PALAEOSMUNDA, A NEW GENUS OF SIPHONOSTELIC OSMUNDACEOUS TRUNKS FROM THE UPPER PERMIAN OF QUEENSLAND

by R. E. GOULD

ABSTRACT. Petrified osmundaceous trunks from the Upper Permian coal measures of the Bowen Basin, Queensland, are assigned to a new genus, *Palaeosmunda*, which possesses an ectophloic, sometimes almost simple but usually dictyoxylic, siphonostele with parenchymatous pith; the stems bear stipulate petiole bases which contain sclerotic rings that are rhomboidal in transverse section, upwards becoming laterally extended into flanges. These are the first Permian Osmundaceae definitely known to exhibit a distinct pith and leaf gaps. A table of morphological comparisons of all known Permian osmundaceous axes is presented. Discovery of *Palaeosmunda* indicates that the family had a greater structural diversity and a wider geographic distribution in the Upper Permian than was previously realized; and hence the Osmundaceae probably developed before the Permian. Two species, *P. williamsii* (type species) and *P. playfordii*, are described in detail; the inner cortex, and sometimes the stipules of the petiole bases of *P. williamsii* contain strands of sclerenchyma, while stipules and inner cortex of the petiole bases of *P. playfordii* consist only of parenchyma. Evidence from association indicates that the trunks probably bore fronds of the types referred to *Sphenopteris lobifolia* Morris 1845, *S. polymorpha* Feistmantel 1876, and *Cladophlebis roylei* Arber 1901.

TRUNKS and rhizomes characteristic of the Osmundaceae are apparently well suited to preservation as fossils and the geological history of the family, based on petrified stems, extends from Upper Permian to Recent (Andrews 1961, Miller 1967). Prior to the present work, all known specimens of Permian osmundaceous stems came from the Soviet Union; where the stele is preserved, these contain a protostele or at least an ectophloic siphonostele without well-developed leaf gaps.

Osmundaceous trunks, petrified with silica, calcite, and ferruginous material, occur at many localities in the Upper Permian coal measures of the Bowen Basin, Queensland (text-fig. 1). These are described as two species of a new genus, *Palaeosmunda* gen. nov., in which the stele is usually an ectophloic dictyoxylic siphonostele, but can appear almost simply siphonostelic; the petiole bases are very similar to those of other stipulate Permian osmundaceous stem genera. The new genus is unusual in that it is the first Permian member of the family definitely known to exhibit a distinct pith and leaf gaps.

The specimens on which the study is based were collected by Dr. J. Armstrong, Mr. R. Lees, Dr. B. Runnegar, Dr. F. W. Whitehouse, Mr. J. H. Williams, and the author. Mr. W. A. Hansen and the management and staff of Utah Development Company provided considerable assistance in the location and collection of specimens from Utah's Blackwater coal-mining lease. One specimen, collected in June 1956, was already held in the collections of the Department of Geology and Mineralogy, University of Queensland. All specimens are housed in the Department and catalogue numbers are prefixed UQ.

In his study of the morphology of the living Osmundaceae, Hewitson (1962, p. 80) used the term 'bundle' when describing the stem xylem in transverse section; he considered two (or more) xylem strands connected by even one tracheid as a single bundle. This terminology avoids any confusion when counting the xylem strands, and is very

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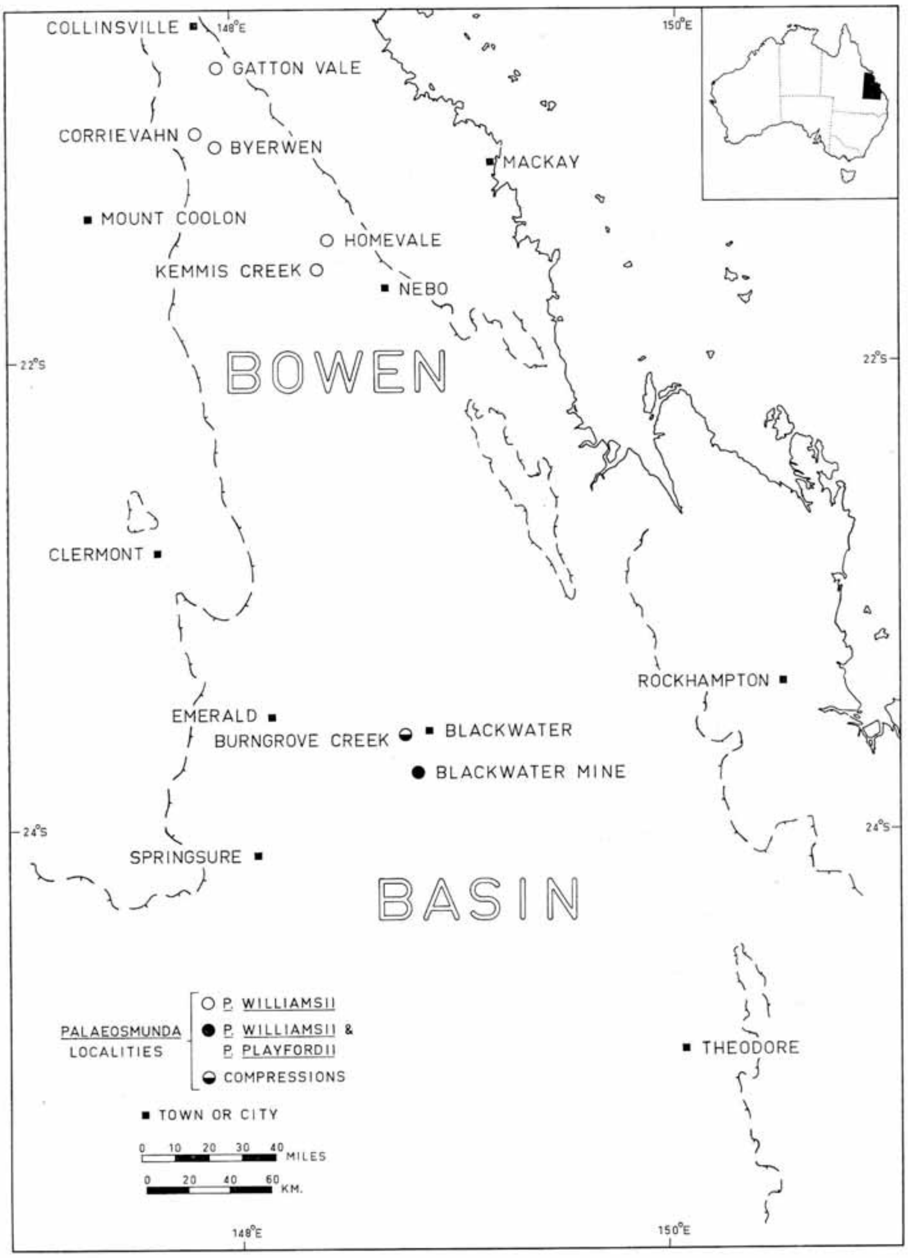


TEXT-FIG. 1. Locality map.

useful in describing the stems of the family where the dictyoxylic stele is well developed. However, where the number of gaps in the xylem ring is small, the number of 'bundles' does not give a complete indication of the structure of the ring. Instead, in the following descriptions, the number of gaps appearing in a transverse section of the xylem cylinder is given. This is equal to the number of bundles in the sense of Hewitson, provided that there are two or more gaps; no gap, or one, results in one 'bundle'. The term 'radial strand' is used in this paper to designate any group of stelar xylem tracheids with a prominent radial dimension when seen in transverse section, regardless of whether the group is connected to adjacent strands or not.

Previous literature. In the second and third parts of their classic memoir on the fossil Osmundaceae, Kidston and Gwynne-Vaughan (1908, 1909) published the first detailed anatomical accounts of Upper Permian osmundaceous stems. They described five species from the Upper Permian of the U.S.S.R., *Zalesskya gracilis* (Eichwald) Kidston and Gwynne-Vaughan 1908, *Z. diploxylon* Kidston and Gwynne-Vaughan 1908, *Thamnopteris schlechtendalii* (Eichwald) Brongniart 1849, *Bathypteris rhomboidea* (Kutorga) Eichwald 1860, and *Anomorrhoea fischeri* Eichwald 1860. The steles of *B. rhomboidea* and *A. fischeri* were not present in their specimens and that of *B. rhomboidea* was described later by Zalessky (1924). Seward (1910) figured some of Kidston and Gwynne-Vaughan's slides and one of these, his frontispiece of *T. schlechtendalii*, had not been figured previously.

In a series of papers, Zalessky (1924, 1927, 1931*a*, *b*, 1935) described and figured further examples from the Upper Permian of the U.S.S.R.; these comprise *B. rhomboidea*, *T. kidstoni* Zalessky 1924, *T. gwynne-vaughani* Zalessky 1924, *Z. uralica* Zalessky 1924, *A. fischeri*, *T. schlechtendalii*, *Z. gracilis*, *Z. diploxylon*, *T. kazanensis* Zalessky 1927, *Z. fistulosa* (Eichwald) Zalessky 1927, *Petcheropteris splendida* Zalessky 1931*a*, *Chasmatopteris principalis* Zalessky 1931*b*, and *Iegosigopteris javorskii* Zalessky 1935. *Thamnopteris kazanensis* was not formally described but a transverse section and some details were figured with explanation (Zalessky 1927, pp. 26, 44, pl. 24, figs. 1–4); the specimen is poorly preserved. Knowledge of *Z. fistulosa* is limited to a photograph of its external surface (Zalessky 1927, pp. 31, 48, pl. 32, fig. 3).

Posthumus (1931) compiled synonymy lists for the genera and species of Permian and other osmundaceous stems that had been described prior to 1928.

STRATIGRAPHY

All specimens of *Palaeosmunda* were collected from the Bowen Basin in freshwater sediments which have been referred to as the Upper Bowen Coal Measures (Smith 1958, Hill and Denmead 1960). Devine and Power (1967) have assigned these sediments in the central western Bowen Basin, including the Blackwater district, to the Bandanna Formation (Power 1967 usage, formerly Upper Bandanna Formation of Patterson *in* Webb 1956, p. 2330). The localities for the osmundaceous fossils (text-fig. 1) are all within the Blackwater Group (Malone 1966) as shown on the geological map of the basin compiled by Malone, Olgers, Mollan, and Jensen (1967); in the Blackwater district the fossil trunks occur in the upper two units of the group, the Burngrove Formation and the Rangal Coal Measures. The Blackwater Group and Bandanna Formation are the same lithological unit in the Blackwater–Springsure area (Power 1967, Devine and Power 1967). The age of the Upper Bowen Coal Measures, Bandanna Formation, and Blackwater Group is generally considered to be Upper Permian (e.g. Runnegar 1968). Webb and McDougall (1967, pp. 483–4) reported an isotopic age of 240 m.y. for a basal part of the Blackwater Group. Ammonoids from horizons below the coal measures in the northern part of the basin are considered to be of Artinskian (Aktastinian–Baigendzhinian) age (Armstrong, Dear, and Runnegar 1967), while microfloras from the Rewan Formation, which overlies the coal measures, are probably in part of Scythian (Otoceratan) age (Evans 1966, p. 59).

SYSTEMATIC PALAEOBOTANY

Division PTEROPHYTA
Order FILICALES
Family OSMUNDACEAE
Genus PALAEOSMUNDA gen. nov.

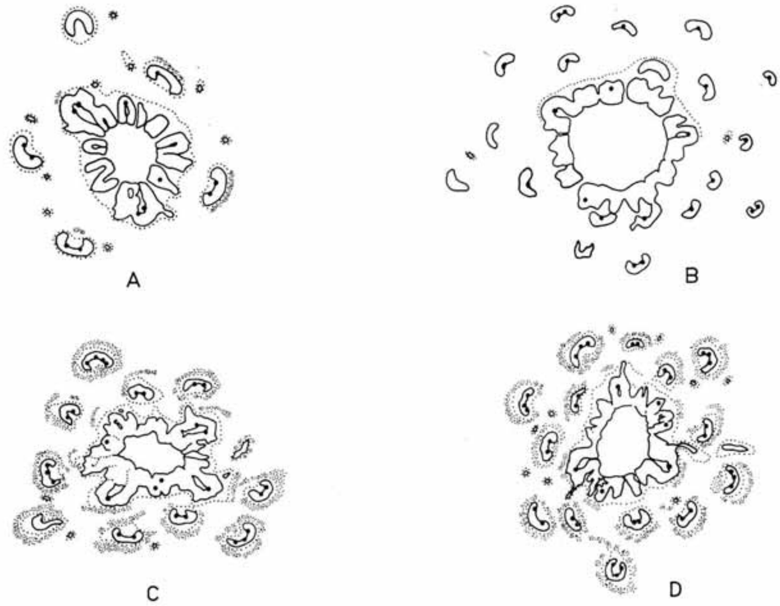
Type species. *Palaeosmunda williamsii* sp. nov.

Diagnosis. Arborescent osmundaceous trunks, each with a stem surrounded by a mantle of leaf bases and adventitious roots; branching of stem dichotomous. Stele an ectophloic, generally dictyoxylic, siphonostele, sometimes almost simply siphonostelic; pith parenchymatous; xylem ring with 0–13 gaps, consisting of 14–28 more or less contiguous radial strands, 9–19 tracheids thick; development of leaf gaps immediate, delayed, or incomplete; gaps very short to long; phloem, pericycle, and endodermis external only. Cortex differentiated into inner parenchymatous zone and outer sclerotic fibrous layer, the latter with short, wide, sclerenchyma cells lining leaf traces and inner cortex; inner cortex about as wide as outer cortex; leaf traces arise at 10–35° to stele, initially with 1 or 2 endarch protoxylem groups; 12–43 traces in a transverse section of cortex. Petiole bases stipulate, containing an adaxially curved, C-shaped vascular strand, inner cortex, and sclerotic ring; sclerotic rings somewhat rhomboidal in cross-section, upwards becoming laterally extended into flanges which partially or completely replace the stipules; rings with gradual increase of fibre diameter towards inner cortex of petiole base, otherwise homogeneous; lateral extremities of ring usually thinner than abaxial and adaxial portions. Roots with diarch xylem strand, arising in pairs from each departing leaf trace usually before it enters inner cortex, or rarely singly, directly from stele; roots often branched and forming dense mat outside mantle.

Discussion. *Palaeosmunda* differs from the Permian osmundaceous stem genera *Bathypteris* Eichwald 1860, *Chasmatopteris* Zalessky 1931*b*, *Iegosigopteris* Zalessky 1935, *Petcheropteris* Zalessky 1931*a*, *Thamnopteris* Brongniart 1849, and *Zalesskya* Kidston and Gwynne-Vaughan 1908, in that the stele is an ectophloic, usually dictyoxylic, siphonostele with homogeneous metaxylem and a parenchymatous pith; the leaf traces in *Palaeosmunda* initially have one or two endarch protoxylem groups whereas the leaf traces of these other genera are initially mesarch. *Palaeosmunda* lacks both the wide cortex of *Zalesskya* and the spinose petiole bases of *Bathypteris*. There is insufficient information available on *Anomorrhoea* Eichwald 1860, for any useful generic distinction to be made. A table of comparisons of the species of Upper Permian osmundaceous stems is given in folder.

Osmundacaulis Miller 1967 (an organ genus based on '*Osmundites*' *skidegatensis* Penhallow 1902), which occurs in Mesozoic and Tertiary strata, would include stems similar to those of the new genus, but the petiole bases of *Palaeosmunda* are quite different. Besides being of specific importance, the arrangement of sclerenchyma within the petiole base in the Osmundaceae, as well as the anatomy of the stele, is of generic and subgeneric significance (Kidston and Gwynne-Vaughan 1907, Hewitson 1962, Miller 1967). The leaf bases of *Palaeosmunda* can be more closely compared with those of *Anomorrhoea*, *Chasmatopteris*, *Iegosigopteris*, *Petcheropteris*, and *Thamnopteris* than with those of *Osmundacaulis*. The generally rhomboidal to laterally extended shape of the sclerotic ring in transverse section is exhibited by all the Permian genera except *Zalesskya*, in which the leaf bases are unknown. In contrast, the sclerotic rings of *Osmundacaulis* are generally rounded; the leaf traces in the outer cortex of the Jurassic *O. gibbiana* (Kidston and Gwynne-Vaughan) Miller 1967, are, however, rhomboidal in transverse section (Kidston and Gwynne-Vaughan 1907). The initial rhomboidal shape, small stipules, and upward lateral extension of the sclerotic ring into flanges which replace the stipules are well developed in *Palaeosmunda*; the shape is not solely due to the close arrangement of the bases around the stem, as they retain and even increase the laterally flanged shape in the outer part of the mantle where they are free of any restriction. The gradual increase in diameter of the fibres of the sclerotic ring towards the inner cortex of the petiole base is also exhibited by *T. schlechtendalii*, *B. rhomboidea*, and possibly by *A. fischeri* and *I. javorskii* (see Kidston and Gwynne-Vaughan 1909, pl. 5, fig. 36; pl. 7, fig. 48; pl. 8, fig. 63; Zalessky 1935, pl. 2, fig. 7), as well as some post-Palaeozoic species of Osmundaceae. At least *I. javorskii* and *P. splendida*, and possibly also *A. fischeri*, *C. principalis*, and *T. schlechtendalii* (see Zalessky 1927, pl. 23, fig. 1), show relatively thin lateral extremities of the sclerotic ring as in *Palaeosmunda*.

The development of the ectophloic dictyoxylic siphonostele in Osmundaceae by Upper Permian is somewhat earlier than had been previously thought (e.g. Hewitson 1962, p. 84), but is not altogether surprising. Leaf gaps are partially formed in the Upper Permian *C. principalis*, and *T. kidstoni*, also of Upper Permian age, contains some parenchyma cells in the inner xylem. Triassic representatives of osmundaceous stems include *Osmundacaulis herbstii* (Archangelsky and de la Sota) Miller 1967, '*Osmundites*' *tuhajkuensis* Prynada (Orlov 1963, pl. 29, fig. 10), and probably '*Osmundites*' *winterpockensis* Bock 1960; all of these are of Upper Triassic age and *O. herbstii*, and probably '*O.*' *tuhajkuensis*, exhibit dictyoxylic siphonosteles. The shape of the transverse section of the sclerotic ring in the leaf bases of '*O.*' *tuhajkuensis* is somewhat intermediate between those of the Permian examples and *Osmundacaulis*; the two masses of sclerenchyma in each arm of the C-shaped petiolar strand of '*O.*' *tuhajkuensis* has, however, only been found in *Osmundacaulis* and *Osmunda*. '*Osmundites*' *winterpockensis* is based on a sandstone cast with no internal structure preserved (C. N. Miller, pers. comm. 1969). Other Triassic fossil stems referred to the Osmundaceae, and used as examples to explain the evolution of the dictyoxylic siphonostele from the protostele (e.g. Daugherty 1960, Emberger 1962, Arnold 1964, Surange 1966), actually belong to other groups. These include *Chinlea campii* Daugherty 1941, and *Osmundites walkeri* Daugherty 1941, which are synonymous and belong to the Lepidophyta (Miller 1968), and the ectophloic siphonostelic *Itopsidema vancleavii* Daugherty 1960, which is also probably not a member of the Osmundaceae (Miller 1969). On the other hand, the plants with protosteles and those with ectophloic dictyoxylic siphonosteles may have already been separate groups by the Upper Permian.



TEXT-FIG. 3. *Palaeosmunda williamsii* gen. et sp. nov. Transverse sections of stele and inner cortex, *c.* ×3·5; where discernible, protoxylem groups of xylem ring and leaf traces represented as black dots; endodermis by a dotted line; and generalized position of sclerenchyma strands in inner cortex by close stipple. A, UQF53542; B, UQF50620; C, D, UQF21571 (holotype).

The oldest known petrified axes referable to the Osmundaceae all occur in Upper Permian strata and these are compared in text-fig. 2. In view of the structural diversity and wide geographic distribution exhibited by these axes, and the relatively stable development of the family from Mesozoic to Recent, it is reasonable to assume that the Osmundaceae originated well before the Upper Permian, probably even before the Permian.

Absence of cataphylls in all specimens of *Palaeosmunda* from the Bowen Basin probably indicates that the climate in which the plant grew lacked severe winters (Steeves and Wetmore 1953; Miller 1967, p. 144). It is interesting to note that cataphylls have not been found in any of the Permian osmundaceous axes.

Palaeosmunda williamsii sp. nov.

Plate 1, figs. 1, 2; Plate 2, figs. 1–7; Plate 3, figs. 1–8; Plate 4, figs. 1–10; text-figs. 2, 3

Holotype. UQF21571; figured in Plate 1, figs. 1, 2; Plate 2, figs. 1, 2, 6, 7.

Type locality. Beside the Collinsville–Mt. Coolon Road in Portion 4, Parish of Corrievahn, central Queensland (shown on text-fig. 1 as Corrievahn); Blackwater Group (formerly Upper Bowen Coal Measures).

Derivation of name. The species is named in honour of Mr. J. H. Williams (Mackay) who kindly assisted in the collection of specimens from the northern part of the Bowen Basin.

Diagnosis. *Palaeosmunda* trunks up to 22 cm. in diameter; stems 1–3·6 cm. wide. Stele an ectophloic dictyoxylic siphonostele, sometimes appearing simply siphonostelic, 3·5–8 mm. in diameter; pith diameter 1–4 mm.; xylem ring 0·7–2·2 mm. wide, with 0–9 gaps, composed of 15–28 radial strands, 9–17 tracheids thick; metaxylem tracheids 35–260 μ (usually 50–150 μ) in diameter, with regular scalariform pitting in 1–5 vertical series on each wall. Inner cortex parenchymatous, sometimes with fibrous sclerenchyma strands surrounding leaf traces; inner cortex 0·8–5·5 mm. wide, including 5–25 leaf traces in a given transverse section; fibrous outer cortex 2·5–9 mm. wide, with 7–26 leaf traces in a transverse section. Leaf traces arise with 1 or 2 endarch protoxylem groups which usually bifurcate before they enter outer cortex; strands of sclerenchyma surround leaf trace in outer cortex of stem, and vascular trace in inner cortex of petiole base. Stipules parenchymatous, or with up to 30, generally small, scattered strands of sclerenchyma fibres.

Description

General. There are 16 specimens, each consisting of a stem surrounded by a mantle of adhering leaf bases and adventitious roots (e.g. Pl. 1, fig. 1; Pl. 3, figs. 1, 7). The specimens are up to 21 cm. long and 22 cm. in diameter, and both ends are broken across. Some trunks are circular in cross-section, but others are oval, presumably due to compression. Three specimens show dichotomy of the stem, but only one contains the actual branching region. The stems, bounded by the sclerotic outer cortex, are 1–3·6 cm. in diameter; the outline in transverse section is undulose due to the emerging petioles.

Stele. The pith is 1–4 mm. in diameter (Pl. 2, figs. 4–7; Pl. 3, figs. 4–6), and consists of vertically elongated, rounded to polygonal, parenchyma cells, measuring 20–110 μ in diameter and 40–300 μ in length; the wall between two adjacent cells is 1–6 μ thick. The parenchyma cells have sometimes partially decayed and separated before preservation.

EXPLANATION OF PLATE 1

Figs. 1, 2. *Palaeosmunda williamsii* gen. et. sp. nov. 1, Transverse section of holotype, UQF21571, from Corrievahn, $\times 2$; section from midway along specimen (top of Plate 2, fig. 1); transmitted and reflected light. 2, Details of stele, inner cortex, and part of outer cortex of fig. 1, $\times 8$; most of pith and inner cortex not preserved; leaf traces depart from stele with 2 protoxylem groups; transmitted light.

EXPLANATION OF PLATE 2

Figs. 1–7. *Palaeosmunda williamsii* gen. et. sp. nov. 1, 2, 6, 7, Holotype, UQF21571. 1, Longitudinal section, $\times 1$; lower half of specimen, details of pith not preserved. 2, Transverse section of petioles showing stipules, $\times 5$. 6, Transverse section from upper part of specimen, $\times 2$. 7, Central portion of fig. 6, $\times 6$; pith partly displaced; note endodermis of stem continuous with sclerotic cortex of root trace at right centre. 3–5, UQF53542, from Homevale. 3, Transverse section, $\times 2$. 4, Detail of stele, $\times 8$; leaf traces leave stele with 2 protoxylem groups. 5, Longitudinal section of pith and xylem of stem, $\times 16$. (1, 3, 6, 7, transmitted and reflected light; 2, 4, 5, transmitted light.)

In one specimen, a few short tracheids are present in the pith (Pl. 4, figs. 1, 2), but these occur where the stem is twisted and are associated with nearby metaxylem strands (cf. Hewitson 1962, p. 81). No internal endodermis is present.

The xylem cylinder is generally similar to that in *Osmunda* and *Osmundacaulis*. It is 0·7–2·2 mm. wide and in transverse section exhibits 0–9 gaps; i.e. in some specimens the xylem is a continuous, but indented ring (Pl. 1, fig. 2; text-fig. 3C, D), while in others it is dissected (Pl. 2, fig. 4; text-fig. 3A, B) and similar to those in most post-Palaeozoic forms of the Osmundaceae. In transverse section the xylem cylinder has 9–24 external lobes, while the cylinder itself consists of 15–28 radial strands, each 9–17 tracheids thick. The protoxylem tracheids, initially mesarch in metaxylem strands below departing leaf traces, are 6–40 μ in diameter, with a wall thickness of 3–14 μ between adjacent cells, and exhibit one series of scalariform pits on each longitudinal wall. Metaxylem tracheids are 35–260 μ in diameter (commonly 50–150 μ), with a wall thickness of 6–23 μ between two adjacent cells. The metaxylem tracheids show regular scalariform pitting in 1–5 vertical series on each wall (Pl. 3, fig. 8); the transverse bars of thickening are 1·1–4 μ thick and 1·5–7 μ apart.

In most of the specimens, except for a dark line marking the position of the endodermis, and strands of sclerenchyma, little cellular detail is preserved between the xylem cylinder and the outer cortex of the stem (Pl. 1, fig. 2; Pl. 2, figs. 3, 4; Pl. 3, fig. 2). A parenchyma xylem sheath, 1–3 cells thick, may be present. Phloem is only preserved in one specimen; it probably formed a continuous layer around the xylem. Metaphloem cells in the wedges between the xylem lobes have a diameter of 27–100 μ with a wall thickness of 3–6 μ. Outside the phloem is a layer of flattened cells up to 7 cells thick, which probably represents the protophloem and pericycle. The endodermis is marked by a dark line or a stained zone, and an abrupt change from pericycle tissue to inner cortex, but cellular detail is lacking. The endodermal diameter is 3·5–8 mm.

Cortex. The inner cortex is 0·8–5·5 mm. wide and consists of parenchyma with, in some specimens, bundles of sclerenchyma fibres. The parenchyma is polygonal to rounded in transverse section, and may be tangentially elongated, measuring 25–70 μ $\times$ 10–60 μ; thickness of the wall between two adjacent cells is 0·7–4 μ, but may appear up to 14 μ thick with deposits of organic and mineral matter. Where present, the bundles of sclerenchyma fibres occur in an intermittent peripheral zone around the endodermis below and adjacent to abaxial surfaces of the departing leaf traces (Pl. 1, fig. 2; Pl. 2, fig. 7); the bundles usually surround the endodermis of the leaf trace as it leaves the stele and they accompany it through the inner and outer cortex of the stem and into the petiole bases. In other cases however, the sclerenchyma does not appear until further out in the inner or outer cortex. In transverse section the bundles measure up to 540 μ tangentially, and up to 210 μ radially. They are composed of sclerenchyma fibres which have a diameter of 13–38 μ, a length of at least 850 μ, and a wall thickness between adjacent cells of 6–18 μ. The primary and secondary walls are clearly shown and the secondary wall may almost completely fill the cell. The inner cortex contains 5–24 leaf traces in a given transverse section.

The dense outer cortex is 2·5–9 mm. wide and consists of sclerenchyma fibres which are polygonal in cross section (Pl. 4, figs. 6, 7). The majority of these fibres have a diameter of 12–45 μ, sometimes up to 70 μ, and length of 270 μ to at least 1100 μ; the end walls are transverse, oblique, or tapering. The primary and secondary walls are clearly preserved and the secondary wall may consist of several layers. Total thickness of wall between two adjacent fibres is 6–30 μ; intercellular spaces of up to 4 μ are sometimes present at the angles. The longitudinal walls may be smooth or exhibit simple, small (3–7 μ), round to oval, irregularly scattered pits. Large, irregularly defined rectangular (3×7 μ–7×23 μ, 1·5–8 μ apart) or annular pits may also be present, but these appear to be formed by shrinkage of the original cell wall. Rare transverse septations may occur. Sometimes the lumen of a fibre is almost filled with secondary wall. A few layers of relatively larger and shorter, although otherwise similar, fibres occur adjacent to the inner cortex of the stem and leaf traces (Pl. 1, fig. 2), and also on the outside of the stem in the depressions behind the departing petioles (Pl. 4, fig. 8); these cells usually have a diameter of 40–85 μ, and a length of 70–300 μ. Part of the outer cortex of one specimen appears inhomogeneous with rings of light-coloured (in thin section) fibres surrounding the leaf traces, and darker, somewhat larger fibres in the areas between the rings (Pl. 3, fig. 1). The outer cortex contains 7–26 leaf traces in a given transverse section. Total number of leaf traces in any one transverse section of the whole cortex is 12–43.

Leaf traces. Traces are formed from the metaxylem strands of the stem in a manner generally similar to that in the subgenera *Osmunda* and *Osmundastrum* of the genus *Osmunda* (Hewitson 1962, Miller 1967). A protoxylem group develops approximately in the centre of the metaxylem strand which gives rise to the leaf trace. Above this point an island of parenchyma develops adaxially to the protoxylem group. This island enlarges upwards and usually becomes connected by a narrow gap with the pith. Thus the xylem strand assumes a U-shape with the narrow open end of the 'U' directed

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EXPLANATION OF PLATE 3

Figs. 1–8. *Palaeosmunda williamsii* gen. et sp. nov. 1–3, UQF57604, from Byerwen. 1, Transverse section, ×1. 2, Transverse section of stele; most of pith and inner cortex filled with silica; leaf traces arise with 1 protoxylem group, ×6. 3, Transverse section of parts of petiole bases showing irregular mass of sclerenchyma in sclerotic ring, and sclerenchyma strands in stipules, ×10·6. 4–6, UQF50624, from Blackwater district. 4, 5, Transverse sections of pith. 4, ×42; 5, ×67·5. 6, Longitudinal section of pith, ×67·5. 7, 8, UQF50620, from Blackwater district. 7, Transverse section, ×1·5; numerous roots and petioles loosely adpressed in outer part of mantle. 8, Longitudinal view of xylem tracheids of stem, ×42. (1, transmitted and reflected light; 2–8, transmitted light).

EXPLANATION OF PLATE 4

Figs. 1–10. *Palaeosmunda williamsii* gen. et. sp. nov. 1, 2, Longitudinal sections showing tracheids in pith, UQF50620. 1, ×42; 2, ×66. 3, Transverse section of roots, UQF53549, from Blackwater Mine, ×10·6. 4, 5, Longitudinal sections of xylem of root. 4, UQF50624, ×99; 5, UQF57604, ×63. 6, 7, Transverse sections of sclerenchyma fibres of outer cortex. 6, UQF53552, from Blackwater Mine, ×60, showing intercellular spaces; 7, UQF53549, ×60. 8, Longitudinal section of outer cortex and part of sclerotic ring of departing petiole, showing shorter fibres at outside of stem; longitudinal axis of section tilted to left; UQF53552, ×40. 9, Longitudinal section of sclerenchyma strand in inner cortex of petiole, showing pitting, UQF50624, ×99. 10, Transverse section of part of petiole base, UQF53541, from Homevale, ×42; note increase in diameter of fibres of sclerotic ring towards inner cortext of petiole.

Fig. 11. *Palaeosmunda playfordii* gen. et. sp. nov. Transverse surface of holotype, UQF53544, from Blackwater Mine, ×0·75; loosely adpressed petioles and numerous roots in outer part of mantle. (1–10, transmitted light; 11, reflected light.)

toward the pith, and the protoxylem group in the centre of the concave surface; the protoxylem group may bifurcate at this stage. The curved part of the 'U' with the adaxial protoxylem group (or groups) then breaks away to form the leaf trace. The leaf gap in the stem xylem may be closed before the leaf trace breaks away, and hence the gap is not evident in any one transverse section, the stem xylem being continuous within the strand or through the departing leaf trace. In other cases the formation of the gap may be delayed until after the leaf trace has entered the inner cortex; sometimes it appears that no complete gap forms although the island of parenchyma is still well developed. A pair of root traces usually arise with the departing leaf trace, one root trace arising from each abaxial lateral angle of the 'U'. However root traces may also be derived from 1 or 2 adjacent strands which partly coalesce with the original radial metaxylem strand.

The leaf traces become progressively larger and more C-shaped as they move out. There are 1–2 adaxial protoxylem groups in the trace when it enters the inner cortex, (1) 2–4 groups as it passes from the inner to the outer cortex, and 4–12 groups when it enters the petiole base. The trace gains encircling layers of phloem, pericycle, endodermis, inner cortex (sometimes including sclerenchyma strands), and outer cortex as it passes through these zones of the stem; except for the sclerenchyma strands around the endodermis, no gaps are left in the tissues concerned. Where sclerenchyma strands are present in the stem, they surround the endodermis of the leaf trace as soon as it enters the inner cortex (Pl. 1, fig. 2); in other cases the sclerenchyma appears further out in the inner or outer cortex, either initially located within the arms of the 'C' or surrounding the leaf trace. The strands of sclerenchyma fibres are always present around the endodermis of the leaf traces within the outer cortex of the stem.

Petioles. The petiole bases arise from the stem at angles of 10–35°; they are usually tightly packed near to the stem, but may be closely or loosely adpressed further out in the mantle (Pl. 2, fig. 6; Pl. 3, fig. 7). The bases consist of a C-shaped vascular strand surrounded by the endodermis, the inner cortex including bundles of sclerenchyma fibres just outside the endodermis, the sclerotic ring, and the stipules (Pl. 2, fig. 2); apart from the stipules, which arise with the petiole, these tissues are continuous with the corresponding zones of the stem. The petiole bases enlarge upwards, ranging from a minimum of 2·5 mm. in radial thickness by 4 mm. wide near the stem, up to 14 mm. thick by 32 mm. wide at the periphery of the mantle of leaf bases, and the ends of the vascular strand become more incurved.

Towards the periphery of the mantle the xylem of the petiolar strand becomes narrower, being 3–4 tracheids thick radially near the stem and only 1–3 tracheids thick further out; the metaxylem tracheids generally decrease in diameter from up to 100–140 μ to 25–70 μ. In one specimen, secondary thickening similar to that of the sclerenchyma fibres occurs in a few tracheids; these have a wall thickness of 13–28 μ. Up to 44 protoxylem groups project on the adaxial sides of the xylem traces in the outermost petioles. In two specimens it appears that there is an intermittent parenchyma sheath around the xylem, consisting of polygonal cells 12–20 μ in diameter. The xylem trace is then completely surrounded by phloem, containing cells which are polygonal in transverse section and 14–40 μ in diameter. The pericycle consists of 2 to 5 layers of polygonal cells 17–30 μ in diameter. Large, apparently schizogenous, mucilage cavities with a diameter of 95–140 μ sometimes occur in the adaxial pericycle region.

The endodermis is often well marked by a dark line or a colour change, but is rarely preserved in detail; it is 1 or 2 cells thick, the cells measuring 14–45 $\mu \times$ 12–30 μ in transverse section, and showing distinct Casparian strips.

The parenchyma cells of the inner cortex of the petiole are polygonal in transverse section with a diameter of 27–95 μ and a wall thickness of 0·8–5 μ. The strands of sclerenchyma that surround the endodermis consist of fibres with a diameter of 13–55 μ, a length of 130 μ to at least 1300 μ, and a wall thickness of 10–34 μ; in some fibres, the secondary wall completely fills the lumen. The end walls may be transverse, oblique, or tapering. The longitudinal walls are usually pitted (pits 2·5–4 μ; Pl. 4, fig. 9) similarly to those of the outer cortex of the stem. Extending up the petiole, the groups at first increase and irregularly coalesce, and then diminish in numbers and size. The concentration of strands varies from a complete spread almost filling the inner cortex, to a single row just surrounding the endodermis. Sometimes 1–4 strands of fibres occur discrete from the others in the lateral extremities of the inner cortex.

The sclerotic ring is usually rhomboidal in cross-section, upwards becoming tangentially elongated; the lateral extremities extend well into the stipules and eventually replace them (Pl. 1, fig. 1; Pl. 3, figs. 1, 7). Adjacent to the stem the size of the ring varies from $3 \times 2{\cdot}5$ mm. to 9×6 mm. with an average thickness of 0·3–0·6 mm.; toward the periphery of the mantle the rings are up to $31{\cdot}5 \times 14$ mm. with a thickness of up to 0·9 mm. The lateral extremities of the rings are usually markedly thinner than the abaxial and adaxial portions. The constituent fibres are similar to those forming the outer cortex of the stem. The fibre diameter increases gradually toward the inner cortex of the petiole base (Pl. 4, fig. 10), although occasionally only a few layers lining the inside of the ring are distinctly larger; the wall thickness (6–24 μ) of all the cells is approximately the same in any one ring. In one specimen, some sclerotic rings contain 1 or 2 masses of large, but short, irregularly arranged, sclerenchyma cells; these are usually in the thin lateral extremities of the ring and appear to have developed where the ring has been broken (Pl. 3, fig. 3).

The stipules consist of polygonal parenchyma cells 14–80 μ in transverse diameter with walls 0·8–3 μ thick, although in many specimens little cellular detail is preserved (Pl. 2, fig. 2). Up to 30, generally small, strands of sclerenchyma develop in the stipular wings of two specimens (Pl. 3, fig. 3). These strands contain fibres with a diameter of 12–55 μ, and a wall thickness between two adjacent cells of 6–28 μ. The secondary wall may completely fill the lumen. The stipular tissue extends well up the petiole base and at least to the periphery of the closely packed mantle of leaf bases. However, the lateral extension of the sclerotic ring replaces more of the stipules further up the petiole base, although in some cases the stipules also increase in length; poor preservation and penetration by adventitious roots prevents definite identification of the parenchymatous stipules at this level.

Roots. The roots usually arise in pairs from the leaf trace before, as, or just after it leaves the stem xylem but before it enters the inner cortex; in one specimen, however, some root traces originate from leaf traces in the inner cortex. Roots occasionally arise from stem xylem strands immediately above, below, or adjacent to departing leaf traces. The xylem trace is diarch (Pl. 1, fig. 2; Pl. 4, fig. 3) and it gains the tissues of the phloem, pericycle, and endodermis as it passes through these zones of the stem. The xylem tracheids are similar to those in the stem (Pl. 4, figs. 4, 5). In the inner cortex the root trace may have a narrow sclerenchyma sheath continuous with the endodermis of the stem, but this is replaced by a sclerotic cortex as the trace enters the outer cortex of the stem (Pl. 2, fig. 7). A few layers of the cells of the inner cortex may accompany the root trace into the outer cortex as there is a gap between the endodermis and the sclerenchyma, but in several cases no inner cortical cells are present. Towards the outside of the mantle, the walls of the cortical fibres nearest to the endodermis usually become progressively thinner, thus giving the appearance of a parenchymatous inner cortex. The endodermis often shows well-defined Casparian strips. The roots vary from less than 1 mm. to 2·5 mm. in diameter and in the majority of specimens, except for the region near the stem, most are cut transversely by a transverse section of the trunk (Pl. 3, fig. 7); this is probably indicative of an arborescent habit (Miller, pers. comm. 1969). They are often branched within the mantle and outside it, sometimes forming an external mat up to 3 cm. wide. The roots freely penetrate the cortex of the stem and the stipules, but not the sclerotic rings or inner cortex of the petiole bases.

Branching. The branching of the stem does not show any abnormal characteristics. However the single specimen containing the branching region is not well preserved.

Discussion. The species is characterized by the sclerotic strands surrounding the leaf traces in the inner cortex of the petiole base. The stele (e.g. Pl. 3, fig. 2; text-fig. 3) is somewhat similar to that in the Jurassic *Osmundacaulis dunlopi* (Kidston and Gwynne-Vaughan) Miller 1967 (see Kidston and Gwynne-Vaughan 1907; Marshall 1926; Edwards 1933, 1934) in that leaf gaps may or may not be completely developed in the xylem ring. Unlike some members of the Osmundaceae, the steles of *P. williamsii* which show the continuous xylem ring are not just associated with branching of the stem (cf. Hewitson 1962). Further variability of the stele is exhibited by the number of protoxylem groups in the developing leaf traces; those which arise from the stele with 2 protoxylems are, like those containing only 1 protoxylem, derived from a single original metaxylem strand of the stele and not from 2 adjacent crozier-shaped strands as is the case in the subgenus *Plenasium* of the genus *Osmunda* (Hewitson 1962, Miller 1967).

Other occurrences. Bowen River crossing, near Gatton Vale Homestead (Blackwater Group); Byerwen Station (Blackwater Group); south-western boundary of Homevale Station (Blackwater Group); Kemmis Creek (Blackwater Group); and south of Utah Development Company's Blackwater Mine, Blackwater district (Rangal Coal Measures of Blackwater Group; or Bandanna Formation). The localities are shown on text-fig. 1.

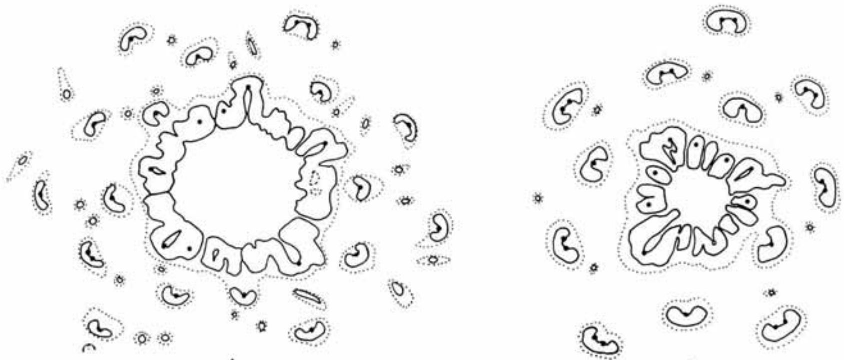
Palaeosmunda playfordii sp. nov.

Plate 4, fig. 11; Plate 5, figs. 1–5; Plate 6, figs. 1–10; Plate 7, figs. 1–9; Plate 8, figs. 1–7; text-figs. 2, 4

Holotype. UQF53544; figured in Plate 4, fig. 11; Plate 5, fig. 1; Plate 6, figs. 2–4, 9, 10; Plate 8, figs. 6, 7.

Type locality. South of Utah Development Company's Blackwater Mine, Portion 3, Parish of Stewarton, near Blackwater, central Queensland; Bandanna Formation, or Rangal Coal Measures of Blackwater Group (formerly Upper Bowen Coal Measures). Locality shown as Blackwater Mine in text-fig. 1.

Diagnosis. *Palaeosmunda* trunks up to 18 cm. in diameter; stems 18–37 mm. wide. Stele an ectophloic dictyoxylic siphonostele, 3·5–11 mm. in diameter; pith diameter 2–6 mm.; xylem ring 1–2 mm. wide, with (?0)3–13 gaps, consisting of 14–20, 27 radial strands, 9–19 tracheids thick; metaxylem tracheids 30–160 μ in diameter, with regular scalariform pitting in 1–7 vertical series on each wall. Inner cortex parenchymatous, 1–6 mm. wide, including 6–21 leaf traces in a given transverse section; fibrous outer cortex 1–10 mm. wide, containing 9–19 leaf traces in a transverse section. Leaf traces arise with one adaxial protoxylem group which usually bifurcates in inner cortex of stem. Stipules and inner cortex of petiole bases parenchymatous.



TEXT-FIG. 4. *Palaeosmunda playfordii* gen. et sp. nov. Transverse sections of stele and inner cortex, *c.* ×3·5; protoxylem groups, where discernible, represented as black dots; endodermis by a dotted line. A, UQF50622; B, UQF53566.

Description

General. This species is the most common in the material collected from the Blackwater district; more than 30 trunks, consisting of a central stem with a mantle of petiole bases and adventitious roots (e.g. Pl. 4, fig. 11; Pl. 5, figs. 1, 3), were used for the description. The specimens are up to 28 cm. long and 18 cm. in diameter with one or both ends broken across. The stems may be dichotomously branched but, although

EXPLANATION OF PLATE 5

Figs. 1–5. *Palaeosmunda playfordii* gen. et sp. nov. 1, Transverse section of holotype, UQF53544, ×1·5; pith and some of inner cortex not preserved. 2, Transverse section of UQF53553, from Blackwater Mine, ×2. 3–5, UQF53566, from Blackwater Mine. 3, Transverse section ×1. 4, Detail of stele and inner cortex, ×5. 5, Longitudinal section of pith and xylem of stem, ×24. (1, transmitted and reflected light; 2–5, transmitted light.)

EXPLANATION OF PLATE 6

Figs. 1–10. *Palaeosmunda playfordii* gen. et sp. nov. 1, Transverse surface of axis above dichotomy (actual branching region not present in specimen), UQF53560, from Blackwater Mine, ×1. 2–4, 9, 10, Holotype, UQF53544. 2, Transverse section of inner cortex, ×66. 3, Longitudinal section of inner cortex, ×66. 4, Longitudinal section of outer cortex showing pitting. ×99. 9, Transverse section of petiole base at point of departure from stem, ×16. 10, Detail of vascular trace in fig. 9, ×66. 5, 6, Longitudinal sections of outer cortex. 5, UQF53566, ×44; 6, UQF53567, from Blackwater Mine, ×63. 7, 8, UQF50622, from Blackwater district. 7, Transverse section of leaf trace at outside of inner cortex, ×16. 8, Transverse section of leaf trace in inner cortex, ×10·6. (1, reflected light; 2–10, transmitted light.)

some specimens contain 2–4 axes in close proximity, the actual branching region is not present (Pl. 6, fig. 1).

Stele. The pith is 2–6 mm. wide and consists of longitudinally elongated, polygonal parenchyma cells with a diameter of 20–83 μ, and a length of 68–300 μ (Pl. 5, fig. 5); wall thickness between two adjacent cells is 1·5–3·5 μ, but may appear up to 10 μ due to organic and mineral matter. There is a slight decrease in the transverse diameter of the pith cells toward the xylem ring.

The xylem cylinder is 1–2 mm. wide and in transverse section exhibits 3–13 gaps (text-fig. 4). It consists of 14–20 (one with 27) radial metaxylem strands, 9–19 tracheids thick, and shows 10–16 external lobes. The protoxylem groups, which appear subcentrally in the metaxylem strands below the departure of leaf traces, consist of tracheids with a diameter of 7–27 μ and a wall thickness of 4–13 μ. Metaxylem tracheids have a diameter of 30–160 μ and a total wall thickness between two adjacent cells of 6–27 μ. These tracheids have 1–7 vertical series of regular scalariform pits on each wall; the bars of thickening are 1–3 μ thick and 2·5–8 μ apart. As in *P. williamsii*, the xylem is dissected by gaps in some specimens (Pl. 5, figs. 2, 4), while in others it is an almost continuous but externally indented ring (Pl. 7, fig. 9). A parenchyma sheath 2–8 cells thick is present in two specimens which both have fully dissected xylem rings. The sheath is prominently developed on the outside of, and in the gaps between, the xylem strands; it does not appear to be present between pith and xylem. The sheath consists of elongated polygonal cells which have a diameter of 13–40 μ, a length of 40–120 μ, and a wall thickness of 1·6–5 μ.

The phloem forms a continuous layer around the xylem and xylem sheath. The metaphloem, which has its greatest development in the indentations between the metaxylem strands, contain cells which are polygonal in transverse section, and presumed to be sieve cells with a diameter of 35–96 μ, a length of at least 550 μ, and a wall thickness between adjacent strands of 1·6–6·8 μ; no sieve areas, however, could definitely be distinguished. Associated with these are some smaller cells, which are rectangular to polygonal in transverse view; these measure from 14–27 μ in diameter to 40 μ × 14 μ. The metaphloem is surrounded by a continuous zone, 68–130 μ wide, of crushed cells, which probably represents the protophloem and pericycle. Some polygonal and tangentially elongated cells, 13–70 μ in diameter with a wall thickness of 3–13 μ, can be distinguished; these have a length of 54–270 μ.

The endodermis is marked by a different colouration and a change from the pericycle to the larger cells of the inner cortex. It consists of slighly darker coloured, more resistant cells which are rounded-polygonal to tangentially elongated in cross-section with a diameter of 12–55 μ; they are rectangular in longitudinal view and up to 200 μ long. No definite Casparian strips are visible. The total diameter of the stele to the endodermis is 3·5–11 mm.

Cortex. The inner cortex consists of slightly tangentially and longitudinally elongated rounded to polygonal parenchyma cells with a transverse diameter of 25–110 μ and a length of 40–170 μ (Pl. 6, figs. 2, 3). The walls may be straight or sinuous, with a thickness between two adjacent cells of 1·5–4 μ. The inner cortex is 1–6 mm. wide; in most specimens this zone contains 6–13 leaf traces in a given transverse section, but one shows 20–1 traces.

The dense sclerotic outer cortical region is 1–10 mm. wide, and consists of fibres which are polygonal in cross-section. The walls between two adjacent cells are 10–30 μ thick and clearly show the primary and secondary walls; intercellular spaces of up to 6 μ commonly occur at the angles. The majority of cells are 13–55 μ in diameter with a length of at least 1300–1800 μ (Pl. 6, figs. 5, 6); the end walls may be transverse, oblique, or tapering. Some relatively wider (28–85 μ, but up to 160 μ) and shorter (200 μ) cells occur on the boundary with the inner cortex of the stem and the leaf traces, and in the depressions beneath the departing petiole bases on the outside of the stem. The longitudinal walls of the fibres may be smooth or with round to oval pits (2·5–8 μ; Pl. 6, fig. 4) as in *P. williamsii*. Larger, more or less rectangular or annular pits appear to be caused by shrinkage of the original wall material. The outer cortex contains 9–19 leaf traces in a given transverse section; total number of traces in the whole cortex in any one section is 18–38.

Leaf traces. These arise from the stem xylem similarly to the traces in the Tertiary–Recent subgenera *Osmunda* and *Osmundastrum*; leaf gaps are usually developed. A mesarch protoxylem group appears in the metaxylem strand of the stem and then an island of parenchyma develops adaxially to the protoxylem. The island of parenchyma enlarges upwards and connects with the pith to form the leaf gap while the outer endarch arch of the xylem breaks away to form the leaf trace. The trace gains the encircling tissues of the xylem sheath, phloem, pericycle, endodermis, inner cortex, and outer cortex as it passes through these respective zones of the stem; each zone of the stem fills in behind the trace and no gaps are formed.

The leaf trace arises with one endarch protoxylem group which usually bifurcates in the inner cortex of the stem (Pl. 6, figs. 7, 8); 4–10 adaxial protoxylem groups are present

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EXPLANATION OF PLATE 7

Figs. 1–9. *Palaeosmunda playfordii* gen. et sp. nov. 1–8, UQF53547, from Blackwater Mine. 1, Transverse section of petioles in outer part of mantle, ×1·5. 2, Part of vascular trace and inner cortex of petiole at left centre of fig. 1, ×10·6. 3, Transverse section of part of vascular trace and inner cortex of petiole (not shown in fig. 1), ×16. 4, Detail of vascular trace from fig. 3, ×42. 5, Further enlargement of part of vascular trace with the adaxial schizogenous mucilage cavities, ×66. 6, Longitudinal section of part of vascular trace of petiole, showing zone of crushed parenchyma cells, ×99. 7, Detail of endodermis of petiolar trace, showing Casparian strips on the radial walls, ×270. 8, Transverse section of sclerotic ring of petiole base; note increase in fibre diameter toward the inner cortex, ×42. 9, Transverse section of stele, UQF50622, ×6; pith and inner cortex not preserved. (1, transmitted and reflected light; 2–9, transmitted light.)

EXPLANATION OF PLATE 8

Figs. 1–7. *Palaeosmunda playfordii* gen. et sp. nov. 1–5, Transverse sections of roots. 1, UQF53564, from Blackwater Mine, ×26·5; 2, Shows triarch xylem trace, UQF59129, from Blackwater Mine, ×10·6. 3–5, Show 2 diarch xylem strands in section, UQF53547. 3, ×16; 4, ×31·5; 5, ×26·5. 6, 7, Xylem tracheids of petiole containing Basidiomycete hyphae with clamp connections, holotype, UQF53544, ×480.

Figs. 8, 9. Dissociated, flanged petioles, with fronds of *Sphenopteris lobifolia–Cladophlebis roylei–S. polymorpha*, and *Glossopteris* sp., from the Burngrove Formation at Burngrove Creek. 8, UQF53582, ×0·66 (the line is a saw cut—see figs. 10, 11); 9, UQF53575, ×0·44.

Figs. 10, 11. Sections of dissociated petioles in specimen shown in fig. 8, ×2.

Figs. 12, 13. Compressions of osmundaceous trunks (probably *Palaeosmunda*) from the Burngrove Formation at Burngrove Creek. 12, UQF53581, ×0·66; 13, UQF53577, ×0·55. (1–7, transmitted light; 8–13, reflected light.)

when the trace enters the base of the petiole. There are up to 44 groups in the trace in the outer zones of the mantle.

Petioles. The petioles arise from the stem at angles of 15–30° and are usually closely adpressed near the stem but loosely arranged in the outer part of the mantle (Pl. 4, fig. 11). The petiole bases consist of a C-shaped vascular trace surrounded by a parenchymatous inner cortex, a sclerotic ring, and lateral stipules; except for the stipules which arise as the petiole emerges from the stem, these tissues are derived from, and continuous with, the corresponding zones of the stem. The bases enlarge upwards, ranging in transverse section from 3·5 mm. thick by 7 mm. wide near the stem, up to 12·5 mm. thick and 35 mm. wide near the periphery of the mantle.

Upwards the C-shaped xylem strands become larger, but thinner, the constituent tracheids narrower, and the ends become more incurved (cf. Pl. 6, figs. 9, 10 and Pl. 7, figs. 1–5). The strands are 1–4 tracheids thick, and the metaxylem tracheids are 30–110 μ in diameter, rarely up to 160 μ. Basidiomycete hyphae showing clamp connections occur within some tracheids in the holotype (Pl. 8, figs. 6, 7). The xylem is surrrounded by a xylem sheath up to 6 cells thick, the phloem, the pericycle, and the endodermis. The pericycle is 2–6 cells thick, and usually contains numerous, apparently schizogenous, mucilage cavities with a diameter of 68–164 μ (Pl. 7, fig. 5; cf. Seward and Ford 1903, p. 247, pl. 30, fig. 45); these cavities are most common on the adaxial side of the trace, but are occasionally present on the abaxial side. Groups of compressed, irregularly arranged parenchyma cells occur in the adaxial xylem sheath, phloem, and pericycle. The groups are quite distinctive in longitudinal section (Pl. 7, fig. 6) and compression probably resulted from the formation of the schizogenous cavities.

The endodermis is 1–2 cells thick (Pl. 7, fig. 7). The cells are polygonal in transverse section (diameter 14–35 μ) and elongated to rectangular in longitudinal view (length 80–330 μ). Casparian strips 6–17 μ wide are present.

The inner cortex of the petiole base consists of parenchyma cells (Pl. 6, fig. 9; Pl. 7, figs. 2, 3) which are polygonal in transverse section with a diameter of 25–100 μ, and rectangular in longitudinal section with a length of 40–280 μ; wall thickness between two adjacent cells is 1–3·5 μ. Sometimes the cells have been partially macerated and separated before preservation.

The sclerotic ring contains sclerenchyma fibres similar to those in the outer cortex of the stem. The fibres are polygonal in transverse section and generally range from 13 to 40 μ in diameter; in any one ring there is usually a gradual increase in diameter towards the inner cortex (Pl. 7, fig. 8). The walls between adjacent fibres are 6–17 μ thick. The sclerotic rings are circular to rhomboidal in shape when they arise and they broaden upwards, contributing greatly to the stipules, eventually replacing them. They range in size from 3–7 mm. in diameter near the stem to 34·5 × 12 mm. in the periphery of the mantle; the thickness of the ring varies from 0·2 mm. to 1 mm. and the lateral extremities are usually thinner than the adaxial and abaxial portions.

The sclerotic ring is surrounded by a sheath of parenchymatous tissue which is extended laterally to form the stipules; the cells have diameters of 25–60 μ.

Roots. The adventitious roots have a diameter of 0·7–2·5 mm. and usually arise in pairs from the leaf traces before their departure from the stele. Roots may also arise irregularly from the metaxylem strands of the stem, especially those immediately below a departing leaf trace. The xylem trace gains the surrounding tissues of phloem, pericycle, endodermis, and sclerotic outer cortex as it passes through these zones of the stem. In most cases no cells of the inner cortex accompany the trace into the outer cortex of the stem, the sclerenchyma being contiguous with the endodermis. In a few examples, however, there is a narrow gap between the endodermis of the root trace and the sclerotic outer cortex as if a layer of inner cortex was present, but no cells are preserved. In a cross-section of the trunk, most roots, except those in the region near the stem, are seen in transverse section (Pl. 4, fig. 11) and this is probably indicative of an arborescent habit (Miller pers. comm. 1969). The root usually has a diarch xylem trace (Pl. 8, fig. 1), but in one case it is triarch (Pl. 8, fig. 2); some show two diarch xylem strands in a section (Pl. 8, figs. 3–5), possibly prior to branching. Sections of roots from the inside to the outside of the mantle show the inner layers of cortical fibres progressively becoming thin-walled, thus appearing as a parenchymatous inner cortex. The roots, which are often branched, penetrate freely throughout the mantle of leaf bases between the sclerotic rings; in one specimen they penetrate through the sclerotic rings into the inner cortex of some of the outer leaf bases, possibly because these were injured while the plant was still living. In several specimens the trunk is surrounded by a mat of roots up to 6 cm. wide; the silt- to very fine sand-sized sediment enclosed within this zone is in contrast to the medium to very coarse sandstone in which the specimens occur.

Discussion. Palaeosmunda playfordii differs from *P. williamsii* in lacking sclerenchyma strands in the stipules and inner cortex of the petiole bases. Speciation on the distribution of sclerenchyma in the leaf bases in Osmundaceae is a well-established principle (e.g. Miller 1967) and the distinction by presence or absence of sclerenchyma is a useful one. The xylem ring in the specimens of *P. playfordii* studied, unlike that in *P. williamsii*, always exhibits some leaf gaps (text-fig. 4); however, the variation shown is of a magnitude that suggests it would be possible for a xylem ring with no gaps to occur. The leaf traces have only been found to arise with 1 protoxylem group.

ASSOCIATED FOLIAGE

The fossil flora of the Upper Bowen Coal Measures has been described and figured by Walkom (1922), Rigby (1962, 1963), Hill and Woods (1964), and White (1964; *in* Malone, Corbett, and Jensen 1964, pp. 70–7, pl. 3–13; *in* Olgers, Webb, Smit, and Coxhead 1966, pp. 49–52, pl. A–D).

Many compressions of osmundaceous trunks, probably referable to *Palaeosmunda*, occur in the silicified, abundantly fossiliferous siltstones of the Burngrove Formation (Blackwater Group) outcropping in a small tributary of Burngrove Creek on 'Tolmies Creek' Station, near Blackwater (Portion 10, Parish of Blackwater; locality shown as Burngrove Creek on text-fig. 1). These specimens show the typical mantle of flanged petiole bases, although other anatomical details are not preserved (Pl. 8, figs. 12, 13). The strata also contain impressions of plants of the types which Walkom (1922) described as *Phyllotheca* sp., *Cladophlebis roylei* Arber 1901, *Sphenopteris polymorpha* Feistmantel 1876, *S. lobifolia* Morris 1845, and *Glossopteris* spp. The portions of fronds referred to *S. lobifolia*, *C. roylei*, and *S. polymorpha* vary from bipinnate to tripinnate and appear to intergrade. Unfortunately, no fertile examples of these fronds have been reported. Some layers of the Burngrove Formation contain masses of the *S. lobifolia–C. roylei–S. polymorpha* fronds, flattened osmundaceous trunks, and dissociated, flanged petioles

(Pl. 8, figs. 8, 9). Transverse sections of some of these dissociated petioles show the sclerotic ring and characteristic C-shaped vascular trace which have been replaced by calcite (Pl. 8, figs. 10, 11). It is thus probable that *Palaeosmunda* trunks bore foliage of this type, but this can only be inferred by association.

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REFERENCES

ANDREWS, H. N. 1961. *Studies in Paleobotany*. New York.

ARBER, E. A. N. 1901. Notes on Royle's types of fossil plants from India. *Geol. Mag.* **8**, 546–9.

ARMSTRONG, J. D., DEAR, J. F., and RUNNEGAR, B. 1967. Permian ammonoids from eastern Australia. *J. geol. Soc. Aust.* **14,** 87–97, 2 pls.

ARNOLD, C. A. 1964. Mesozoic and Tertiary fern evolution and distribution. *Mem. Torrey bot. Club* **21** (5), 58–66.

BOCK, W. 1960. New American Triassic tree ferns. *Proc. Pa Acad. Sci.* **34,** 92–5.

BRONGNIART, A. 1849. *Tableau des genres de végétaux fossiles considérés sous le point de vue de leur classification botanique et de leur distribution géologique: dictionnaire univ. histoire nat.* **13,** 1–127. Paris.

DAUGHERTY, L. H. 1941. The Upper Triassic flora of Arizona. *Publs. Carneg. Instn* **526,** 108 pp., 34 pls.

—— 1960. *Itopsidema*, a new genus of the Osmundaceae from the Triassic of Arizona. *Am. J. Bot.* **47,** 771–7.

DEVINE, S. B. and POWER, P. E. 1967. Permian stratigraphic revisions and rock-unit correlations, central western Bowen Basin, Queensland. *Qd. Govt. Min. J.* **68,** 511–20.

EDWARDS, W. N. 1933. *Osmundites* from central Australia. *Ann. Mag. nat. Hist.*, ser. 10, **11,** 661–3.

—— 1934. Jurassic plants from New Zealand. Ibid., ser. 10, **13,** 81–109, pl. 4, 5.

EICHWALD, E. 1860. *Lethaea Rossica ou paleontologie de la Russie.* **1.** Stuttgart.

EMBERGER, L. 1962. L'intérêt des Osmundacées Triassiques récemment découvertes. *Naturalia monspel.* ser. Bot. **14,** 41–5.

EVANS, P. R. 1966. Mesozoic stratigraphic palynology in Australia. *Australas. Oil Gas J.* **12** (6), 58–63

FEISTMANTEL, O. 1876. On some fossil plants from the Damuda Series in the Raniganj coalfield, collected by Mr. J. Wood-Mason. *J. Asiat. Soc. Beng.* **45** (2), 329–82.

HEWITSON, W. 1962. Comparative morphology of the Osmundaceae. *Ann. Mo. bot. Gdn.* **49,** 57–93.

HILL, D. and DENMEAD, A. K. (eds.). 1960. The geology of Queensland. *J. geol. Soc. Aust.* **7,** 474 pp., 8 pls., 2 maps.

—— and WOODS, J. T. (eds.). 1964. *Permian index fossils of Queensland.* Brisbane.

KIDSTON, R. and GWYNNE-VAUGHAN, D. T. 1907–9. On the fossil Osmundaceae. Part I. *Trans. R. Soc. Edinb.* **45,** 759–80, pl. 1–6. Part II. Ibid. **46,** 213–32, pl. 1–4. Part III. Ibid. **46,** 651–67, pl. 1–8.

MALONE, E. J. 1966. *Geology. Fitzroy region, Queensland. Resources series.* Canberra.

—— CORBETT, D. W. P., and JENSEN, A. R. 1964. Geology of the Mount Coolon 1:250,000 sheet area. *Rep. Bur. Miner. Resour. Geol. Geophys. Aust.* **64,** 78 pp., 15+4 pls.

—— OLGERS, F., MOLLAN, R. G., and JENSEN, A. R. 1967. *Geological map, Bowen Basin, Queensland.* Scale 1:500,000. Canberra.

MARSHALL, P. 1926. A new species of *Osmundites* from Kawhia, New Zealand. *Trans. N.Z. Inst.* **56,** 210–13, pl. 48–54.

MILLER, C. N., JR. 1967. Evolution of the fern genus *Osmunda*. *Contr. Mus. Paleont. Univ. Mich.* **21,** 139–203, pl. 1–4.

—— 1968. The lepidophytic affinities of the genus *Chinlea* and *Osmundites walkeri*. *Am. J. Bot.* **55,** 109–15.

MILLER, C. N., JR. 1969. (In press.) The evolution of the fern family Osmundaceae. *Contr. Mus. Paleont. Univ. Mich.*

MORRIS, J. 1845. *Fossil Flora.* Pp. 245–4, pl. 6, 7, in STRZELECKI, P. E. de. *Physical descriptions of New South Wales and Van Diemen's Land.* London.

OLGERS, F., WEBB, A. W., SMIT, J. A. J., and COXHEAD, B. A., 1966. Geology of the Baralaba 1:250,000 sheet area, Queensland. *Rep. Bur. Miner. Resour. Geol. Geophys. Aust.* **102,** 58 pp., D+3 pls.

ORLOV, YU. A. 1963. *Osnovy paleontologii.* **(14)** *Vodorosli, Mokhoobraznye, Psilofitovye, Plaunovidnye, Chlenistostebel'nye, Paporotniki.* Moscow (in Russian).

PENHALLOW, D. P. 1902. *Osmundites skidegatensis* n.sp. *Trans. R. Soc. Can.* Sect. 4, 2nd ser., **8,** 3–18, pl. 1–6.

POSTHUMUS, O. 1931. *Catalogue of the fossil remains, described as fern stems and petioles.* Malang.

POWER, P. E. 1967. Geology and hydrocarbons, Denison Trough, Australia. *Bull. Am. Ass. Petrol. Geol.* **51,** 1320–45.

RIGBY, J. F. 1962. The taxonomic position of *Actinopteris indica* Srivastava. *Proc. Linn. Soc. N.S.W.* **86,** 299–304, pl. 10A.

—— 1963. On a collection of plants of Permian age from Baralaba, Queensland. Ibid. **87,** 341–51, pl. 11, 12.

RUNNEGAR, B. 1968. (In press.) The Permian faunal succession in eastern Australia. *Proc. Specialist Symposium, Geol. Soc. Aust., Canberra, 1968.*

SEWARD, A. C. 1910. *Fossil Plants. A Text-book for Students of Botany and Geology. II.* Cambridge.

—— and FORD, S. O. 1903. The anatomy of *Todea,* with notes on the geological history and affinities of the Osmundaceae. *Trans. Linn. Soc. Lond.* 2nd ser. Bot. **6,** 237–60, pl. 27–30.

SMITH, E. M. 1958. *Queensland. Lexique stratigraphique international* **6** (5a). Paris.

STEEVES, T. A., and WETMORE, R. H. 1953. Morphogenetic studies on *Osmunda cinnamomea* L.: some aspects of the general morphology. *Phytomorphology* **3,** 339–54.

SURANGE, K. R. 1966. *Indian fossil Pteridophytes.* New Delhi.

WALKOM, A. B. 1922. Palaeozoic floras of Queensland. Part I. The flora of the Lower and Upper Bowen Series. *Publs. geol. Surv. Qd.* **270,** 65 pp.

WEBB, A. W., and MCDOUGALL, I. 1967. Isotopic dating evidence on the age of the Upper Permian and Middle Triassic. *Earth Planet. Sci. Letters* **2,** 483–8.

WEBB, E. A. 1956. Review of exploratory oil wells penetrating Permian section in central Queensland, Australia. *Bull. Am. Ass. Petrol. Geol.* **40,** 2329–53.

WHITE, M. E. 1964. Reproductive structures in Australian Upper Permian Glossopteridae. *Proc. Linn. Soc. N.S.W.* **88,** 392–6, pl. 22–4.

ZALESSKY, M. D. 1924. On new species of Permian Osmundaceae. *J. Linn. Soc.,* Bot. **46,** 347–58, pl. 32–4.

—— 1927. Permskaya flora ural'skikh predelov Angaridy. Atlas. Flore Permienne des limites ouraliennes de l'Angaride. Atlas. *Trudÿ geol. Kom.* **176,** 152 pp., 46 pls. (in Russian and French.)

—— 1931*a*. Structure anatomique du stipe du *Petcheropteris splendida* n. g. et sp., un nouveau représentant des Osmundacées Permiennes. *Izv. Akad. Nauk. SSSR* 7th ser. (1931), 705–10, pl. 1, 2.

—— 1931*b*. Structure anatomique du stipe du *Chasmatopteris principalis* n. g. et sp., un nouveau représentant des Osmundacées Permiennes. Ibid. 715–20, pls. 1, 2.

—— 1935. Structure anatomique du stipe d'une nouvelle Osmondée du terrain Permian du Basin de Kousnetzk. Ibid. (1935) 747–52, pls. 1–3.

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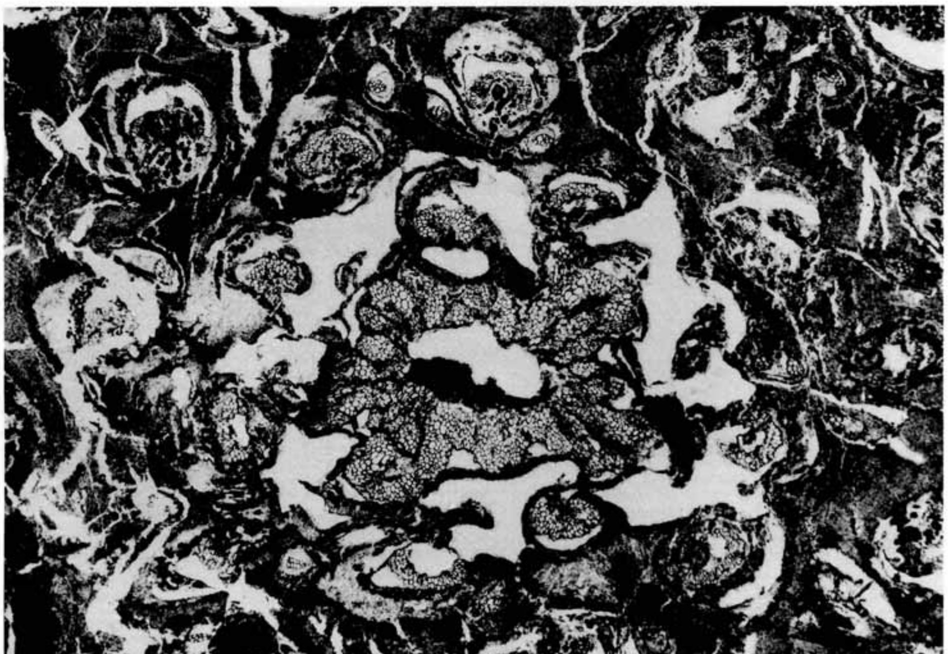

2

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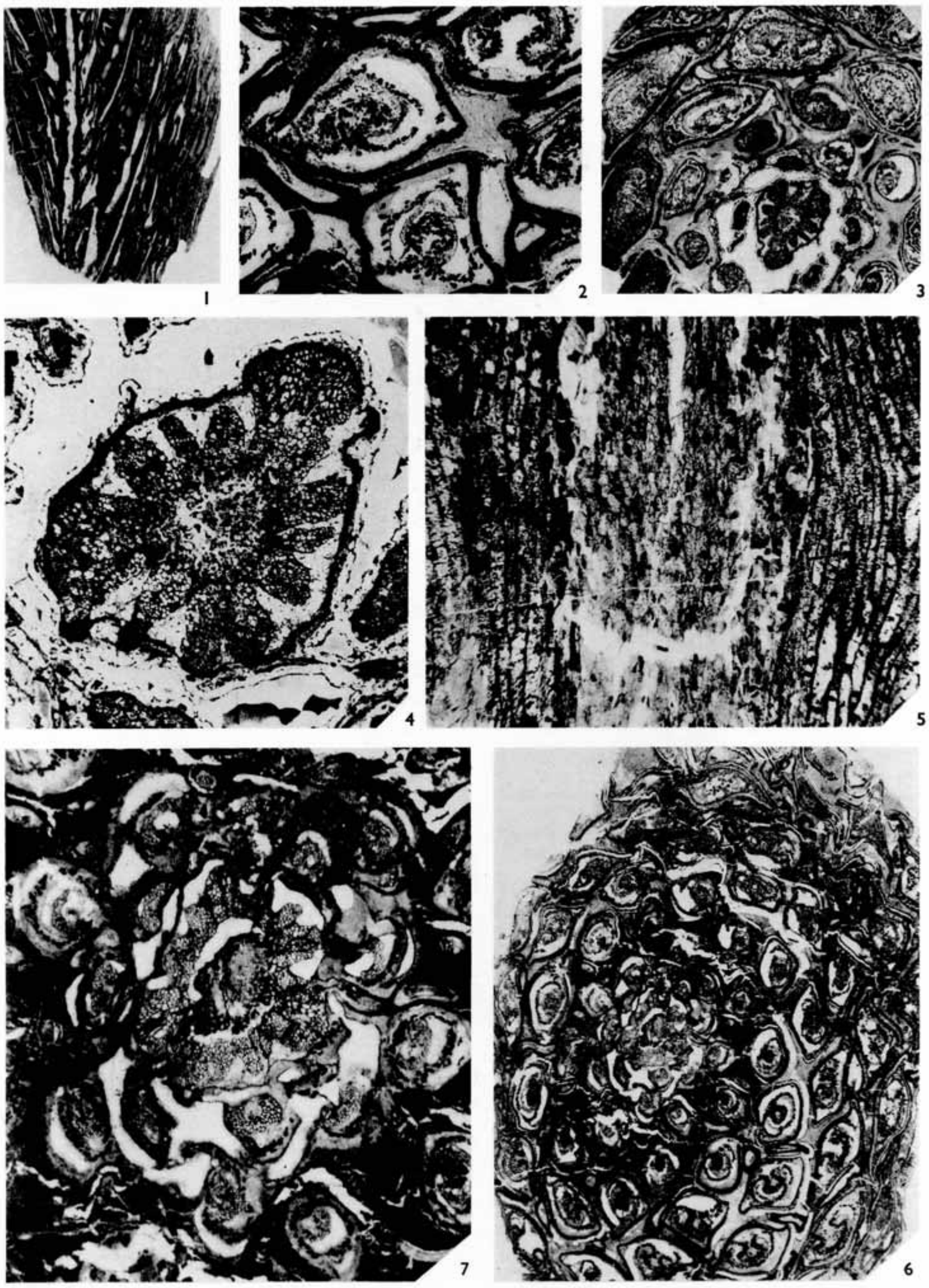

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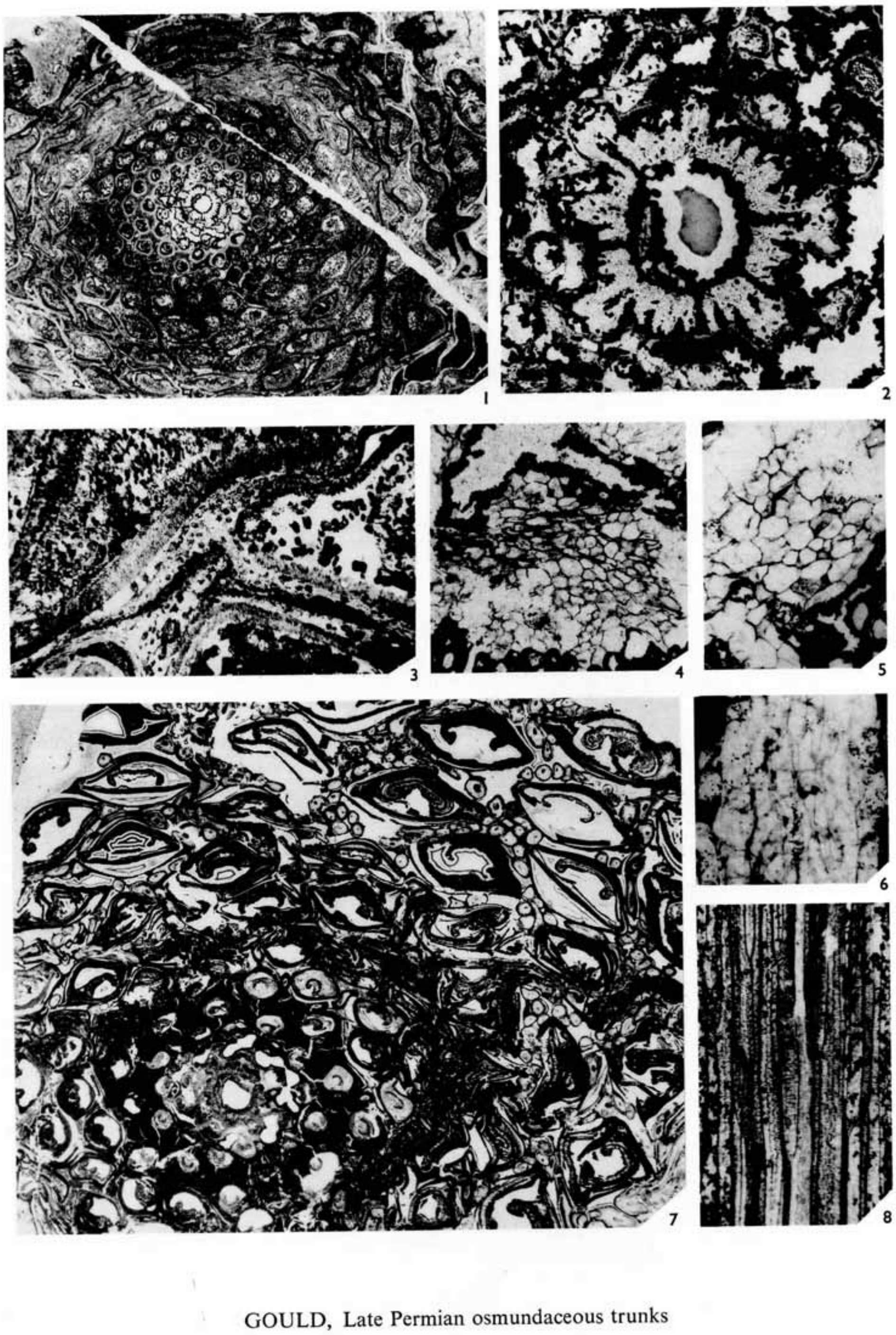

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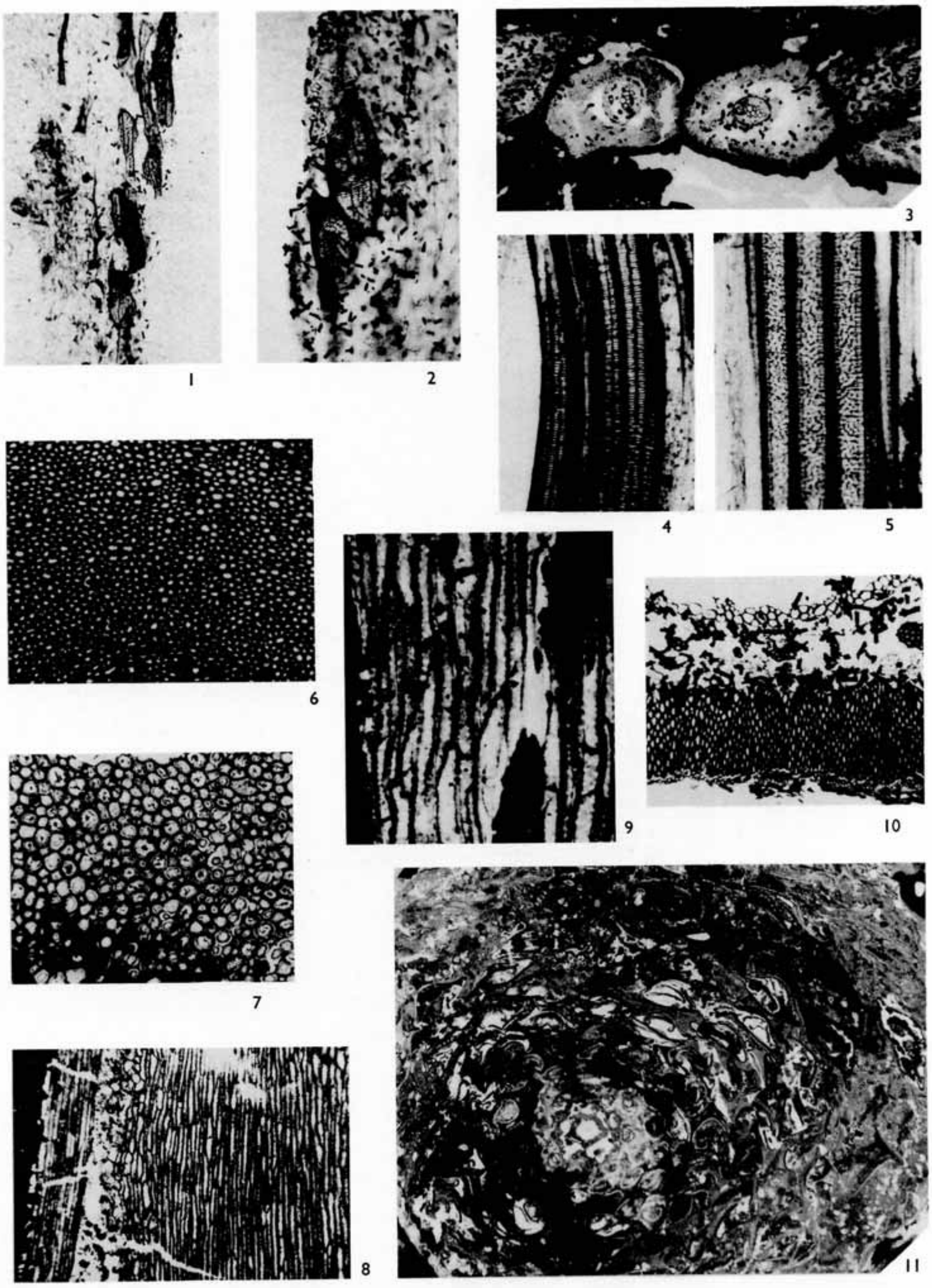

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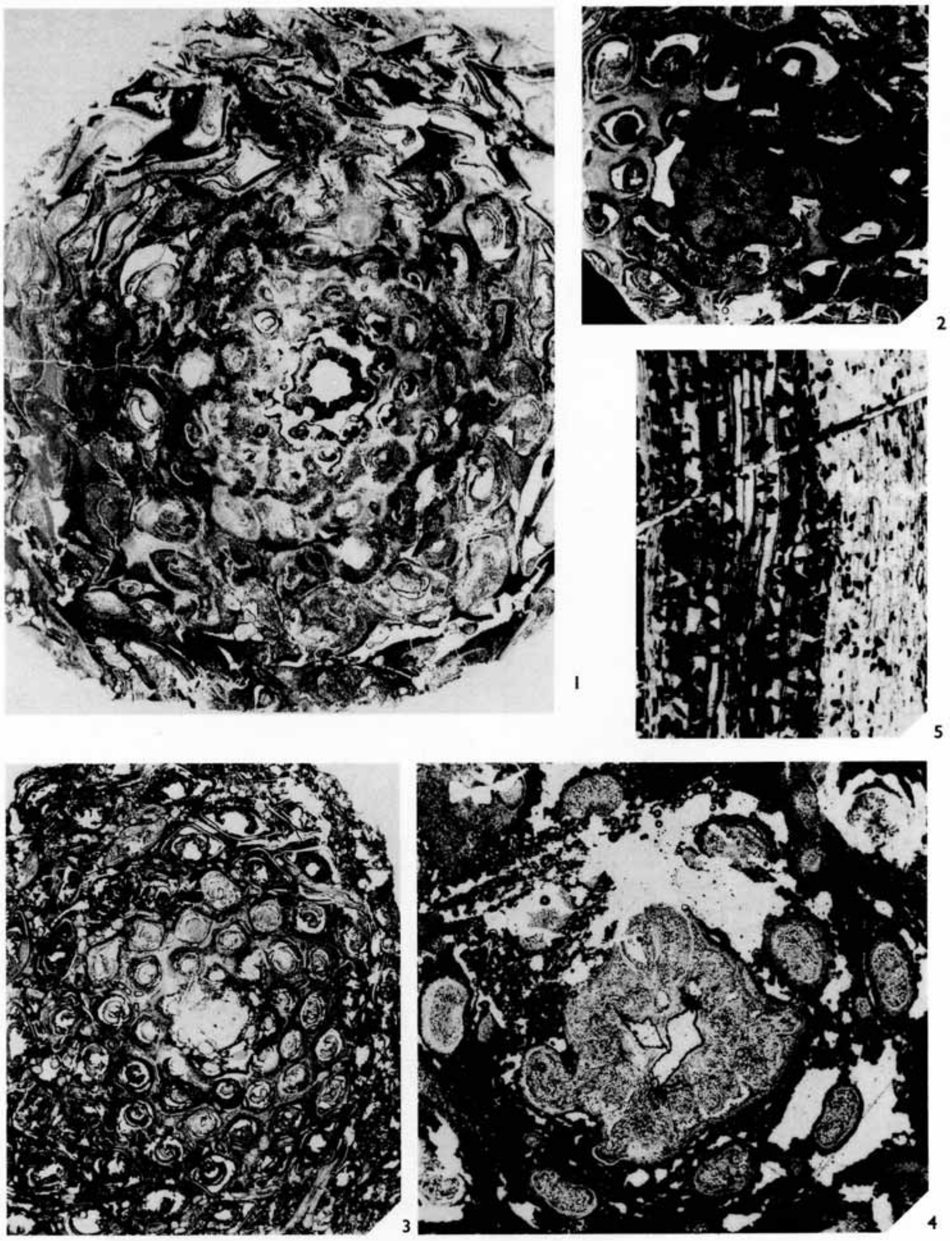

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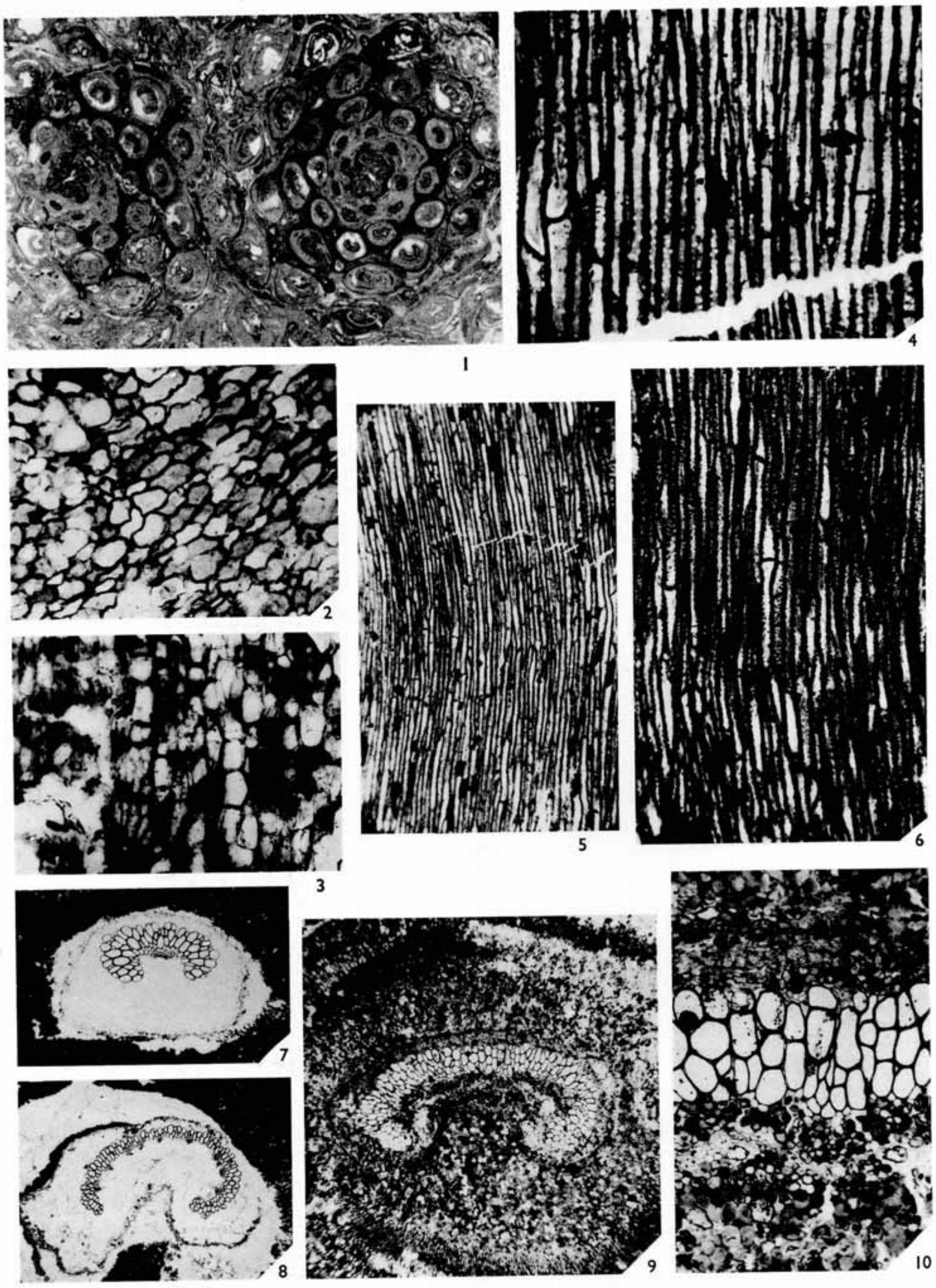

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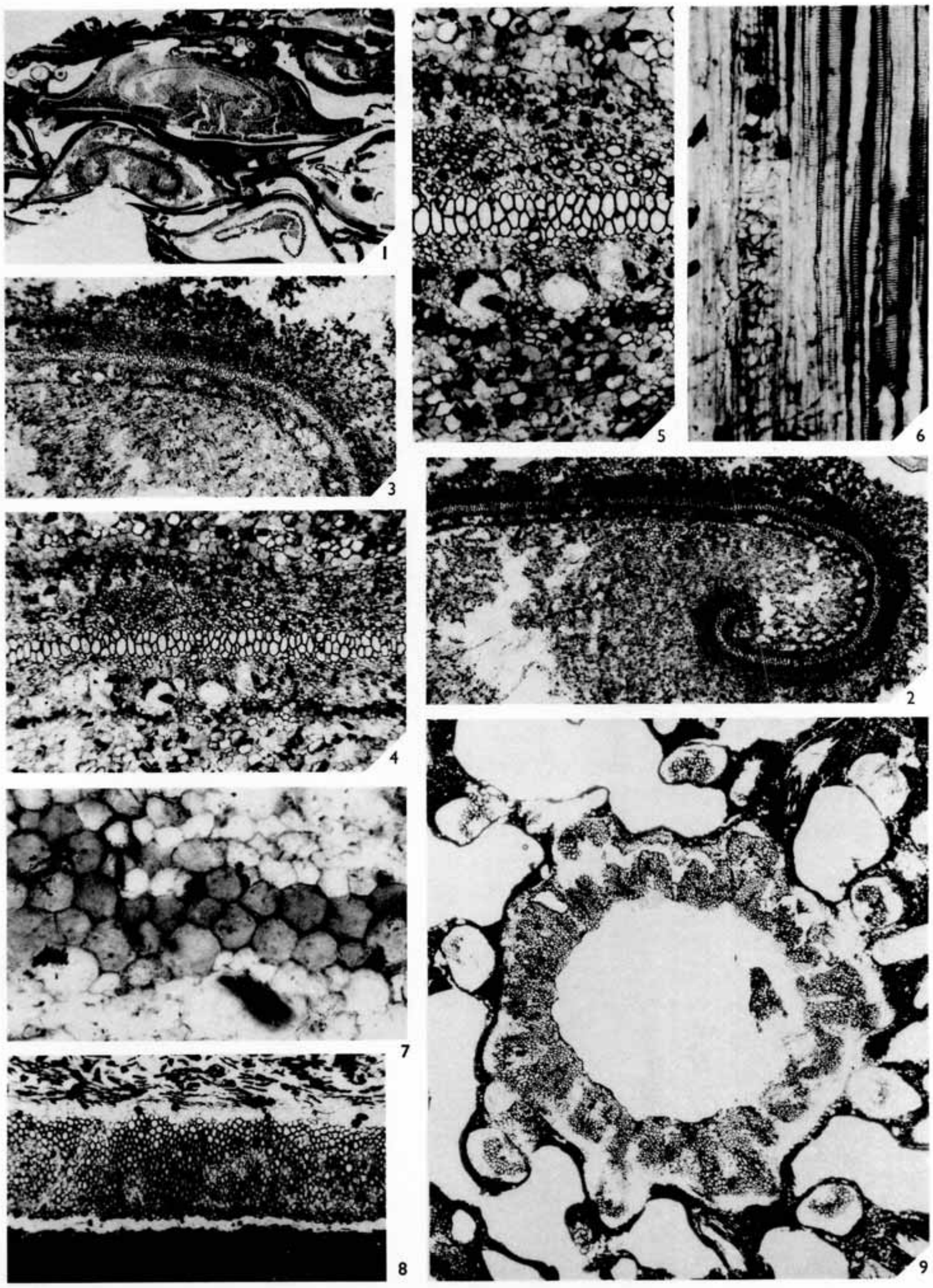

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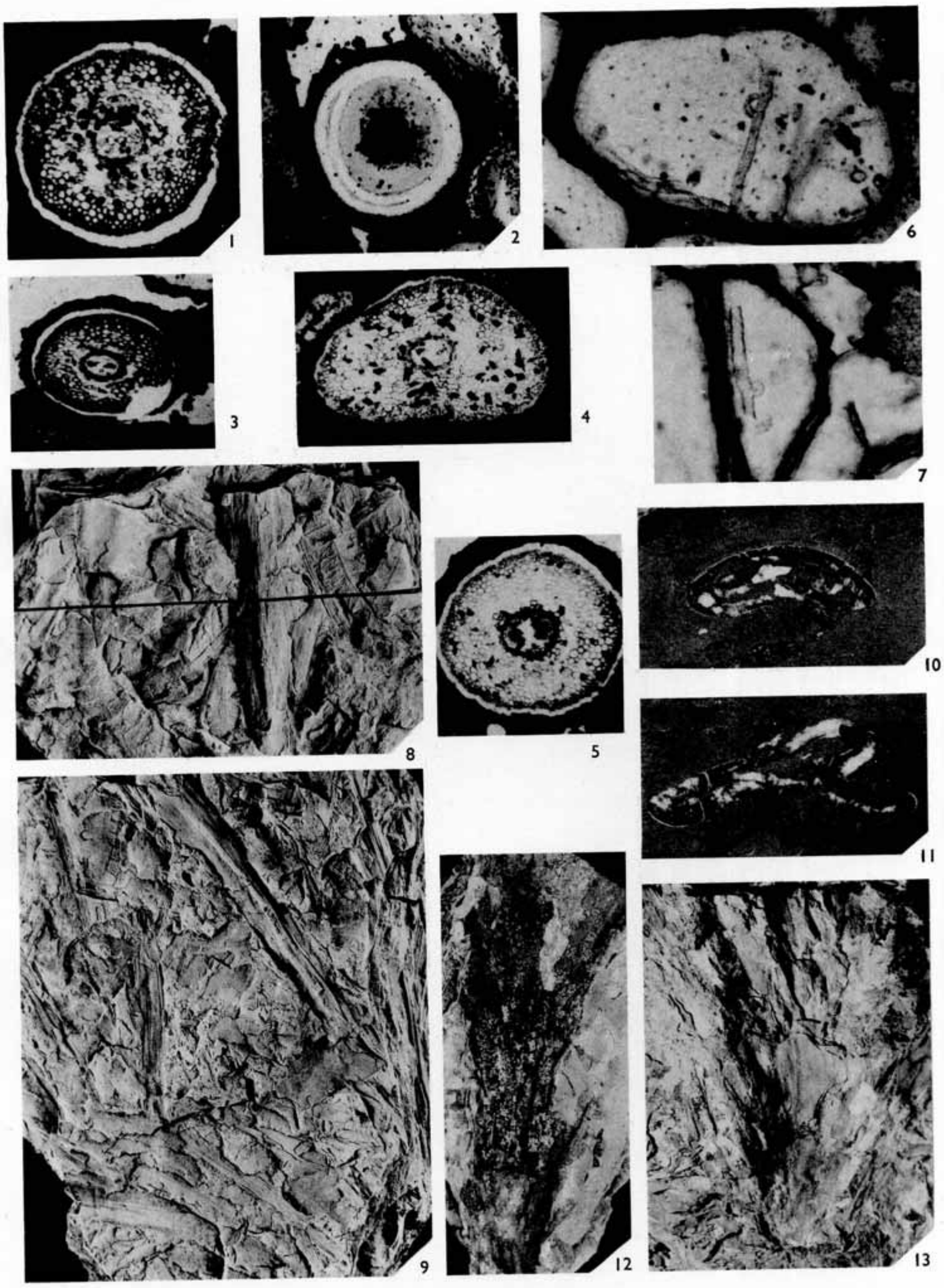

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