

# A NEW GENUS OF OSMUNDACEOUS STEM FROM THE UPPER TRIASSIC OF TASMANIA

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**ABSTRACT.** Petrified osmundaceous trunks from the Late Triassic east of Woodbury in central Tasmania are assigned to a new genus and species, *Australosmunda indentata*. This species possesses an ectophloic siphonostele with a parenchymatous pith, but in other respects is similar to *Millerocaulis*, *Osmundacaulis*, or *Osmunda*. Although leaf gaps are absent the stele is deeply indented where leaf traces arise. *A. indentata* is the first osmundaceous species described which has a stele lacking leaf gaps but a parenchymatous pith, and offers convincing support for the hypothesis that the evolution of the parenchymatous pith and the evolution of leaf gaps in the xylem were independent transitions. Because of the relatively advanced nature of the leaf traces, and the presence of species with leaf gaps earlier in the record (*Palaeosmunda* from the Upper Permian of Queensland), *A. indentata* is unlikely to have been an intermediate stage in the development of leaf gaps, but probably represents a relatively advanced species which has maintained a primitive stelar feature.

THE Osmundaceae contains three living genera with about twenty-one species (Hewitson 1962), but importantly has a long and impressive fossil record (e.g. Miller 1967, 1971; Gould 1970) beginning in the Upper Permian. Of particular interest in the family is the development of the modern stelar types from the earliest fossil types. Since petrified stems are very common a great deal of literature has developed concerning stelar development. Although the evolutionary pathway is now generally beyond debate, newly found fossil species are constantly adding information in this area.

The Osmundaceae are relatively common in Permian to Jurassic strata in Australia (Gould 1970, 1973; Tidwell 1987; Tidwell and Jones 1987, and references therein) and some of the species are of particular evolutionary significance. The discovery of specimens from the Upper Triassic of central Tasmania which belong to a new genus adds substantially to the record of the family in the southern hemisphere and provides evidence of a previously undescribed stelar type.

## LOCALITIES AND GEOLOGY

Petrified tree-fern stems were found at three separate localities east of Woodbury during mapping of the Interlaken Quadrangle of the Tasmanian Geological Survey Geological 1 : 50 000 atlas series (Forsyth 1986). The geology of the area consists essentially of gently dipping volcanic lithic sandstone and coal measures of the Upper Parmeener Supergroup intruded by small and large-scale dolerite sheets and dykes elsewhere radiometrically dated as being of mid-Jurassic age (Schmidt and McDougall 1977). The strata and some dolerite bodies were faulted and eroded prior to the extrusion of tholeiitic lava flows that occur a few kilometres north of the fossil localities. The basalt flows are inferred to be of Early to Middle Miocene (Late Oligocene?) age (Sutherland and Wellman 1986) and probably previously extended closer to the fossil localities. The basalt overlies thin veneers of Tertiary rocks that include silcrete and groundwater ferricrete. Quaternary deposits include veneers consisting largely of dolerite clasts but also containing notable components derived from Parmeener strata. They occur as talus, alluvial fans, higher level alluvial terraces above the modern flood plains, and as lag deposits.

Two of the fossil localities can be directly related to Upper Parmeener strata, the third locality consists of loose material inferred to be derived from Upper Parmeener Supergroup strata and found in a Quaternary high-level terrace deposit. The similarity of the tree-fern fossils at all localities suggests that the third locality is not related to Tertiary silicification.

*Locality 1.* The best stratigraphic control is provided by this locality which occurs high on the northern side of Brents Sugarloaf and is estimated to be 30 m topographically below the summit (Co-ordinates 55 GEP 412296 (Universal Grid Reference), 147° 29' 53" E., 42° 11' 04" S.). Here a conspicuous block of silicified material, probably transported peat, contains much plant material including tree-ferns and *Dicroidium*, and occurs probably almost *in situ* in volcanic lithic sandstone of the Upper Parmeener Supergroup. Further loose pieces of the silicified material occur at the same elevation nearby, suggesting that a lens containing the material is present. Volcanic lithic sandstone beds at a similar horizon on the eastern side of Brents Sugarloaf are well exposed. They include breccia beds with intra-basinal lutite clasts up to 1 m in diameter, beds with silicified stems or tree stumps from a few mm to over 1 m in diameter, and beds with thin layers or isolated pebbles, cobbles, and boulders of rounded extra-basinal clasts. Exotic clasts include cleaved and veined quartzite and acid igneous porphyries. The highest beds at Brents Sugarloaf include black lutite and several tuff layers just below a capping Jurassic dolerite sill.

*Locality 2.* This locality (55 GEP 401284, 147° 29' 10" E., 42° 11' 43" S.) occurs 1.5 km south-west of locality 1 and is probably separated from it by one or more faults. Tree-fern fossils and the long-ranging late Palaeozoic to early Mesozoic pollen *Falcisporites australis* occur in several loose blocks of silicified material to which volcanic lithic sandstone matrix adheres. Two hundred metres further south and higher the fine-grained base of a minor Jurassic dolerite sheet is exposed and is probably faulted against an extensive area of coarse-grained dolerite. Extra-basinal clasts of exotic lithologies similar to those at Brents Sugarloaf but including Lower Parmeener Supergroup lithologies with Permian shelly fauna occur in lag deposits, and in talus shed from the fine-grained dolerite sheet near locality 2. From the rock distribution it is concluded that the extra-basinal clasts and tree-fern fossils are shed from the approximately 40 m of strata underlying the fine-grained dolerite intrusion.

*Locality 3.* Abundant silicified wood and a solitary silicified tree-fern (holotype of *Australosmunda indentata*) were found as loose clasts in a higher level Quaternary alluvial terrace deposit (55 GEP 398326, 147° 29' 15" E., 42° 09' 26" S.). The deposit straddles a Jurassic fine-grained dolerite dyke that probably marks the structural boundary between Upper Parmeener volcanic lithic sandstone upstream to the south and older quartz sandstone to the north. Dolerite clasts are the most common constituent of the deposit and the relatively coarse grain-size of many clasts indicates that they have not been derived locally, but have undergone a minimum transport of 2-5 km. Other clasts include well-rounded quartz porphyry, fossiliferous Lower Parmeener rocks and other exotic rocks for which no other source exists within the catchment other than the extra-basinal clast-bearing beds of the volcanic lithic sandstone sequence.

Although the majority of silicified wood clasts appear indistinguishable from silicified wood in the volcanic lithic sandstone sequence, some clasts could be derived from other (?Tertiary) sources.

*Age.* The tree-fern fossils from localities 1 and 2 are clearly derived from the Upper Parmeener Supergroup volcanic lithic sandstone sequence. This sequence is probably best known in eastern and north-eastern Tasmania where it has been penetrated by numerous fully cored coal exploration bores and has been recently mapped (Turner *et al.* 1984). In particular, beneath Fingal Tier the main coal-bearing interval of the sequence is about 220 m thick and contains coal seams known informally from top to bottom as seams A-H (Threader and Bacon 1983). Exotic cobbles and boulders like those found at Woodbury are not known below about seam E and tuff beds appear to be confined to above B seam (Calver, in Turner and Calver 1987). Although the volcanic lithic sandstone and coal measures sequence is widely distributed in Tasmania, neither exotic clasts nor tuff beds have been commonly reported away from the north-eastern to eastern area except for the occurrence of one or both of the features at a few localities in the Tasmanian Midlands (Forsyth 1984, in press *a*). Where indications are available the exotic clasts and tuff appear to occur in the uppermost beds of the sequence in the Midlands area.

The similarity of the tree-fern fossil from locality 3 with those from localities 1 and 2 plus the occurrence of exotic clasts at all localities suggests the tree-fern fossils may all be derived from a restricted interval of the volcanic lithic sandstone sequence above the equivalent horizon of seam E and possibly in proximity to seam B.

Quartz sandstone occurs about 45 m below seam H at Fingal Tier and nearby at Nicholas Range the interval with quartz sandstone hosts two partly extrusive basalt 'flows'. Interbedded sediments contain a microflora probably best compared with the less distinctive microflora of the upper part of the Bowen Basin Moolayember Formation (de Jersey and Hamilton 1967) and the overlying basalt has been radiometrically dated at  $233 \pm 5$  Ma (Calver and Castleden 1981). At Fingal Tier the interval from seam A to seam G and possibly to seam H can be correlated with the *Craterisporites rotundus* Zone (de Jersey 1975; Forsyth, in

press *b*) although from the incomplete palynology carried out to date the nominate zone fossil and *Polycingulatisporites densatus* have not been recorded below seam B.

Thermal effects of an overlying dolerite intrusion may prevent the top of the *C. rotundus* Zone from being recognized at Fingal Tier, but further south a tuff bed associated with coal near the top of the sequence has been radiometrically dated at  $214 \pm 1$  Ma (Bacon and Green 1984). Rocks immediately below the tuff and a lithocorrelate of the coal contain *C. rotundus* Zone microfloras, whereas 20 m above the coal correlate the microflora from an overlying dominantly grey lutite sequence has been referred to the lower (Assemblage A) *Polycingulatisporites crenulatus* Zone (de Jersey 1975; Forsyth, in press *b*).

An approximate Carnian age has been indicated for the *C. rotundus* Zone (de Jersey 1975; Helby *et al.* 1987) and this is supported by the New Zealand range of *Annulispora follicularis* and *A. microannulata* (N. J. de Jersey, pers. comm.). Assemblage A (de Jersey 1976) of the *P. crenulatus* Zone is probably of Norian age (Stevens 1981; Helby *et al.* 1987; Tozer 1984). The coal seam sequence seam A to seam G at Fingal Tier is therefore considered to be of Late Triassic (Carnian) age and good agreement is shown between the radiometric dates and the time scale of Webb (1981); the date of  $214 \pm 1$  Ma for tuff near the top of the sequence comparing favourably with the Norian/Carnian boundary  $215 \pm 5$  Ma, and the date of  $233 \pm 5$  Ma for basalt underlying the sequence being probably of Middle Triassic age,  $225 \pm 5$  Ma to  $240 \pm 5$  Ma.

Although the volcanic lithic sandstone sequence has yielded *C. rotundus* Zone microfloras or slightly older microfloras with *A. folliculosa* from several localities in Tasmania (Forsyth, in press *a*), palynological data from Woodbury are lacking. Within 15 km of Woodbury, *A. folliculosa* is present either in the volcanic lithic sandstone sequence or in underlying rocks, and 35 km south-west from Woodbury at Spring Hill, a microflora from a sequence either below the volcanic lithic sandstone sequence or alternatively interpretable as a lutite dominated basal facies of the volcanic lithic sandstone sequence, indicates a *C. rotundus* Zone age (Forsyth 1984, in press *a, b*).

Macrofloras at Woodbury immediately underlying a tuff overlain by a sandstone bed with exotic cobbles, includes *Johnstonia coriacea* indicating a Late Anisian to Norian age (Retallack 1977). The stratigraphic position of other beds with *Dicroidium odontopteroides* and *Heidiphyllum elongatum* cannot be determined with respect to the interval with fossil tree ferns.

Based on the lithological correlation of the interval with tree-fern fossils at Woodbury with the upper part of the coal measures at Fingal Tier outlined above, the tree-fern fossils are considered to be Late Triassic (probably Carnian or early Norian) in age.

## MATERIAL AND METHODS

One fossil specimen represents an isolated section of a trunk (Pl. 35, fig. 1). Transverse sections of this specimen were taken from the apex and base, and a longitudinal section from the apex. Several other specimens were found embedded with other plant remains in larger pieces of rock, and transverse sections of several of these were also cut. However, the best anatomical preservation was found in the isolated specimen, and the description is based largely on it.

The sections were produced by the lapidary section of the Tasmanian Department of Mines. First, blocks were cut from the fossils using a diamond saw. The appropriate block faces were then polished on a Logitech LP30 Production Lapping and Optical Polishing Machine before bonding to ground microscope slides using the bonding/mounting medium epo-tek 301. Excess material was then removed using a Micro-Trim saw, a lapping machine, and the Logitech LP30, adjusted to produce sections of  $30 \mu\text{m}$  thickness automatically. Coverslips were applied using epo-tek 301. Material removed from the trunk apex of the holotype to produce a transverse section was utilized to make a longitudinal section, which cut the central stele at about  $5^\circ$ . The remaining offcuts are stored with the type specimen.

## DESCRIPTION OF SPECIMENS

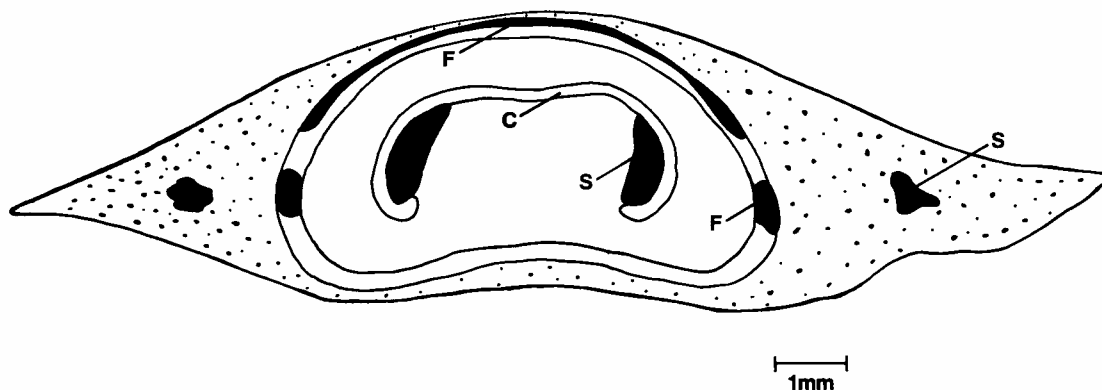
The fossils (Pl. 35, figs. 1–4) are clearly osmundaceous in affinities, with the characteristic stelar structure and leaf trace arrangement described by Miller (1967, 1971). The stele is very small (about 3–5 mm in diameter), and despite some deep indentations where the leaf traces arise, a leaf gap was not observed (Pl. 35, fig. 4). Inside the xylem ring only a single cell type was observed, and longitudinal section confirmed that this was parenchyma (Pl. 35, figs. 4–7). On this basis the fossil can be said to have a simple siphonostele, with a parenchymatous pith. The metaxylem elements have conspicuous scalariform pitting (Pl. 35, fig. 8).

Each departing leaf trace has only one protoxylem bundle, in an endarch arrangement (Pl. 36, figs. 1 and

2). The protoxylem divides into two usually at the outer edge of the outer cortex (Pl. 36, fig. 3), and continues dividing beyond there until there are eight or more protoxylem groups present (Pl. 36, fig. 4). The metaxylem in the leaf trace increases in cell number and in overall size as it departs from the stem, and develops into the C-shape characteristic of many ferns including the Osmundaceae. As the leaf trace moves through the inner and then the outer cortex, it becomes surrounded by a ring of cells from these two areas, first, parenchyma and then sclerenchyma. Beyond the outer cortex there is clear development of stipular expansions, but the sclerenchyma ring maintains a rounded shape and does not extend into these extensions (Pl. 36, fig. 5). Hewitson (1962) noted the taxonomic importance of the presence and positioning of sclerenchyma in stipular expansions. In these fossils there is one large, rounded bundle in each stipular expansion, as well as several smaller, scattered bundles (text-fig. 1; Pl. 36, fig. 5). The sclerenchyma ring can also have a characteristic distribution of thick-walled fibres, and in the fossil they occur in an abaxial arch and as two lateral bundles (text-fig. 1). There are also two large sclerenchyma bundles within the concavity of the C-ring of metaxylem (text-fig. 1; Pl. 36, fig. 6).

One root with a diarch xylem strand arises from each departing leaf trace (Pl. 36, figs. 2, 3, 7), probably before it enters the inner cortex. There is no sign of a mat of external roots, which is common in many fossil and living osmundaceous species, in any of our fossil specimens. The roots consistently run parallel to the stem, suggesting that the species had an upright habit.

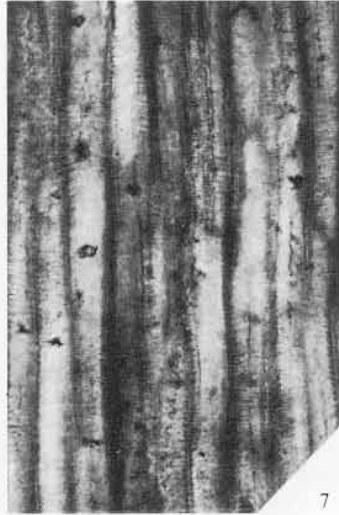
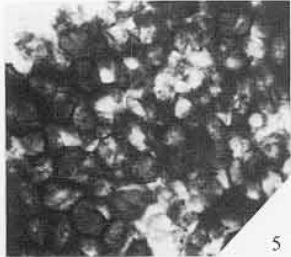
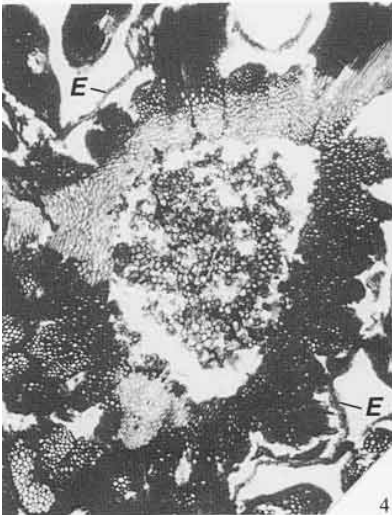
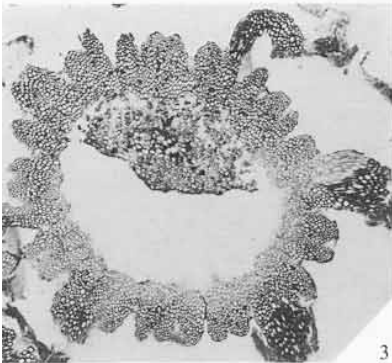
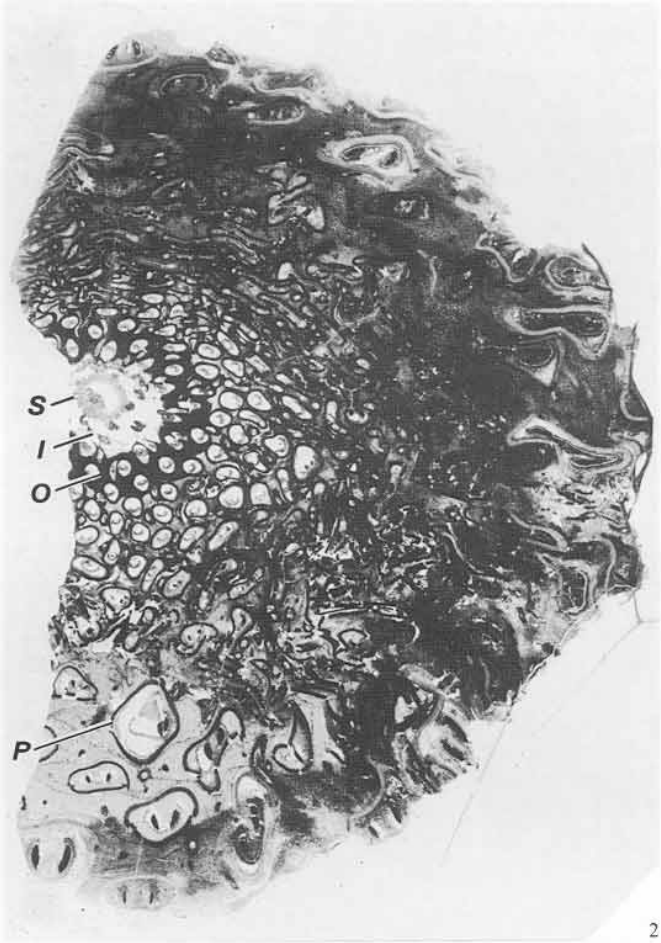
The phloem is completely degenerated, but occasional signs of what is probably the endodermis can be seen external to the central xylem (Pl. 36, fig. 5). There is no sign of either phloem or endodermis on the inside of the xylem ring, and since the parenchymatous pith almost fills the central area in some sections (e.g. Pl. 35, fig. 5) it is assumed that phloem was absent there. The position of the inner cortex is quite clear



TEXT-FIG. 1. Drawing of a transverse section of a petiole base of *Australosmunda indentata* gen. et sp. nov. Note that the thick-walled fibres (F) in the sclerenchyma ring occur in an abaxial arch and as two lateral bundles. Sclerenchyma (S) occurs in each concavity of the C-ring of metaxylem (C) and as one large, rounded bundle in each stipular expansion, surrounded by numerous smaller, scattered bundles.

#### EXPLANATION OF PLATE 35

Figs. 1-7. *Australosmunda indentata* sp. nov. 1, holotype of *A. indentata* (GST 10001), showing upright habit and petiole scars,  $\times 0.5$ . 2, transverse section of the basal end (GST 10001A) showing the small stele (S), the inner cortex (I), the outer cortex (O), the leaf traces in the cortex, and the petiole bases towards the edge of the section (P),  $\times 1.6$ . 3, stele (GST 10001A), from the basal end of the stem, showing a continuous metaxylem cylinder which is deeply indented, but not pierced, by departing leaf traces,  $\times 15$ . 4, stele (GST 10001B), showing the parenchymatous pith which fills the cavity within the metaxylem cylinder. Traces of the endodermis (E) can be seen,  $\times 14$ . 5, transverse section of the pith parenchyma (GST 10001A),  $\times 225$ . 6, longitudinal section of the pith parenchyma (GST 10001C),  $\times 225$ . 7, longitudinal section of the metaxylem elements of the stele (GST 10001C). Scalariform pitting can be seen in some areas,  $\times 150$ .



HILL et al., *Astralosmunda indentata*

(Pl. 35, fig. 2), but again cell detail is absent. It is probable that this area was parenchymatous. The outer cortex is well preserved and is sclerenchymatous (Pl. 35, fig. 2; Pl. 36, fig. 8).

These fossils do not, in our opinion, fall within the range of any described genera of the Osmundaceae. All extant species have an ectophloic, dictyoxylic siphonostele, or something more advanced, and the same is true for all fossil species which have been assigned to extant genera or to the form genus *Osmundacaulis* (Miller 1971), which has recently been separated into two genera, *Osmundacaulis* and *Millerocaulis* (Tidwell 1986). Most other fossil genera have a protostele (e.g. *Zalesskya*, *Bathypteris*, *Chasmatopteris*, *Iegosigopteris*, *Petcheropteris*, and *Thamnopteris*). *Palaeosmunda*, from the Upper Permian of Queensland, usually has an ectophloic-dictyoxylic siphonostele, but can sometimes be simply siphonostelic (Gould 1970). However, although this is the closest genus to the fossils in terms of stele structure, *Palaeosmunda* differs in several other important ways, especially in the extension of the sclerotic ring in the leaf traces out into the stipular expansions. Therefore, a new genus is required to accommodate these fossils.

### SYSTEMATIC PALAEONTOLOGY

Division PTEROPHYTA

Order FILICALES

Family OSMUNDACEAE

Genus AUSTRALOSMUNDA gen. nov.

*Type species. Australosmunda indentata* sp. nov.

*Derivation of name.* Named for the southern occurrence of these osmundaceous fossils.

*Diagnosis.* Arborescent osmundaceous trunk, with a stem surrounded by a mantle of leaf bases and adventitious roots; unbranched. Stele an ectophloic siphonostele; pith parenchymatous; xylem ring consisting of approximately twenty contiguous radial strands, up to eighteen tracheids thick; leaf gaps incomplete, extending up to three-quarters through the metaxylem ring; phloem, pericycle unknown, endodermis external only. Cortex differentiated into inner zone where cells are not preserved, and an outer sclerotic fibrous layer, with short, wide, sclerenchyma cells lining leaf traces and inner cortex; inner cortex about as wide as outer cortex; leaf traces arise at about 30° to stele, initially with one endarch protoxylem group; about forty 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 remain rounded or elliptical in transverse section, not extended into stipules. Roots with diarch xylem strand, arising singly from each departing leaf trace usually before it enters inner cortex.

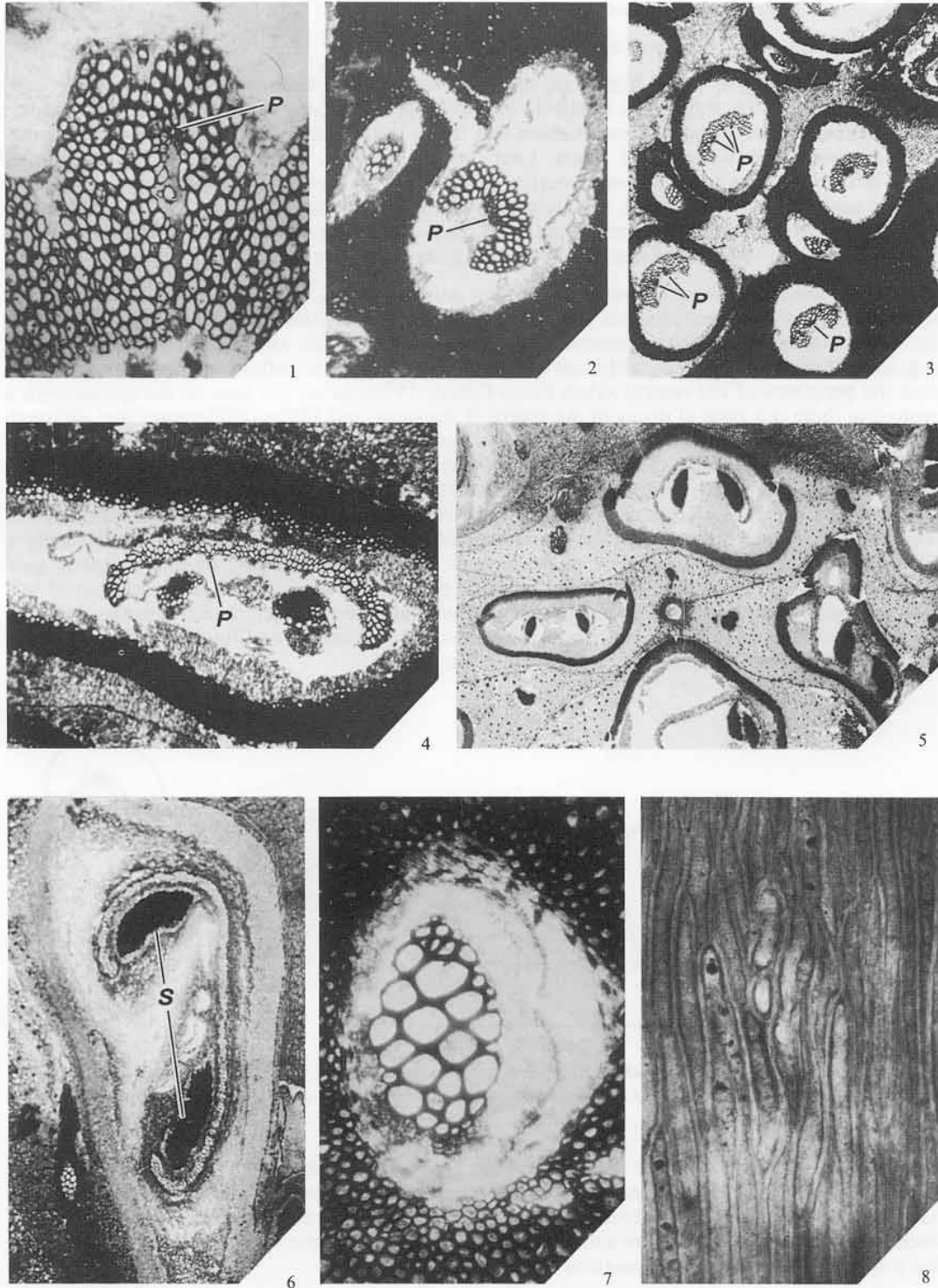
*Australosmunda indentata* sp. nov.

Plate 35, figs. 1-8; Plate 36, figs. 1-8

*Holotype.* GST 10001; figured in Plate 35, fig. 1, housed at the Tasmanian Department of Mines, Hobart.

#### EXPLANATION OF PLATE 36

Figs. 1-8. *Australosmunda indentata* gen. et sp. nov. 1, departing leaf trace from the central stele (GST 10001A). Note the single protoxylem group (P) and the lack of a complete leaf gap, × 70. 2, leaf trace in the outer cortex (GST 10001A), still with one protoxylem group (P). Note the root to the left of the leaf trace which has arisen from the leaf trace soon after its formation, × 40. 3, leaf traces in the outer cortex (bottom right) (GST 10001A) and beyond. Note that the protoxylem bundle (P) divides into two at about the outer edge of the outer cortex and then continues to divide, × 15. 4, metaxylem bundle in a petiole base (GST 10001A) containing a large number of protoxylem groups (e.g. P), × 30. 5, petiole bases (GST 10001A) with stipular expansions. Note the sclerenchyma bundles in the stipular expansions and in the concavity of the C-ring of metaxylem, × 6. 6, C-ring of metaxylem in a petiole base (GST 10001A). Note the two sclerenchyma bundles (S) in the concavity of the C-ring, × 12. 7, diarch root trace (GST 10001A) soon after its formation from the leaf trace. A protoxylem bundle can be observed at the top and bottom of the root trace, × 40. 8, longitudinal section of the sclerenchyma in the outer cortex (GST 10001C), × 150.



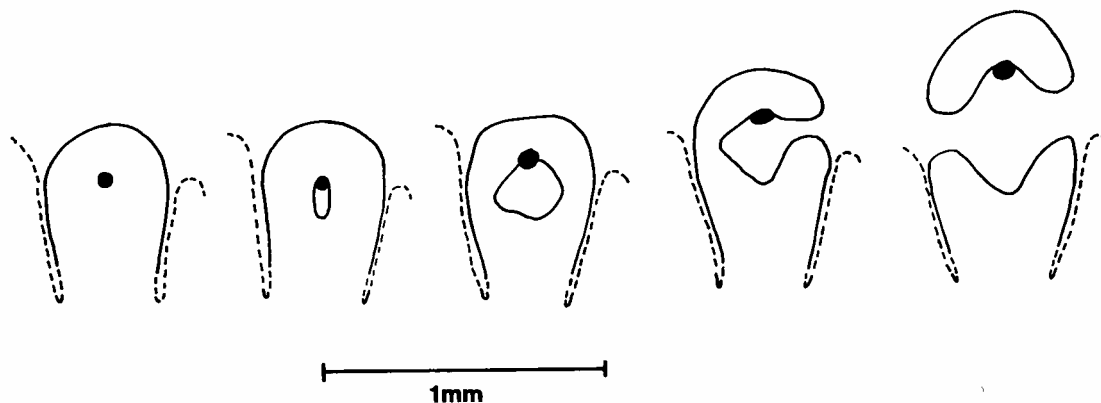
HILL et al., *Astralosmunda indentata*

*Type locality.* Locality 3 east of Woodbury, Tasmania.

*Derivation of name.* Named for the indented nature of the stele.

*Diagnosis.* Trunks up to 12 cm high, 7 cm diameter; stem 14 mm diameter. Stele 3.5 mm diameter, pith 2.2 mm diameter; metaxylem tracheids  $36\ \mu\text{m}$  (range  $15\text{--}55\ \mu\text{m}$ ) in diameter, with scalariform pitting. Inner cortex includes about thirteen leaf traces in transverse section, fibrous outer cortex includes about twenty-seven leaf traces. Leaf traces arise with one endarch protoxylem group which bifurcates at the end of the outer cortex. Leaf bases with C-shaped vascular strand containing eight or more protoxylem groups, with sclerenchyma bundle in each concavity; sclerenchyma ring with an abaxial arch and two lateral bundles of thick-walled fibres; stipular expansions each with one large mass and numerous smaller masses of thick-walled fibres.

*Discussion.* *Australosmunda indentata* is the first osmundaceous species described with a simple siphonostele and a parenchymatous pith. Osmundaceous fossils exhibit a range of stelar types with the simplest being protosteles composed of central short tracheids and peripheral long tracheids (e.g. *Zaleskya*, *Thamnopteris*), although in *T. kidstoni* parenchyma cells occur singly or in clusters near the periphery of the central xylem tissue (Miller 1971). In all but four of the species with a protostele there is a zone of decay in the centre of the stem, and Miller (1971) notes that although typical central xylem tracheids border the vacant zone, other cell types may have occurred within. *Chasmatopteris principalis* exhibits an early indication of the formation of leaf gaps, with the metaxylem cylinder being conspicuously indented (but never pierced) opposite certain leaf traces (Miller 1971). There is a large morphological distinction between these stelar types and those of other osmundaceous stems described to date which have conspicuous leaf gaps and usually a distinct pith of parenchyma and/or sclerenchyma. *A. indentata* fills part of this morphological hiatus. There is no trace of short tracheids in the pith of this species, and the formation of leaf gaps is almost complete (text-fig. 2). The metaxylem cylinder is heavily and frequently indented opposite the point of origin of leaf traces, but in several sections viewed (including both the base and apex of the holotype), a leaf gap was not observed.



TEXT-FIG. 2. Stylized series of ascending transverse sections showing the separation of a leaf trace from the stelar xylem of *Australosmunda indentata* gen. et sp. nov. The black dot represents the protoxylem.

It is notable that this Late Triassic species was growing long after the Upper Permian *Palaeosmunda* species from Queensland, which show clear evidence of well-developed leaf gaps (Gould 1970). However, as has been noted earlier, the arrangement of the sclerenchyma in the leaf traces of *Palaeosmunda* was more similar to the primitive protostelic species, whereas *A. indentata* has a more advanced sclerenchymatous arrangement.



Miller (1971) nominated six characters on a primitive to advanced scale which he used for numerical analyses of osmundaceous stems. The first of these characters is stelar type. The stelar type of *A. indentata* is not recorded in Miller's list, and does not fit easily into his sequence, since it is relatively advanced in having a parenchymatous pith and relatively primitive in not having fully developed leaf gaps. The second character concerns the cell types in the cortex, and in this *A. indentata* is intermediate on the scale in having parenchymatous and sclerotic layers of about equal breadth. The third character concerns the petiole bases, which are primitive in *A. indentata* in being closely adhering, although this condition is generalized in the family (Miller 1971). The fourth character refers to the xylem arrangement in the leaf trace at its point of divergence, and *A. indentata*, with its endarch arrangement, is considered to be advanced. The fifth character refers to the number of leaf traces visible in one cortical cross-section. *A. indentata*, with about forty, is considered to have a medium number between the high primitive number of 100–150 and the advanced condition of only about five to fifteen. The final character deals with the position in which the first protoxylem bifurcation in the leaf trace takes place, and in this *A. indentata* exhibits the primitive condition, with the bifurcation taking place near the outer edge of the outer cortex.

Therefore, on this basis *A. indentata* has a mixture of primitive, intermediate, and advanced characteristics. Although *A. indentata* exhibits an important intermediate type of stelar development, it must be assumed that this type occurred much earlier, since *Palaeosmunda* exhibits a more advanced form in the Permian. The development of leaf gaps in *Australosmunda* would give rise to a stem type which would be typical of many fossil *Millerocaulis* and *Osmundacaulis* species, and it is possible that *Australosmunda* is a precursor of at least some of these species. Several *Osmundacaulis* species have recently been described from Australia (Edwards 1933; Gould 1973; Tidwell 1987; Tidwell and Jones 1987), but none appear to be closely related to *Australosmunda indentata*.

The occurrence of a wholly parenchymatous pith in a stele without leaf gaps in *A. indentata* offers convincing support for the hypothesis that the evolution of the parenchymatous pith and the evolution of leaf gaps in the xylem were independent transitions. Previously, the occurrence of 'delayed' and 'incomplete' leaf gaps in species that also have a mixed pith (e.g. *Millerocaulis dunlopi*, *M. kolbei* (Miller 1971) and *M. beardmorensis* (Schopf 1978)) left support for the hypothesis quite ambiguous.

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