bank and Hill House Nab (both Lower Deltaic), and this reinforces Florin's view.

Florin discusses the classification of *E. laxus*. He concludes that it may well belong to the Taxodiaceae and I agree; every one of its vegetative characters is found in one or another living genus of the family. However we have no information about reproductive organs. A small lump on the specimen shown in Fig. 55 e–g looks like a possible scar of a missing male cone, but the leaf base seems to continue past the lump and I conclude that it is caused by a minute nodule in the substance of the stem.

The shoots of *E. laxus* may have been deciduous like *Taxodium*. The very thin cuticle and delicate substance suggest this and so does the distribution of bud scales. Bud scales, in general, mark a dormant period and their position in *E. laxus* agrees with the deciduous *Taxodium* rather than the evergreen *Sequoia sempervirens* (D. Don) Endlicher. Each caducous branch system of *Taxodium* has bud scales at its base but its side branches have no bud scales for they grow out early in the same season. They merely have small basal foliage leaves. *Sequoia*, which has caducous branch systems lasting about four years, has bud scales at the base of the main shoot and at each branch shoot, for they grow out in the following season.

**Comparison.** Florin (1958: 332) identifies some specimens collected long ago in the Stonesfield Slate as *Sewardiodendron laxum*, but I reject them. The leaves narrow slightly as they
Fig. 56. 

**Elatocladus laxus** (Phillips)

A, upper cuticle, midrib to left; V.58520a, ×200. B, upper cuticle with margin (opened) to right; V.58520a, ×200. C, cells of upper cuticle near margin, showing dark plaques on surface; V.58520a, ×500. D, lower cuticle with broad stomatal band and transversely orientated stomata; V.58520b, ×50. E, stoma drawn from within, walls at deeper focus (i.e. on outer surface) shown by broken lines, darker cuticle stippled; V.58520b, ×500. F, stoma from outside; darker cuticle stippled, oblique shaded part coated on inside with resinous matter; V.58520a, ×500. G, lower cuticle near leaf apex, midrib to left; V.58520a, ×200. All the preparations are from one shoot from the Gristhorpe Bed, V.58520.
approach the stem (particularly in his pl. 45, figs 1, 3) whilst they become broader in *E. laxus*. No microscopic details of these Stonesfield specimens are known.

**Occurrence.** Middle Deltaic, Gristhorpe Series: Gristhorpe Bed (frequent). Lower Deltaic: Whitby (? Long Bight Plant Bed); Beast Cliff, Petard Point (rare); Roseberry Topping (locally frequent); Hasty Bank (locally frequent); Hill House Nab (rare).

*Elatocladus zamioides* (Leckenby) Seward

Figs 57, 58

1864 *Cycadites zamioides* Leckenby: 71; pl. 8, fig. 1.
1875 *Cycadites zamioides* Leckenby; Phillips: 228; lgn. 58. (Sketch of holotype)
1900 *Taxites zamioides* (Leckenby) Seward (in part): pl. 10, fig. 5. (Shoot, refigured by Florin 1958: pl. 30, fig. 5.)

Not the references to *Taxites laxus*.

1919 *Elatocladus zamioides* (Leckenby) Seward: 431. (Name)
1958 *Thomasiocladus zamioides* (Leckenby) Florin: 311; pl. 29, figs 2–4; pl. 30, figs 1–7. (Holotype refigured in pl. 30, fig. 4)

**Diagnosis** (slightly emended). Length of ultimate shoots exceeding 6 cm (shoot bases and branching unknown but axillary buds present). Apical and axillary buds covered by minute scale leaves. Stem 2 mm wide below, tapering, each surface marked by 3 or 4 prominent decurrent cushions; cushions each passing two nodes but overlapped at third node below. Leaves borne in opposite pairs. Successive pairs at about 70° making a double helix with 2 + 4 parasitiche.

Leaves mostly straight, normally borne at 80°–90° to stem but at a smaller angle at stem apex. Blade widest in lower third, tapering to acute or acuminate apex, base rounded, petiole present but very short. Leaf typically 15–25 mm long, 1-2-1-5 mm wide (widest 2-0 mm), leaves near stem apex short and narrow. Leaf surfaces mainly flat but midrib sharply raised adaxially; abaxially margins slightly prominent, midrib becoming prominent near leaf base. Leaf substance thin but slightly darker near midrib and margins (no fibres visible). Stomatal bands inconspicuous.

Cuticles fragile, about 1–2 μm thick but up to 3 μm at margin. Cells of upper surface almost uniform, square or moderately elongated, forming long files ending in a point; cells over midrib rather longer and more thickly cutinized, cells near margin rather narrower. Anticlinal walls marked by a fine ridge; interrupted, straight or very slightly waved. Surface walls nearly flat; often thin near anticlinal walls but thicker in interior (though not forming a papilla). Surface mottled with darker spots. Leaf edge formed by flange of cuticle 2–3 μm wide (no marginal teeth present).

Lower cuticle thinner, stomatal bands typically narrower than midrib but about as broad as lateral regions without stomata. Cells of lateral regions mostly rectangular and in long files; anticlinal walls as on upper surface but middle region of cell often forming dark ridge (which may be nearer margin than midrib); surface mottled and often showing faint longitudinal striae. Cells in middle of midrib may be slightly longer and more cutinized than on upper surface and longer also in marginal regions; only narrowed at extreme edge of leaf.

Stomatal band typically showing 3–4 files of stomata. Stomata all longitudinal, sometimes sharing a terminal subsidiary cell; lateral subsidiary cells never shared and usually separated by ordinary cells from other subsidiary cells. Subsidiary cell group elongated, terminal cells little specialized, one or two lateral cells present on each side of pit, their surface thickened next to pit and further out having a thin strip. Curved lateral encircling cells often present (terminal encircling cells absent). Stomatal pit rectangular or oval, very shallow but edges usually over-hanging guard cell margins; guard cell aperture distinct, nearly as long as the pit. Poles of guard
Fig. 57. Elatocladus zamioides (Leckenby)
A, V.58531, as collected, ×1. B, same specimen in transfer, showing two buds near apex (one terminal, one lateral) and three others further back, ×2. C, apices of four leaves from A, midrib forming faint ridge, ×6. D, details from middle region of A, ×6. E, details from B, including bud, ×10. F, shoot with crowded leaves and possibly irregular phyllotaxis; V.25882, ×2. G, details from middle region of B, ×10.
cells often reaching the surface but exposed area small and faintly marked. (Trichomes absent, hypodermal cells absent or not preserved.)

**Holotype.** Specimen figured by Leckenby (1864: pl. 8, fig. 1). Sedgwick Museum, Cambridge, no. K.286.

**Discussion.** All the figured cuticles came from just two shoots and though I prepared others they gave poor results and merely provide general confirmation. The broader leaves may possibly have more than four stomatal files in each band. Florin’s statement that the cuticle may attain moderate thickness must refer to the leaf edges since it is otherwise delicate, over both surfaces.

The main additions are details of phyllotaxis and the buds, the lateral buds being unknown until specimen V.58531 was transferred, when four became visible. Florin did not give close attention to the phyllotaxis, including *E. zamioides* (1958: 355) among the conifers with ‘sub-opposite’ leaves and perhaps bijugate phyllotaxis, but he gave no other details. All the specimens I have seen with well-spaced leaves certainly do have opposite pairs, and the pairs are not at 90° but nearer 60° or 70°. The specimen figured by Seward (1900), for example, shows this, and V.25882 shows it more precisely. In the transferred specimen V.58531, 16 nodes are clearly visible and a few others poorly; although the divergence between two successive pairs cannot be stated accurately, the mean divergence for the 16 is close to the ideal of 69°, i.e. half the Fibonacci angle of 137.5° (Harris 1976). I could not, however, make out the precise phyllotaxis in shoots with crowded leaves, but I note that the leaf cushions pass two nodes, conforming to the normal pattern.

No specimen shows a shoot base but some have a ragged end. I imagine that all the Museum specimens of shoots may be ones torn off prematurely by storm. The separate leaves, however, which are rare, were probably abscissed naturally.

**Classification.** Florin called attention to the many points of agreement between *E. zamioides* and the living Cephalotaxus. He noted the unusual midrib, projecting upwards, and called attention to several features of the cuticle. He concluded it was ‘highly probable’ that it belonged to the Cephalotaxaceae. Such new points as have been learnt mostly agree also, and though no character taken alone is exclusive to Cephalotaxus their combination is shared by that genus alone and most of the differences are relative. Cephalotaxus leaves, for example, are larger and more robust. Florin particularly emphasized the fewer stomatal files of *E. zamioides* (3–4) as against 13–21 in *Cephalotaxus*. This, however, may be because the fossil leaves are narrower. Narrow Cephalotaxus leaves at the end of a year’s growth have only 4–8 files.

*E. zamioides* stomata have less frequent encircling cells than *Cephalotaxus*, in which they are normally present on both sides and terminal ones are frequent. I saw no convincing terminal encircling cell in the fossil; of 18 clearly seen stomata almost half had no encircling cell at all. In general *E. zamioides* is much less xeromorphic than *Cephalotaxus* in its delicate leaf, thin cuticle and very shallow stomatal pit. These features suggest that *E. zamioides* may have dropped its leaves at the end of the first growing season, unlike *Cephalotaxus* which only drops them after 3 to 4 years.

**Comparison.** *Cephalotaxus ussuriensis* Krasilov (1967) from the Lower Cretaceous of eastern Siberia is the most similar Mesozoic fossil known to me, although it has more robust leaves, like the living *Cephalotaxus*. Its cuticle is fairly thick but like *E. zamioides* it has many monocyclic stomata.
Fig. 58. Elatocladus zamioides (Leckenby)

A, strip of upper cuticle, midrib on left, ×200. B, diagram of three fragments of lower cuticle, showing stomata and leaf margin; square representing 1 mm². C–E, stomata, ×400. F, edge of leaf with cuticles opened, ×200. Upper cuticle to left, cells crushed along margin. G, lower cuticle, ×200. H, leaf edge showing small cutinized knobs, ×500. I, details of upper epidermal cells, ×500. J, details of lower epidermal cells, ×500. The figures are drawn from Florin’s preparations of specimen V.44968 and are all based on slide b except the middle fragment of B which is in slide c.
Occurrence. *E. zamioides* is rare, known from about 20 specimens, and its only locality is the Gristhorpe Bed. Florin mentions field records from other localities but as they are unsupported by specimens he rejects them.

*Elatocladius setosus* (Phillips) comb. nov.  
Figs 59, 60

Yorkshire specimens:

1875  *Brachyphyllum setosum* Phillips: 229, lignon. 60. (Specimen refigured here)
1900  *Cheirolepis setosa* (Phillips) Seward: 294 (in part), text-fig. 53 b. (Not text-fig. 53 A which may be *Geinitzia rigida*).
1952  *Haiburnia setosa* (Phillips) Harris: 362, text-figs 1, 2, 3 A–C. (Figures repeated here)
1958  *Haiburnia setosa* (Phillips); Florin: 317; pl. 34, figs 1–8.

Foreign material is discussed below.

Diagnosis (slightly emended from Harris and Florin). Shoot systems dropped with their side branches and leaves intact. Main axis long, straight, up to 3 mm wide; laterals distant, often alternate, spreading horizontally, often arising at an angle of 45° but secondary branchlets at a smaller angle. Stem marked with conspicuous leaf base cushions, on small stems each cushion continuing past one node and ending at second node below. Phyllotaxis varied; leaves often in opposite pairs forming a double helix but often also attached singly in a simple helix.

Leaves on main shoot and on some of laterals either pointing radially or only spreading horizontally to a small extent, these leaves borne at an angle of less than 30° and concealing stem. At bases of side branches and in occasional portions of long shoots leaves short and almost scale-like. On most lateral branches all leaves spreading in horizontal plane by bending and twisting of their bases, blades diverging at an angle of 70°–90° and commonly separated by gaps wider than the leaves.

Foliage leaf attached at apex of cushion, its base not or only slightly narrowed; linear lanceolate, dorsiventrally flattened; adaxial surface mostly flat but concave near leaf base, abaxial surface keeled below. Longest leaves 7 mm but most leaves 5 mm or less; width 0.5–0.8 mm. Basal cushions 1.5–3.0 mm long × 0.3–0.5 mm. Leaf blade normally straight but occasionally bending forwards (falcate) in its apical region, substance of leaf opaque except near edges where a band of cuticle, 5 μm broad, is translucent. Margins of leaf entire to near apex but then varied, either entire or showing multicellular bulges (or occasional minute teeth or marginal cells projecting to form a scarious edge). Apex commonly acuminate.

Cuticles 2–4 μm thick on both surfaces but thinner adaxially in appressed leaves; mainly similar on the two surfaces but stomata evenly scattered adaxially whilst avoiding keel abaxially. On decurrent cushion, cuticle as on abaxial leaf surface but rather thicker. Stomatal frequency low everywhere. Stomata all orientated longitudinally, not forming files, seldom close enough for encircling cells to be in contact. Epidermal cells small, forming well-marked longitudinal files, either square or rectangular (2–3 times as long as broad); anticlinal walls forming conspicuous ridges, straight or slightly waved, sometimes interrupted. Surface wall flat, either without sculpture or with faint longitudinal striations. Keel (midrib) in lower part of leaf marked by long cells.

Stomata varied; subsidiary cells often four, with two lateral and two terminal ones, but often six and forming a uniform ring. Stomatal pit usually elongated but sometimes round, lateral subsidiary cells usually overhanging guard cells slightly, sometimes concealing them but sometimes leaving them exposed; terminal subsidiary cells usually overlapping guard cell poles.
Fig. 59. Elatocladus setosus (Phillips)
A, shoot system, V.29279, ×1. B–E, apices of leaf fragments, ×10. B, V.58535; C, with marginal bulges, V.58532; D, marginal unicellular teeth, V.58533; E, V.58534, extreme end of leaf missing. F, medium-sized stem showing leaf attachment, V.29281, ×8. G, shoot system, V.29278, ×1. H, details of portion of A, ×5. I, Phillips' holotype, V.21111, ×1. J, transfer of portion of shoot in G, ×8; V.29278a. The specimens in A, F–H, J are from Whitby Plant Bed and were figured by Harris (1952), but J is redrawn. B is from Stainsacre Beck, C from Marske Quarry, D from Beast Cliff, E from Bransdale. I, figured by Phillips (1875) and Harris (1952), is probably from Haiburn Wyke Plant Bed.
Guard cells thinly cutinized except along aperture. Surface of lateral subsidiary cells usually strongly thickened next to the pit, thickened also further out with narrow thin strip between; outer anticlinal wall often projecting strongly inwards. Terminal subsidiary cells varied; sometimes small and thickened like lateral ones, thickening round pit then forming well-marked and very slightly raised rampart bounded by thin strip, but often scarcely thickened. Lateral encircling cells nearly always present, unspecialized; terminal encircling cells sometimes occurring (but often doubtfully recognizable). (Trichomes absent, no hypodermal cells preserved.)

Fig. 60. Elatocladus setosus (Phillips)
Holotype. V.21111, first figured by Phillips (1875: 229; lign. 60). Fig. 59 i.

Discussion. The older accounts of *E. setosus* were inadequate but all the hand specimens in the British Museum bearing this name appear to be rightly determined. Although no shoots with spreading leaves were figured, several specimens show such shoots, connected to or associated with shoots having constricted leaves.

The present diagnosis of *E. setosus* differs little from those of Harris (1952) and Florin (1958). I stated that the cuticle was 1 μm thick, an error, and neither author considered phyllotaxis. Certain specimens with well-spaced leaves show them in opposite pairs, successive pairs being at nearly 90° (Fig. 59 h). The shoot shown in Fig. 59 i, when first drawn in 1952, seemed to show leaves in disorder, but on fresh study the 14 lowest leaves are interpreted as forming 7 successive pairs at angles of about 60°. I could not fit the upper leaves into a double helix but perhaps they would fit a simple helix.

The stomata of *E. setosus* are remarkably sparse. Counts of cells of two different leaves on the upper surface gave 1 for every 32 ordinary cells and 1 for every 60 ordinary cells but the number of stomata included was too small for a reliable stomatal index. The frequency of stomata on the lower surface, taken as a whole, is roughly similar.

The cone attributed to *E. setosus* by Thomas (1913) belongs to *Elatides thomasii*.

Comparison. No other Yorkshire conifer shares the two shoot forms of *E. setosus*, but the constricted form is somewhat like *Cyparissidium blackii*. The cone-bearing shoot figured by Turutanova-Ketova (1963: text-fig. 100) as *Elatides setosa* is certainly different and suggests rather a *Selaginella*. (We know nothing about the reproductive organs of *Elatocladus setosus* nor of its affinities.)

Specimens resembling Seward’s figures of *E. setosus* from several parts of the Soviet Union have been identified with it but not one is known in detail and without fine details I am unwilling to identify even a Yorkshire specimen. The shoots figured by Delle (1967) from the Russian Middle Jurassic resemble the constricted Yorkshire shoots macroscopically and those from the Upper Jurassic of Russia figured by Stanislavskii (1957: 73; pls 15, 16) include specimens with spreading leaves.

Occurrence. Shoots are known from four Lower Deltaic localities. Haiburn Wyke Plant Bed, the type locality, a few specimens collected in the nineteenth century. Whitby, fallen blocks of sandstone from just above the plant bed, locally frequent. Marske Quarry, several shoots. Beast Cliff *Ctenozamites* Bed, one fragment.

A problematical Hasty Bank specimen quoted (on my advice) as *E. setosus* by Hill & van Konijenburg-van Cittert (1973) is probably *E. laxus*.

Detached leaves were obtained by bulk maceration from four Middle Deltaic localities, of which two belong to the Sycarham Series and two doubtfully to the Grishorpe Series, and also from one Lower Deltaic locality. In none of the macerations was this species frequent.

*Elatocladus sideriticus* (Bose) comb. nov.

Figs 61, 62

1955 *Taxulus sideriticus* Bose: 116, text-figs 3, 4. (Figures repeated here)
1958 *Taxulus sideriticus* Bose: Florin: 319; pl. 35, figs 1–4; pl. 36, figs 1, 2. (Photos of cuticle)

Diagnosis. Ultimate shoots known only; simple, slender, dropped with their leaves still attached. Axis very slender (0·4–0·8 mm), bearing leaves on all sides but leaf bases bending and
Fig. 61. Elato cladus sideriticus (Bose)
twisting to bring each lamina into the horizontal plane and at right angles to the axis; lamina of adjacent leaves often in contact. Leaf contracting below to about half its maximum width but not forming a petiole; continuing onto the stem as a decurrent cushion about 0·5 mm to 3 mm long, cushion prominent until overlapped by lower leaves. Surface of axis commonly showing two decurrent cushions in a simple helix, probably with 1 + 2 parasichies.

Lamina ovate lanceolate, broadest at middle, typically 2·0–2·5 mm × 0·8–1·0 mm (extremes noted 1·0–4·5 mm long and 0·4–1·6 mm wide). Apex rounded, obtuse, acute or shortly mucronate; base of lamina narrowed to about half, clasping stem (appearing asymmetric because of oblique compression). Lamina rather thin, flat above but midrib prominent below. Margins usually entire but occasionally bearing minute tooth formed by a single cell.

Cuticles moderately thick (up to 3 µm in folds), thicker along margins. Adaxial surface showing stomata thinly scattered over middle region, orientation mainly longitudinal. Epidermal cells nearly uniform (midrib scarcely distinguished), mostly shortly rectangular or polygonal, tending to form files; anticlinal walls usually well marked, straight or slightly waved, occasionally interrupted. Surface wall slightly raised, often showing slight median ridge or 1–4 weak papillae; marked with minute granules.

Abaxial surface showing well-marked midrib, marginal regions and two stomatal bands midway between midrib and margins. Cells of midrib rather large, rectangular, surface not much thickened. Cells of marginal region rectangular, papillose near stomatal band. In stomatal band cells isodiametric polygons, anticlinal walls often ill-marked; surface wall raised and thickened to form one or more papillae; papillae often solid and moderately prominent or hollow and very prominent. Stomata nearly all longitudinal, scattered or forming ill-marked files but some not placed in any file, mostly separated from one another by ordinary cells.

Stomata of both surfaces surrounded by 4–7 subsidiary cells resembling other cells but forming round or angular pit; edges of pit forming raised rampart of concrescent papillae, a second papilla often present on outer part of subsidiary cell. Guard cells thinly cutinized, rather deeply sunken. Unspecialized encircling cells sometimes present. (Trichomes apart from marginal teeth absent; cutinized hypodermis absent.)

**Holotype.** V.30608.

**Discussion.** Nearly all the material is from the type locality where it is represented by abundant fragments in a thin layer. Many of the shoots have undergone oxidative decay, ultimately leaving nothing but a pale double cuticle; when less decayed they have value because they show that the only robust cell walls inside the leaf are in the midrib. There are no hypodermal fibres and the margins only look dark when folded. Sometimes mesophyll cells are preserved and sometimes in folds in the cuticle the papillae are seen in lateral view.

The leaves of different shoots vary moderately in size and also in the development of papillae, but papillae are never absent from the stomatal bands. As in *Marskea*, leaves with strongly developed papillae tend to have obscure cell outlines in the stomatal band. The fine mottling of the cell surface noted by Florin may be caused by pits but requires examination by electron microscopy.

**Classification.** I agree with Florin that *E. sideriticus* cannot be classified on present evidence. Its delicate shoot looks more like a *Selaginella* than a conifer, but *Selaginella* leaves have a different epidermal anatomy and scarcely any cuticle. *E. sideriticus* has a well-developed cuticle, occasionally 10 µm thick at the top of papillae. The stoma of *E. sideriticus* is like that of *Marskea* but the stomatal distribution is different. I searched the matrix for pollen where it is
Fig. 62. *Elatocladus sideriticus* (Bose)

the commonest species but saw nothing peculiar, nor were there any significant seeds or cone scales.

**Occurrence.** The type locality is in the Middle Deltaic Sycarham Series, a few metres above the Iron Scar (Eller Beck Bed) at Haiburn Wyke. *E. sideriticus* is abundant in a thin layer which seems to be of limited horizontal extent and has been difficult to find again. Leaf fragments have been obtained by bulk maceration of rocks from three localities of the Sycarham Series about 2 km north of the type locality, and at Trough House, Glaidsdale Moor. The hand specimen shown in Fig. 61 L, M is also from Trough House, a locality of the Middle Deltaic but of unknown relation to the Eller Beck Bed.

**Genus Bilsdalea** Harris 1952

**Emended Diagnosis.** Ultimate shoots known only; stiff, straight, unbranched. Leaves borne in a simple helix, uppermost small but not forming bud scales, persistent though ultimately breaking off irregularly near their bases.

Leaf linear, flat, apex normally obtuse; base tapering but not forming a petiole, twisted and bent to spread lamina horizontally and then continued as a decurrent cushion; margins sharply angular, midrib well marked on lower surface but not very prominent; probably including a resin canal. Scattered fibres present in lamina except at margins; no thickened hypodermis present.

Stomata limited to two abaxial bands, orientation longitudinal, mostly forming short files. Guard cells sunken in narrow pit; surface of lateral subsidiary cells thickened near pit and near outer edge but with thin strip between thickenings. Terminal subsidiary cells scarcely specialized but covering guard cell poles. Unspecialized lateral subsidiary cells often present.

Ordinary epidermal cells typically rectangular, elongated; not or only obscurely papillose. (Trichomes absent apart from occasional bulging cells at leaf apex.)

**Type Species.** *Bilsdalea dura* Harris (1952: 374).

*Bilsdalea dura* Harris 1952

Figs 63–65

1952 *Bilsdalea dura* Harris: 374, text-figs 6–8, 9 A, D, F. (Figures mostly repeated here)
1958 *Bilsdalea dura* Harris; Florin: 315; pl. 31, figs 1–9; pl. 32, figs 1–4; pl. 33, figs 1–6. (Shoots, cuticle, discussion)

**Emended Diagnosis.** Axis of ultimate shoots at least 1·5 mm broad below, tapering upwards, bearing leaves in 2 + 3 parastichies, blades spreading at about 45°, rather crowded and often in contact. Decurrent cushions prominent, continuing undiminished until overlapped, separated by narrow grooves; internode surface at any level commonly showing three cushions.

Leaves usually straight, commonly 20–30 mm long and 1·5–2·0 mm wide (but shorter and narrower near stem apex). Distal part of leaf tapering only slightly and commonly ending in rounded or obtuse apex, occasionally tapering to acute or acuminate apex; proximal part tapered gradually to one-third of full width but remaining broader than thick to point of attachment.

Leaf surfaces glossy, interior normally opaque; if leaf cleared by decay midrib conspicuous as dark strand and lamina traversed by separate fibres about 2 mm long. In most leaves (ones with obtuse apex) midrib becoming broader and denser near apex, substance of lamina at sides of midrib also becoming denser and finally merging with midrib at apex. At apex epidermis and
Fig. 63. *Bilsdalea dura* Harris

Shoots and leaves, all isolated by bulk maceration except L–N, A–F, ×4; G, ×12.5; H–N, ×2. A, B, both sides of V.29318 from Cloughton. C, D, both sides of the lectotype, V.29310, from Cayton. E, F, both sides of V.29311 showing cups of scales. G, same cups in detail, Cayton; see also Fig. 65 D. H–K, short leaves from Cayton and Cloughton; H, V.29321; I, J, V.29312; K, V.29320. L–N, long leaves from Whitby, V.29317. All figures are from Harris (1952).

cuticles missing, interior tissues exposed. (In acute or acuminate leaves midrib slightly or not at all enlarged and cuticle often intact.)

Leaf margins entire, showing one or two superimposed files of elongated thick-walled cells; near leaf apex files meeting margin at a small angle (but never projecting as teeth or as scarios frill).

Cuticles very firm, about 7 µm thick (but less in stomatal bands), upper slightly thicker over midrib and at extreme edges. Cells of upper nearly uniform, length typically four times width.
but sometimes broader and shorter over midrib. Anticlinal walls strongly marked by inwardly-projecting ridge, straight or slightly undulating, often interrupted. Surface wall either flat and evenly thick or slightly thicker in middle region, never papillose; occasionally showing median thin strip or a number of small thickened areas.

Lower cuticle divided into midrib region, lateral regions and stomatal bands placed half way between midrib and margins. Cells over midrib often longer than on adaxial side and anticlinal walls occasionally showing jagged extensions onto cell surface. Cells of marginal regions as on adaxial surface but interior often showing a thinner marginal area round a slightly thickened middle area or two elongated thicker strips separated by thin strip.

Stomatal bands up to 0.4 mm wide, narrowing towards leaf base and at apex; up to 10 files of stomata and some scattered stomata present, spacing of stomata in a file uneven; occasionally two stomata sharing a terminal subsidiary cell but lateral subsidiary cells never shared (though sometimes in contact). Exceptionally terminal cells thickened, continuing thickenings of the lateral subsidiary cells. Thickening of subsidiary cells scarcely raised above general surface.

Epidermal cells at apex of obtuse leaves short and of irregular shape, cell surface occasionally raised to form a hollow bulge. (Apex of acute leaves not specialized.)

Lectotype. V.29310, selected by Florin (1958).

Discussion. About 90 per cent of Bilsdalea leaves have obtuse apices, 5 per cent acute and 5 per cent transitional. Those with acute apices show nothing unusual, the midrib diminishing upwards, the interior remaining unchanged and the cuticle being intact to the apex. In all the obtuse leaves, however, the apical region is specialized in a way unlike any other conifer known to me. Over most of the leaf the coaly interior is uniform, whether partly cleared by decay or not, but just below the apex it becomes much denser. The midrib also becomes broader and thicker (darker) and at the apex merges with the other interior substance. The cuticle of the apical region is fairly normal except that the cells are shorter and some may bulge; then, just short of the tip, both upper and lower cuticles are abruptly and unevenly broken, the fracture being across cells and occasionally across a stoma. A tiny portion of the interior tissue may project above the cuticle as a crumbly coal of dull surface, contrasting with the glossy cuticle. The coal dissolves completely on maceration, revealing no recognizable structure.

After search through about a hundred obtuse leaves isolated by gentle bulk maceration with cold water, two leaves were found which possibly show intact apices. One of these was in process of breaking away and maceration completed the break. The cuticle which broke away was fairly thick, so I concluded that the break was caused by weakness of the internal tissues rather than by the cuticle. The other apparently intact leaf was preserved without further study. I feel sure that most of the broken ends of obtusely pointed leaves were broken before extraction by bulk maceration for the break is obvious in leaves exposed in unmacerated hand specimens. Compressed leaves show the nearly transverse break as a slit in the cuticle. Ordinarily the cuticle may be paler and softer below the break but this is artificial and caused by the more rapid entrance of the Schultz’ mixture through the break, an effect avoided if leaf tips are cut off before maceration so that it can enter from below as well.

I cannot offer a satisfactory explanation for the specialized leaf apex of these obtuse leaves of Bilsdalea. A possibility considered was that it represents a hydathode; the enlargement of the midrib, the short cells, the irregular stomata and the massive internal tissue (a possible epithem) all being consistent with this. The break in the epidermis is not, however, consistent. Many angiosperms have apical hydathodes but I do not know a conifer that has one. Another
Fig. 64. Bilsdalea dura Harris
possible comparison is with the 'food bodies' produced by a few tropical angiosperms, for example certain species of *Acacia*.

Although the biological reason for the specialized leaf apex of *Bilsdalea* is open, the gap in the cuticle provides a useful and unusual taxonomic character. It was missed by Harris (1952) and by Florin (1958) but once recognized is easily seen.

I imagine the rare intact leafy shoots of *Bilsdalea* were torn off prematurely by violence, but I do not believe the detached leaves, even though sometimes found in large numbers, had been abscissed. The evidence suggests instead that they died while still attached to the shoot, later

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Fig. 65. *Bilsdalea dura* Harris

A. upper cuticle, V.29315. B, lower cuticle, cells unusually narrow, V.29323. C, lower cuticle of a leaf with few encircling cells, V.29324. D, cuticle from one of the scales forming the cup shown in Fig. 63 G, V.29311a. E, stomatal band under phase-contrast lighting to show thickenings of cells, V.29322. F, whole lower cuticle to show distribution and orientation of stomata, V.29315. G, one stomatal band of F. Figures from Harris (1952); all ×200 except E, ×500 and F, ×20.
breaking off irregularly near their bases when they had become brittle. Although in living conifers this is an unusual method of leaf shedding, it does occur. It is normal for example in *Araucaria araucana* (Molina) K. Koch and a few other species of *Araucaria*, and also occurs occasionally in some species of *Picea*. Unfortunately we do not yet know a defoliated shoot of *Bilsdalea dura* which might test this idea.

The available leafy shoots of *B. dura* have rather short leaves, up to 2.5 cm long, though longer leaves are known detached. Leaves longer than 3.5–4.0 cm are rare, and my earlier statement (1952) that the leaf may be up to 8 cm long is doubtfully correct.

The statement that there may be a resin duct is based on certain naturally cleared leaves in which there is a paler streak along the midrib. The same leaves often show scattered fibres and sometimes various mesophyll cells but never show any hypodermal cell walls beneath the epidermis.

A shoot showing rosettes of scales which may mark the bases of male cones is shown in Fig. 63 e–g. Each rosette is about 1–2 mm wide and under 1 mm long, and in the centre is a scar 0.75 mm wide. The scales have rather thin cuticles. Harris (1952), besides suggesting that these rosettes might be bases of male cones, also suggested that they might be basal scales of taxaceous ovules or of vegetative buds. However, *Trulla*, the female cone now assigned to *Bilsdalea*, cuts out the ovule idea. The possibility of vegetative buds is also unlikely because the shoots have diminutive leaves at their apices, not buds enclosed in broad scales. If *Bilsdalea* should prove to have borne its male cones in little cups of scales it would be like many living conifers.

**Comparison.** *Bilsdalea angustifolia* Florin 1958: 339, from the Jurassic of Bornholm, is distinguished by its narrow acuminate leaves with fewer stomatal files.

**Occurrence.** *Bilsdalea* occurs throughout the Deltaic Series but is rare in the Upper Deltaic. Occasional leaves are met with in nearly all the rich plant beds and its robust cuticle, bright brown colour and well-marked structure make it easy to recognize among the fragments obtained by bulk maceration. It was only twice found as the most abundant species, in the classic beds of Gristhorpe and Cloughton, and there it was abundant for only one or two metres horizontally. In these horizons alone intact shoots and reproductive fragments were found. The distribution suggests a species that occurred widely in the flood plain, but in small numbers.

<table>
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<th>Horizon</th>
<th>No. of locs</th>
<th>% of locs with determinable plants</th>
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<td>2%</td>
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<tr>
<td>Middle Deltaic Gristhorpe Series</td>
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<td>Middle Deltaic Sycarham Series</td>
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<td>Lower Deltaic</td>
<td>22</td>
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**Genus TRULLA nov.**

**Diagnosis.** Female cone (known from detached fragments only): axis of cone bearing radiating fertile appendages probably in a globose mass. Appendages elongated, spaced widely, each consisting of a slender stalk expanding distally into a flat, rounded head. Stalk and abaxial surface of head thickly cutinized; adaxial surface of head cutinized only at its edges, inner region (imperfectly known) forming pad with denuded surface but probably bearing several seeds. Seeds attributed to cone oval, flat.
NAME. From the Latin trulla, a small spoon, referring to the shape of the appendages.

TYPE SPECIES. Trulla nitens sp. nov., the only species.

Trulla nitens sp. nov.

Fig. 66; Pl. 7, figs 11–14

DIAGNOSIS. Cone nearly 2 cm wide; length of fertile appendages about 8 mm, the distal 2.0–2.5 mm of which is the expanded head. Stalk of appendage about 0.7 mm wide, probably oval in section and enclosing three thick vascular strands, its surfaces glossy and smooth. Abaxial surface of head also glossy but adaxial surface denuded (after loss of seeds) and uneven, not glossy. Cuticle of stalk and of head about 10 μm thick, becoming thinner near margins of head. Cells on most of stalk mainly rectangular and forming longitudinal files, dimensions varied, typically 140 μm × 30 μm, becoming shorter and less regular near head. Anticlinal walls marked by strong, straight, inwardly-pointing ridges, occasionally interrupted and sometimes showing minute jagged extensions onto cell surface; surface wall flat, finely mottled or obscurely marked by longitudinal striations. Stomata few, in two narrow bands near margin of abaxial surface only; other surface similar except for absence of stomata. Each stomatal band comprising about two files of stomata near base of stalk but stomata near head more widely scattered. (Trichomes absent.)

Stomata on most of stalk longitudinal; pit narrow, elongated and surrounded by elongated group of subsidiary cells but near head subsidiary cell group irregular or rounded. Typically two lateral subsidiary cells present on each side of pit, surface of lateral cell thickened near pit and near outer margin but with thin strip between. Lateral encircling cells often present, unspecialized. Terminal subsidiary cells usually unspecialized. (Stomata of irregular shapes also occurring.)

Cuticle of abaxial surface of head divided into inner and marginal regions. Marginal region scarious, less thickly cutinized than inner region, composed of single layer of radially elongated cells up to 200 μm × 20 μm, but often divided transversely into two cells about 100 μm long. Margin irregularly divided into lobes or teeth composed of more than one cell. Cells of inner region of irregular or isodiametric polygonal shape, anticlinal walls sharply marked, straight; surface wall flat, unmarked. A very few scattered stomata present, their shapes irregular but subsidiary cell group often rounded. (No trichomes present.)

Adaxial surface retaining only a few cutinized epidermal cells next to marginal region; cells like abaxial ones.

Seeds attributed to cone about 1.1 mm × 0.9 mm, substance thin, delicate; surface showing small cells in longitudinal files (probably related to those in cuticle). Cuticle 1–2 μm thick, showing isodiametric cells about 30 μm wide, anticlinal walls straight, finely marked, surface flat. (Internal cellular cuticles present but details uncertain; no megaspore membrane observed.)

HOLOTYPE. V.58853; Fig. 66 D, J–L, N, O; Pl. 9, figs 13, 14.

NAME. Latin, nitens, shiny.

DISCUSSION. The available material consists of two broken cones and a few separately-preserved cone appendages which were macerated out of the matrix providing the cones. The smaller specimen had been broken before deposition but the larger may well have been complete, becoming broken only during collection.

I feel sure that Trulla belongs to Bilsdalea. The specimens were collected in a small region of
Fig. 66. *Trulla nitens* sp. nov.

A–C, detached cone scale seen from above (A), below (B) and as cuticle (C), latter showing stomata of abaxial surface and edge of adaxial cuticle (dotted line); V.59022, ×16. D, two seeds, macerated fragments, V.58853a, ×16. E–G, detached cone-scale from above, below and as cuticle; hole caused in preparation; V.59023, ×16. H, I, imaginary transverse and longitudinal sections through E; cuticle shown by firm line, bare coal surface without line. J, K, seed cuticle fragments macerated from holotype; short lines indicating direction of cell files, J showing possible micropyle; V.58853b, ×50. L, abaxial cuticle of cone-scale stalk, from holotype. V.58853c, ×200. M, stomata from stalk of G, ×200. N, possible nucellar cuticle; O, integument cuticle; from same seeds as J, K, ×200. P, stoma on head of G, ×400. Q, margin of G, transverse lines representing torn bits of adaxial cuticles; ×200. All specimens from Cloughton *Solenites* Bed, cliff exposure.
the Cloughton Solenites Bed where most of the Bilsdalea shoots were found, whereas elsewhere in the bed only occasional Bilsdalea leaves are met with and Trulla was not seen. There is also structural agreement between Bilsdalea leaves and the appendage stalks. Both are brown and glossy and a stalk might easily be taken for a leaf. Their ordinary epidermal cells are exactly similar and so are many of the stomata.

There are, however, differences. The appendage stalk is probably thicker than the leaves and its edges are rounded rather than angular. It seems to have three vascular bundles instead of one. The stalk has fewer stomata and these are in narrow bands near the margin. The expanded head has no resemblance in form to the leaf and its cuticle is also different.

The attribution of Trulla to Bilsdalea rules out many possibilities about classification, for instance my idea that Bilsdalea might be allied to Amentotaxus, an idea which Florin (1958: 316) rejected on other grounds. However, though I feel sure that Trulla is a female cone, the only secure morphological facts are that it is composed of spoon-shaped appendages with a denuded surface. I cannot even be sure that the ill-known seed-like bodies really belong to it or are seeds at all. Only by adding imaginary data can anything approaching normal cone scales be envisaged; for instance that the appendage is a combined bract and ovuliferous scale, the lower surface being the bract and the pad part of the ovuliferous scale denuded of its upper surface and seeds.

I should stress that no definite seed was seen, merely that a fragment of a head accidentally removed in degagement yielded delicate cuticle fragments which might represent integument, micropyle and nucellus; and that two small oval bodies lying over an appendage stalk when macerated yielded delicate cuticles rather like the supposed integument. Much rock surface from near where the specimens were found was searched carefully but no separate seeds were found, nor were any recovered when the waste rock was macerated in bulk with water.

There is clearly much to learn about this cone.

**Genus LINDLEYCLADUS** nov.

**Diagnosis.** Ultimate shoots caducous, unbranched; of strictly limited growth (main stems unknown). Leaves borne helically, bent and twisted at their bases to spread the leaf blades in the horizontal plane; readily abscissed from axis. Leaf lanceolate, base strongly contracted but scarcely petiolate, distal end tapering to blunt point. Veins numerous, equal, forking near leaf base but then unbranched; becoming parallel briefly and then converging towards apex but outer veins ending by meeting margins at a small angle. (Veins not observed at extreme base of leaf; no ducts or secretory bodies observed between veins.)

Cuticles delicate; upper epidermal cells almost uniform, straight-walled. Lower epidermis divided into vein strips with rectangular cells forming files and stomatal strips with smaller, polygonal cells. Stomata orientated longitudinally and forming files separated by ordinary cells, guard cells slightly sunken in rectangular pit. Terminal subsidiary cells elongated, sometimes shared with next stoma but usually separate; lateral subsidiary cells broad, often one on each side of stoma (but sometimes two), cuticle thickened but scarcely overhanging at edge of pit, surface sometimes showing faint ridge parallel with pit. Lateral subsidiary cells never shared with next stoma and usually separated by ordinary cells. (Encircling cells absent; trichomes absent.)

**Type species.** Zamia lanceolata Lindley & Hutton 1836: pl. 194.

**Name.** After the pioneer palaeobotanist Dr J. Lindley.
DISCUSSION. *Lindleycladus* is distinguished from *Podozamites* by its longitudinally rather than transversely orientated stomata, which are placed in longitudinal files. In its longitudinally orientated stomata it is more like *Araucariodendron* Krasilov (1967), though it differs in that the stomata are regularly monocyclic rather than dicyclic.

*L. lanceolatus* has, however, been included for many years in *Podozamites* Braun. This imperfectly typified genus was established by Braun (1843: 36) for part of *Zamites*. I quote him verbatim.


Zur ihr gehören: Zamites distans. Presl; Zamia lanceolata. Lindley and Hutton; und noch die 4 neuen Arten von hier etc.’

Though Braun designated no species as type of *Podozamites* I consider that the first species he mentioned was intended as Type, in this as also in other genera he described. The first species is generally the one which fits the diagnosis best and is not necessarily the earliest described (*lanceolatus* was in fact described before *distans*). In this I agree with other authors, including Andrews (1955). Thus when a generic difference is recognized between the two species of *Podozamites*, it is *P. lanceolatus* that needs a new generic name. Most Recent conifers have longitudinal stomata, but some have them transverse and some at random orientation; no genus has some species with longitudinal, others with transverse stomata. At family level, however, e.g. among Taxodiaceae, different genera may have different stomatal orientations.

Cuticles of *Podozamites* showing transverse stomata, determined either as *P. distans* or as some other species, have been figured by Harris (1935), Florin (1953), Turutanova-Ketova (1963), Doludenko (1966) and Krasilov (1967). (Schenk (1867: pl. 36, figs 9a, b) figured a stoma of *P. distans* so different from anything figured later that I suppose there was some mistake.)

I have no doubt that what I call *Podozamites distans* (Presl) and *Lindleycladus lanceolatus* (Lindley & Hutton) belong to wholly distinct genera, distinguishable microscopically. However, there may be doubt about their correct specific names since the cuticle of neither of the holotypes is known, merely that of specimens identified with the holotypes. *P. distans* (with transverse stomata) has its leaves broadest in their middle region where the margins and veins are parallel and it has rather conspicuous veins at slightly under 2 per mm. It has scales at the base of the shoot, the permanent stem is very thick (Weber 1968) and it is linked with the female cone or cone scale *Cycadocarpidium* (though for some reason only in the older part of its range). On the other hand the leaf of *L. lanceolatus*, with longitudinal stomata, is broadest well below the middle and then tapers to the apex; the veins are very slender and typically 3 per mm. Basal scales, main stem and fructifications are unknown. It should be noted that the main stems figured by Weber (1968) were called *P. lanceolatus* because he treated *P. distans* as a synonym. We know nothing about the main stem of *Lindleycladus*.

Nathorst (1911) was the first to show that the leaves of *P. distans* are attached in a helix. Florin (1953) gives an interesting account of the change of opinion from Braun’s (1843) idea that *Podozamites* is a simply pinnate cycad leaf to the idea that it is a conifer shoot bearing simple leaves, a change extending over almost a century. Seward (1900) came near to Nathorst’s idea when he observed that a Yorkshire specimen had some of its leaves attached laterally, others on top, but he left *Podozamites* as a vaguely classified cycad.

Though not all the leaf bases of Seward’s specimen, 39303, can be seen clearly, re-examination showed that the lower 13 conform to a helix in which successive leaves are at 140°, just over the ideal angle of 137.5° (Harris 1976), but the upper leaves require a larger angle. The irregular attachment mentioned by Seward remains possible for this and indeed for other specimens too.
**Taxonomic Position.** I have no doubt that *Lindleycladus* is a conifer but as it is not securely linked with any cone it can only be placed in a family tentatively. In this spirit I place it in the Podozamitaceae (*Cycadocarpidium*), a family consisting of a compact and satisfactory core of *Cycadocarpidium, Podozamites distans (sensu stricto)* and a few other species resembling it. Alvin *et al.* (1967) use the family name in this sense, but most authors include less satisfactorily known fossils which have no better family assignment and form a diffuse mantle. These include ill-known as well as microscopically different specimens determined as *Podozamites*, besides the rather similar *Angariella Prinada*, the less similar *Caveophyllum Migatcheva*, the very different female cone *Swedenborgia* (linked with species of *Podozamites*) and some rather diverse associated male cones and dispersed pollen grains. All authors agree about the core of the Podozamitaceae, but each has his own idea of what should be included in the mantle (Sze 1931, Turutanova-Ketova *et al.* 1963, Krasilov 1967, Němecj 1968, Stanislavskii 1971). I now include *Lindleycladus* in the mantle though others may disagree.

*Lindleycladus lanceolatus* (Lindley & Hutton) comb. nov.
Figs 67, 68

Yorkshire specimens.
1843 *Podozamites lanceolatus* (Lindley & Hutton) Braun: 36. (Name)
1875 *Zamites lanceolatus* (Lindley & Hutton) Phillips: 225, lign. 54. (Rough sketch of holotype)
1900a *Podozamites lanceolatus* (Lindley & Hutton) Seward: 15. (Notes on holotype)
1900 *Podozamites lanceolatus* (Lindley & Hutton); Seward: 242, text-fig. 44. (Drawing of specimen 39303; discussion)

**Emended Diagnosis.** Axis of caducous shoot 13 cm or more long, width near base 2 mm but tapering distally to less than 1 mm; base slightly expanded, truncate, without scale leaves. Surface of axis smooth apart from ridges and furrows decurrent from leaf bases. Leaves borne either singly, probably in a simple helix, or in opposite pairs in a double helix; gaps between blades variable but typically as wide as blade. Lowest leaves borne at 90° to axis but most leaves at 30°–60°, uppermost leaves almost parallel with axis.

Leaf blade lanceolate, almost straight; largest known about 11 cm × 1 cm but most leaves 7–8 cm × 6–7 mm at their broadest point; smallest observed 5-5 cm × 3.0 mm. Blade at its broadest below the middle, often at 1.5–2.0 cm from base; tapering almost evenly from this point but apex a semicircle about 1 mm wide. Base of leaf narrowed to 1.5 mm (often compressed obliquely and appearing narrower), often curved in direction of shoot base, particularly in lower leaves. Veins typically about 25 per cm at widest point but barely 20 in broadest leaves and up to 30 in narrowest leaves; in all leaves veins converging towards apex and becoming less distinct, in distal half some veins meeting margins at about 1° and only two-thirds of veins reaching apical regions; ultimate concentration about 6 per mm. Margins originally rounded in section (cuticle showing several crushed cells at edge).

Upper surface of lamina mostly flat but slightly hollowed near base, veins and margins scarcely raised. Whole surface marked with close-set longitudinal ridges 60 μm broad and up to 500 μm long (? hypodermal fibres), epidermal cells only faintly marked. On lower surface veins distinctly raised and margins often more strongly raised and broader than veins. Epidermal cells over veins and by margins forming long files, those between veins short and files less distinct.

Upper cuticle about 2 μm thick; epidermal cells nearly uniform, more or less rectangular, typically 50 μm × 25 μm, forming longitudinal files; end cell of file pointed, veins not marked or
Fig. 67. *Lindleycladus lanceolatus* (Lindley & Hutton)
A, detached leaf, V.58854. B, shoot with narrow leaves, Yorkshire Museum. C, lower region of shoot, V.58855. D, typical shoot, Yorkshire Museum. E, shoot and separate detached leaves, Hancock Museum, Newcastle; see also Fig. 68 B, D, F. Leaf pairs are numbered and detached leaves marked x. Specimens A, C are from Whitby Plant Bed, the others unlocalized. All figures ×1.
possibly marked by about two files of narrower cells. Anticlinal walls straight, occasionally interrupted, finely marked; surface walls flat, evenly thick, cell corners often thickened.

Lower cuticle about 1 μm thick but thicker at margins, divided into vein regions and stomatal tracts between veins. Anticlinal walls as on upper epidermis but more finely marked. Cells over veins large, 60–100 μm × 20 μm, forming well-marked files. In stomatal tracts, cells nearly isodiametric polygons often about 30 μm × 20 μm, files indistinct. Stomata forming 3–4 well-marked files. Polar subsidiary cells slightly thickened near ends of pit (but thickening possibly belonging to guard cells); lateral subsidiary cells forming continuous thickened rim next to pit, guard cell surface very thinly cutinized. (Cutanized hypodermal cells and trichomes absent from both surfaces.)

**Holotype.** Specimen figured by Lindley & Hutton 1836: pl. 194.

**Discussion.** Specimen K.284 in the Sedgwick Museum shows the shoot base, but only as an imprint. The stem increases to 3 mm wide at the very base, which is truncate, and the surface is smooth apart from faint grooves.

The form of the leaf base is only seen undistorted in detached leaves. In some it is symmetrical but in others it is rather more extended and also bent laterally, a feature shown well in Sedgwick Museum specimen K.460.

The attached and separate leaves range from 3–10 mm wide, the broader ones being longer than the narrow ones. Many authors have distributed such leaves under several specific names, for instance Fig. 67 A corresponds to specimens named *P. schenkii* Heer and Fig. 67 C to ones named *P. distans* (Presl). I feel sure, however, that all the Yorkshire specimens belong to a single species. Their visible features agree except that the veins are consistently rather more concentrated in the narrower leaves than in those which are broader. There is supporting evidence from their occurrence in the field. For instance, one surface of Phillips’ Whitby block, Oxford Museum J.5001, shows about 25 leaf fragments ranging from the broadest to the narrowest, and intermediate ones, 6–7 mm wide, are most frequent. It seems unlikely that leaves of more than one rare species should be found together in this way on a single bedding plane.

Of the intact Yorkshire shoots known to me, nine have leaves attached singly at a node, two have opposite pairs and I presume that in all these the phyllotaxis is a simple or a double helix. But no specimen is sufficiently well preserved to exclude the possibility mentioned by Seward that the leaves were borne irregularly.

The cuticles of *L. lanceolatus* are delicate and difficult to prepare, the matrix being somewhat coarse-grained. None of the cuticle fragments was more than 1 mm² in area and they included no compression folds which would have shown the original thickness. I base my estimate on the rims of the tiny holes caused by mineral grains. At the folded leaf edge the thickness is 3 μm. All the figures are drawn from fragments of a single leaf, other leaves yielding similar but less good cuticles.

Like those of several *Podozamites* species the leaves of *L. lanceolatus* lack xeromorphic characters of thick cuticles and protected stomata which are normal in evergreen conifers. They agree rather with the deciduous foliage of *Taxodium, Metasequoia* and *Larix*.

Beyond the middle of the leaf the veins approach and end in the margin at intervals of about 1 cm and at a very small angle. The margin is thick (and I assume fibrous). The veins end similarly in certain species of *Podozamites*. In *Araucaria araucana* (Molina) K. Koch the veins reaching the margin end there separately without forming a continuous marginal fibrous strand. In the rather similar leaf of *Ferganiella* the veins meet the margin at a wider angle, about 30°, and appear to end there.
Fig. 68. *Lindleycladus lanceolatus* (Lindley & Hutton)

A, C, E, G, cuticles prepared from one leaf of Phillips' Whitby specimen, J.5001, in Oxford University Museum, duplicate slides in British Museum. B, D, F, details from Hancock Museum specimen shown in Fig. 67 E. A, lower cuticle, vein on left, × 400. B, upper region of leaf 3 right, × 2. C, stoma, × 800. D, veins at apex of B, × 5. E, upper cuticle, a tract of narrow cells possibly marking a vein, × 400. F, lower region of leaf 5 left, showing veins and thick margins, × 5. G, upper cuticle, × 200.
Comparison. *Podozamites distans* (Presl) from the German Rhaeto-Liassic has been identified by many authors with the Yorkshire Bajocian *Lindleycladus* (*Podozamites*) *lanceolatus* (Lindley & Hutton). Both species were based on drawings of a single leafy shoot, the main differences being in the shape of the leaves, broadest below the middle in *L. lanceolatus* but broadest over the whole middle region (where the edges are parallel) in *P. distans*, a small difference. However the several leafy shoots of *L. lanceolatus* known from Yorkshire as well as the more numerous separate leaves all agree in this character and all have slender, crowded veins. Many specimens from Germany and from Rhaeto-Liassic floras of other lands agree with Presl’s type of *P. distans* in leaf shape and in having rather coarser and more widely spaced veins. The cuticles of *L. lanceolatus* and *P. distans* are of course quite different.

Schenk (1867) described numerous shoots which I consider belong to *P. distans* (Presl) and others which I suspect are different. Heer (1876) described a great many specimens from the Lower Cretaceous of Siberia as *P. lanceolatus* which differ from Yorkshire specimens. Since then many specimens have been identified as belonging to one or other of the two species, which, if all were to be accepted, would remove any possible distinction between them. Some authors have named older specimens *P. distans* and younger ones *P. lanceolatus*.

There is as yet no proof that a specimen both agreeing with *L. lanceolatus* in form and matching it in cuticle occurs outside Yorkshire. I have surveyed the records of *Podozamites* and give a list below of those with the best claim to be identical, the slender stems bearing leaves of a size and shape matching one of the Yorkshire specimens. I have in general excluded specimens figured as having coarser and more widely spaced veins but I am not sure that the figures were accurate. The specimens range the Jurassic and Lower Cretaceous of the northern hemisphere.

List of references to leafy shoots agreeing macroscopically with a Yorkshire specimen.

1876 Heer: pl. 27, fig. 8; excluding many other less similar specimens. (Upper Jurassic; Amurland)
1900 Ward: pl. 63, fig. 4; pl. 64, fig. 1, but veins rather few. (Jurassic; California)
1905 Yokoyama: pl. 1, fig. 6 only. (Upper Jurassic; Japan)
1914 Counillon: pl. 4, figs 3, 5; pl. 5, fig. 3 only. (Indochina)
1925 Kawasaki: pl. 33, figs 90–93 only. (Lias; Korea)
1928 Yabe & Oishi: pl. 3, figs 6, 7, 9. (Jurassic; China)
1930 Hollick: pl. 10, figs 2, 3a, 4 only. (Cretaceous; Alaska)
1931 Sze: pl. 7, fig. 1 only. Includes a useful general review of *Podozamites*. (Lower Jurassic; China)
1939 Kawasaki: pl. 15, figs 59–61; pl. 16, fig. 63. (Lias; Korea)
1955 Kimura: pl. 2, fig. 8. (Lias; Japan)
1959 Kräusel: pl. 2, figs 8, 9; pl. 3, figs 12a, b; other specimens are *P. distans*. (Rhaeto-Liassic; south-west Germany)
1964 Benda: pl. 10, fig. 5 only. (Middle Jurassic; Afghanistan)
1966 Genkina: pl. 55, fig. 8; pl. 56, figs 1–5. (Issyk-Kul, central Asia)
1971 Stanislavskii: text-figs 50, 52, 53 only. (Rhaetic, Donbass)

Besides these specimens with the best claim to be identical there are, in order of decreasing claim, detached leaves of suitable macroscopic character, records without figure or figures of indeterminable specimens, leaves whether separate or attached of different shape and, finally, a few records of leaves of known but clearly distinguished cuticle structure. These include *P. ex gr. lanceolatus* Krasilov (1967) from the Lower Cretaceous of eastern Siberia.

Occurrence. *Lindleycladus lanceolatus* is restricted to a few localities in Yorkshire. Detached leaves were abundant in a layer of the Whitby Plant Bed when it was well exposed in about 1950. Blocks collected there by Phillips and by Halle are represented at Oxford and Stockholm respectively. There are similar leaves on Whitby blocks in the Sedgwick Museum, but intact shoots are rare and the only specimen definitely from Whitby is one collected by
Hamshaw Thomas and shown in Fig 67 c. The other shoots figured here, as well as the one figured by Seward (1900) and three at the Sedgwick Museum, are unlocalized. They are all in a similar hard matrix and may have been collected at the same place, possibly Haiburn Wyke where Williamson collected the holotype. There is also a specimen in Stockholm collected by Mr Sewell in Westerdale. Probably all the material is from the Lower Deltaic.

Genus CARPOLITHES Schlotheim 1820

Carpolithes (or Carpolithus) may be used for any kind of fossil seed or fruit and has no type species (Andrews 1955). It is used here for a seed that has sufficient specific peculiarities for its description as a binomial but is insufficiently known to be included in a more precisely defined genus.

Carpolithes cepa sp. nov.

Pl. 7, figs 7, 9


Diagnosis. Seed of broadly oval shape, 8–12 mm long × 8–16 mm broad, substance thick at basal end becoming thinner towards apex and margins. Surface, ? denuded before preservation, showing numerous ribs running from base to apex; each rib consisting of a loose bundle, about 300 μm broad, composed of thick-walled elongated cells up to 500 μm long × 70 μm broad.

Traces of a thick cuticle (?) = outside of integument) with large, straight-walled approximately rectangular cells about 150 μm × 70 μm. Thin cellular cuticule (?) = nucellus) with finely marked narrow cells. Megaspore membrane robust, probably rounded (its thickness was not satisfactorily measured), composed of granules 1–2 μm wide separating cavities of same width. (No rod-like bodies observed and no cellular marks visible on membrane surface.)


Name. Latin, cepa, an onion.

Discussion. The specimen figured by Phillips and here selected as lectotype is from Whitby, as are a number of other specimens in the British Museum and at the Riksmuseum, Stockholm. There is a block collected by Dr E. M. Berridge and thought by her to be from Whitby which has several seeds including one that gave cuticles on maceration. The specimens are mostly uninformative, being mere imprints or retaining little of the coaly substance.

The onion-like outline and markings suggested the name cepa but it is likely that the seed was originally rather flat in section, particularly near the edges, as there is no apparent distortion of the matrix.

The large megaspore membrane of C. cepa shows that it is a seed. Phillips (1875: 233) suggested that it might belong to his 'Sphaereda paradoxa', another name for Beania gracilis Carruthers, but that fossil has different seeds. He also suggested that it might belong to the obscure fossil of his lign. 66.

There are no structural details of C. cepa known to me that suggest its family or origin. However, the field occurrence suggests a possible link with Lindleycladus. The lectotype has two Lindleycladus leaves, and another specimen (Sedgwick Museum K.1203) has three at least. This establishes that they sometimes occur in the same assemblage at Whitby but does not link them;
I merely record the association so that when the Whitby Plant Bed is again well exposed further material may be searched for.

If *C. cepa* should prove to be the seed of *Lindleycladus* it would differ considerably from that of *Cycadocarpidium* in being 5–10 times as large, with a weight doubtless correspondingly greater. *Cycadocarpidium* cone scales look well suited to have been wind-dispersed but I imagine that *C. cepa* was borne and dispersed differently.
REFERENCES


The Yorkshire Jurassic Flora


Lebour, A. G. 1877. Illustrations of fossil plants: being an autotype reproduction of selected drawings prepared under the supervision of the late Dr Lindley and Mr W. Hutton . . . (c.) vi + 139 pp., 64 pls. Newcastle-upon-Tyne.


Lindley, J. & Hutton, W. 1831–37. The fossil flora of Great Britain; or, figures and descriptions of the vegetable remains found in a fossil state in this country. 1 (1831–33), li + 223 pp., pls 1–79, 2 (1833–35), xxviii + 208 pp., pls 80–156, 3 (1835–37), 208 pp., pls 157–230. London. (See also Lebour 1877.)


Solms-Laubach, H. Graf zu 1891. Fossil Botany, being an introduction to Palaeophytology from the standpoint of the botanist. 401 pp., text-figs. Oxford.


Turutanova-Ketova, A. I. 1950. [Some Jurassic seeds and flowers of gymnosperms from central Asia and southern Khazakstan.] Vop. Paleont., Leningrad, 1: 273–347, 5 pls, text-figs. [In Russian.]


Vakhrameev, V. A. 1964. [Jurassic and Early Cretaceous Floras of Eurasia and the paleofloristic provinces of this period.] Trudy geol. Inst. SSSR, Moscow, 102. 263 pp., 49 figs. [In Russian.]

——, Dobruskina, I. A., Zaklinskaya, E. D. & Meen, S. V. 1970. [Palaeozoic and Mesozoic floras of Eurasia and phytogeography of this period.] Trudy geol. Inst. SSSR, Moscow, 208. 426 pp., 47 figs, 4 tables. [In Russian.]


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**Bold type** indicates a new generic name.
ERRATA

This being the final volume of the *Yorkshire Jurassic Flora*, the opportunity is taken to make a number of corrections to earlier volumes.


p. 72, diagnosis of *Marattia anglica*, line 5. Vein concentration 10–12 per cm, not per mm.

p. 133, Fig. 46 D. Not V.25840; possibly slide no. V.52378.


1: Omissions

The following British Museum registration numbers are now available for specimens figured in volume IV.

p. 18, Fig. 5: *Ginkgo sp. cf. sibirica* Heer. A, V.56445; B, V.58618; C, E, V.58619; D, V.58620; F, V.58621; G, V.58619; H, V.56638; I, V.56445; J, V.56640.

p. 23, Fig. 6: *Ginkgo longifolius* (Phillips) Harris. A, V.58629; B, V.58630; C, V.58631; F, 39280.

p. 24, Fig. 7: *Ginkgo longifolius* (Phillips) Harris. B, V.58632.

p. 45, Fig. 15: *Sphenobaiera longifolia* (Pomel) Florin. B, V.58635; C, V.58636.

p. 49, Fig. 16: *Sphenobaiera ophioglossum* Harris & Millington. D, also from V.56466.

p. 58, Fig. 19: *Eretmophyllum pubescens* Thomas. B, V.58643; D, V.58644; E, V.58645; F, V.56467; H, V.58646; I, V.58647.

p. 64, Fig. 20: *Eretmophyllum whithiense* Thomas. B, V.58694; C, V.58695; D, V.58696; F, V.58697; G, V.56469; H, V.58698; I, V.58699.

p. 69, Fig. 21: *Pseudotorellia tibia* Harris & Millington. B–E, V.56464a.

p. 96, Fig. 28: *Czekanowskia furcula* Harris & Miller. B, V.28393b.

(The specimens in Figs 19 C and 20 A appear to be lost.)

2: Errors and re-registrations

p. 19, line 4. Continue first sentence as ‘, 0° 26’ 52” W., the Beast Cliff *Ptilophyllum* bed’.

p. 21, line 13. Insert ‘g’ in ‘Ginko’ to read ‘Ginkgo’.

p. 24, last line. Figs A, D, F–I are from Harris 1946a, not 1946.

p. 25, last line. Figs B, C are from Harris 1946a, not 1946.


p. 31, line 1. Replace ‘slide A’ with ‘slide V.6475a’.

p. 33, caption line 3. Replace ‘fig. 4A, B’ with ‘fig. 5A, B’.

p. 39, diagnosis line 2. Replace ‘distant’ with ‘distinct’.


p. 50, discussion, line 12, second sentence. Delete ‘shown in Text-fig. 17 B’ and replace by ‘so far collected’.

p. 60, line 8. Insert ‘are’ after ‘thickening’.


p. 64, fig. E is V.56469a, not V.56469.


p. 92, synonymy. Delete Fig. 1 F.

p. 94, Holotype. Replace with V.28393a, b (Pl. 5, fig. 2; Text-figs 26, 27 A, B, 28 A, B).

p. 95, caption, line 1. ‘V.28393’ should read ‘V.28393a’.


p. 100, *Czekanowskia thomasi*. Insert synonymy, ‘?’ Harris, 1951. *Solenites vimineus*. T. fig. 1 F.

p. 103. caption, line 1. Replace 'V.56492' with 'V.56421a' and 'V.56491' with 'V.56423a'. Insert after 'C-E', 'slide V.56420a'.

p. 104. Discussion and occurrence, line 4. Replace 'are the same as' with 'are the same species as'.

p. 105. caption, lines 5 and 6. Replace 'V.56497' with 'V.56429a' and 'V.56496' with 'V.56431a'.

p. 106. line 7. Insert 'walls' after 'surface'.

p. 108. line 2. Replace '1,500' with '600 productive'.

p. 111. Replace 'Pl. 6, fig. 6.' with 'Pl. 6, figs 5, 6;'.

p. 116. description, line 3. Replace 'Spaereda' with 'Sphaereda'.

p. 117. caption, line 4. Replace 'V.28508' with 'V.28568'. Caption, line 6. A–D are all new drawings.

p. 123. line 16. Replace 'Tsugipollenites' with 'Tsugaepollenites'.

p. 125. line 5. Replace 'three' with 'two'. Line 6. Replace 'three' with 'four'.

p. 130. last line. Replace 'Txaites' with 'Taxites'.

p. 132. caption, line 3. C–E are from V.56392a and V.56392c. Caption, line 6. Replace 'V.56392a' with 'V.56392b'.

p. 149. For 'Leakholm' read 'Lealholm' and for 'Leptosrobus' read 'Leptostrobus'.

p. 150. For 'Tsugipollenites' read 'Tsugaepollenites'.

Plate 4, caption to Fig. 2. Replace 'V.56477' with '13518a'. Caption to Fig. 3. Replace 'V.56483' with 'V.56419b'.

Plate 5, caption to Fig. 2. Replace 'V.28393a' with 'V.28393b'. Caption to Figs 3, 4. Replace 'V.56489' with 'V.56413a'.

Plate 6, caption to Fig. 2. Replace 'V.56497' with 'V.56429a'. Caption to Fig. 3. Replace 'V.56496' with 'V.56431a'. Caption to Figs 5, 6. Replace 'V.56499' with 'V.56410b'.

Plate 7, caption to Fig. 1. Replace 'V.56499' with 'V.56410b'.
PLATES
PLATE 1

**Brachyphyllum mamillare** Lindley & Hutton ex Brongniart

Fig. 1. Thick shoot showing xylem core and broad leaves partly separated by decay. V.56931, × 1. Beast Cliff *Otozamites* Bed.

Fig. 2. Sturdy shoot showing unusually regular branching. V.57363, × 1. Hillhouse Nab, Farndale.

Fig. 3. Slender shoots showing somewhat irregular branching (the commonest form). V.27207, × 1. Long Bight, Whitby.

Fig. 4. Two shoots, that on the right somewhat rotted and xylem core exposed. V.56930, × 1. Cloughton Wyke, *E. laterale* Bed.

Fig. 5. Main axis showing large leaves. V.56763, × 1. Fallen block, Burniston Wyke.

Figs 6–9. Shoots with more or less prominent leaves (*scalbiensis* form). Fig. 7 showing xylem core. Fig. 6, V.56756, × 2, Cloughton Wyke Fern Bed. Fig. 7, V.56929, × 2, fallen block, Gnipe Howe, Hawsker. Figs 8, 9, V.58794, × 2, Hasty Bank.

Figs 12–13. Imprints of male cones showing sporophyll heads, × 2. Fig. 12, V.56933. Fig. 13, V.56934. Fallen blocks, Haiburn Wyke.

Fig. 14. Interior of male cone exposed by splitting. V.56932, × 4. See also Fig. 3E, p. 9. Haiburn Wyke.

**Araucarites phillipsii** Carruthers

Figs 10, 11. Part and fragment of counterpart of cone, from block V.27626 (b and c), × 1. About half-way along Beast Cliff, perhaps c. 3 km SE of Ravenscar.

**Pagiophyllum maculosum** Kendall

Fig. 15. Shoot fragment of small form with short leaves. V.56775, × 1. Cloughton Wyke *Nilssonia* Bed.

Fig. 16. Shoot of slender form. V.56808, × 1. Cloughton Wyke *Anomozamites* Bed.

Fig. 17. Small shoot with undeveloped apical bud, V.57393, × 4. Cloughton Wyke *Zamites* Bed.

**Hirmerella kendalliae** sp. nov.

Figs 18, 22. Ovuliferous scale showing lobed margin. V.58360, × 4 and × 6. Cloughton Wyke *Zamites* Bed.

**Hirmerella estonensis** (Kendall) comb. nov.

Fig. 19. Ovuliferous scale, V.57391, × 2.


Both specimens are from Big Quarry, Eston Moor, at 54° 32' 29" N.
PLATE 2

Elatides williamsonii (Lindley & Hutton) Nathorst

Fig. 1. Male cones covering surface of a block, some unexpanded and full of nearly mature pollen. V.24680, ×1.

Figs 2, 3. Empty male cones, ×2. Fig. 2, V.56723. Fig. 3, V.56720.

Figs 4, 6. Male cone still with pollen, partly petrified and split longitudinally. V.56722, ×2 and ×6.

Fig. 5. Male cones expanded to different extents. V.45266, ×2.

Fig. 7. The cone named Mascolostrobus harrisii van Konijnenburg-van Cittert, possibly an expanded male cone of E. williamsonii. Specimen no. 1354, University of Utrecht, ×4.

All from the Gristhorpe Bed, Cayton Bay.

Elatides thomasi sp. nov.

Figs 8, 13. Leafy shoots, ×1. Fig. 8. holotype, V.56730. Fig. 13, V.56728. Hasty Bank.

Fig. 9. Three female cones and fragment of a main shoot. V.56734, ×1. Fallen block, Whitby.

Fig. 10. Female cone, V.56736. ×2. Roseberry Topping.

Figs 11, 12. Empty male cones. ×2. Fig. 11, V.58827. Fig. 12, V.56735. Hasty Bank.

Geinitzia divaricata (Bunbury) comb. nov.

Fig. 14. Shoot system, ×1. V.57369. Beast Cliff Equisetum Bed.
PLATE 3

*Geinitzia divaricata* (Bunbury) comb. nov.
Fig. 1. Small shoot, V.57370, ×2. Fallen block, Beast Cliff.
Fig. 2. Main shoot with radially-pointing leaves and lateral with complanate leaves. V.57371, ×1. Fallen block, Beast Cliff.

*Geinitzia rigida* (Phillips) comb. nov.
Fig. 3. Shoot, V.57373, ×2. Fallen block at about 54° 20' 37", Cloughton Wyke.

*Pagiophyllum kurrii* (Schimper) Salfeld

*Pagiophyllum maculosum* Kendall
Figs 6, 7. Leaf cuticle, ×200. V.57525. At top left of Fig. 6 the hypodermal cell outlines are seen whilst in Fig. 7 the epidermal cell outlines are clear. Birk Brow Quarry Coal.
Schizolepis liasokeuperianus Braun

Figs 1–8. Detached cone scales, ×2. The figures are in pairs, that on the left being the specimen under paraffin, that on the right dry. Specimens in the Section for Palaeobotany, Riksmuseum, Stockholm, labelled 'Scarbro Nya lagret A.N. 1879'. Figs 1, 2, specimen 271, see also Fig. 45E, p. 100. Figs 3, 4, specimen 277a, see also Fig. 45C. Figs 5, 6, specimen 277b, see also Fig. 45D. Figs 7, 8, specimen 274, see also Fig. 45B.

Pityocladus scarburgensis sp. nov.

Fig. 13. Holotype and loose-lying leaves attributed to it. ×2. Specimen no. 278, Section for Palaeobotany, Riksmuseum, Stockholm.

Cyparissidium rudlandicum sp. nov.

Fig. 9. Holotype before preparation of transfer. V.57415, ×2.

Cyparissidium blackii (Harris) comb. nov.

Fig. 10. Exceptional specimen with somewhat diverging leaves. V.57383, ×2. Fallen block, Cayton Bay. Sandstone matrix.

Fig. 11. Shoot with rather long leaves. V.57378, ×2. Scalby Ness (sandstone).

Fig. 12. Shoot showing short basal leaves. V.57382, ×2. Scalby Wyke (shale).

Fig. 14. Richly branched shoot with primary and secondary branches. V.57381, ×2. Scalby Ness (sandstone).
Plate 4

British Museum (Natural History) *The Yorkshire Jurassic Flora, V*
**PLATE 5**

*Pityanthus scalbiensis* van Konijnenburg-van Cittert

Fig. 1. A cone exposed in median longitudinal section by grinding, ×8. The microsporophylls bend downwards.

Fig. 2. Cone V.58839 as originally exposed, ×4.

Figs 3–5. Same cone at levels 420 μm, 660 μm and 910 μm below the surface as exposed by grinding; ×8. See also Fig. 39, p. 84.

Fig. 6. A cone in very oblique section, ×8.

Fig. 7. Cone V.58840 in oblique section, ×8.

Fig. 8. Two cones associated with shoot fragments of *Cyparissidium blackii*. V.57384, ×2.

Fig. 9. Dispersed pollen grain associated with *C. blackii*, ×500.

The cones in Figs 1, 6, were destroyed by further grinding.

*Scarburgia hillii* sp. nov.

Figs 10–14. Transfers showing cone scales attached to cone axis. Figs 10, 12, V.58963, ×1, ×2. Figs 11, 13, 14, V.58964, ×1, ×2, ×4. See also Fig. 41A, p. 88.

Figs 15, 16. The Cayton group of seeds with closely associated fragments of *Cyparissidium blackii* as first found, later entirely used for maceration, ×2.

Fig. 17. **Holotype** cone at top right, with other cone fragments and fragments of *Coniopteris*. V.58842, ×2.

Figs 1–14, 17 from Scalby Ness.
**Plates 6**

**Scarburgia hillii** sp. nov.

**Fig. 1.** Inner cuticles of seed nucellus projecting beyond megaspore at top. V.59067b, × 20.

**Fig. 2.** Cuticles of the cover (epimatium) and the integument. In the upper half of the photo the cover is torn away and the pale integument alone is seen, while in the lower half both cuticles are seen, showing the cells obscurely. V.59065d, × 100.

**Fig. 3.** Cuticle of cover, anticlinal walls very uneven. V.59072c, × 280.

**Fig. 4.** Upper half cover cuticle with uneven anticlinal walls; lower half (dark) top of integument cuticle and overlying cover cuticle. Integument cells here elongated. V.59073, × 100.

**Fig. 5.** Cuticle of integument from seed illustrated in Fig. 42E, F. p. 90. V.59072c, × 260.

**Fig. 6.** Cuticle of nucellus with top of megaspore membrane below. V.59063, × 660.

**Fig. 7.** Granular megaspore membrane with cell outlines of nucellus over it; at edge the nucellus extends beyond the megaspore. V.59067b, × 660.

**Fig. 8.** Fragment of seed showing at top the nucellar beak enclosing two pollen grains and at bottom right a little of the megaspore membrane. There is an extraneous mineral particle above the nucellus and another one, almost black, below the pollen grains. V.59065c, × 120. See also Figs 9, 10, below and Fig. 41E, F, J, p. 88, and Fig. 42A, B, J, p. 90.

**Figs 9, 10.** Views at high and at low focus of the two pollen grains seen in Fig. 8 above, × 600.
PLATE 7

**Poteridion hallei** sp. nov.

Figs 1, 2. **Holotype** as originally exposed and in transfer, ×10. See also Fig. 54A–E, p. 120.

**Marskea jurassica** (Florin) comb. nov.

Figs 3, 4. Male cone near end of a shoot and connected to it by an imprint, indistinct tissue to left of the cone base possibly the apical bud. Fig. 3, dry; Fig. 4, under paraffin. See also Fig. 50G, p. 110. V.57623, ×4. Whitby.

Figs 5, 6. Ovule surrounded by scales, detached entire from the rock. Fig. 5 from below, broken base to left. Fig. 6 from above, the micropyle at left and above middle surrounded by a triangular ridge, the edge of the aril. V.34698, ×10. See also Fig. 50A–D, p. 110. Beast Cliff *Otozamites* Bed.

Figs 8, 10. Shoot and attached ovule showing scales. Fig. 8, dry; Fig. 10, under paraffin. V.34702, ×4; first figured by Florin. 1958: pl. 9, fig. 7. See also Figs 48G (p. 106) and 50F (p. 110). Beast Cliff *Otozamites* Bed.

**Carpolithes cepa** sp. nov.

Fig. 7. Several seeds, V.58857, ×1.

Fig. 9. Two seeds in transfer showing the fibrous coat. V. 58857a, ×2.

**Trulla nitens** sp. nov.

Figs 11, 12. Part and counterpart, V.58852, ×4.

Figs 13, 14. **Holotype**, part and counterpart, V.58853, ×4.