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Paurodendron stellatum: A new Permian permineralized herbaceous lycopsid from the Prince Charles Mountains, Antarctica

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ABSTRACT

Diminutive, silica-permineralized lycopsid axes, from a Guadalupian (Middle Permian) silicified peat in the Bainmedart Coal Measures of East Antarctica are described and assigned to *Paurodendron stellatum* sp. nov. Axes consist only of primary-growth tissues with a vascular system characterized by an exarch actinostele with 6–20 protoxylem points. Stems have a relatively narrow cortex of thin-walled cells that are commonly degraded, but the root cortex typically contains more robust, thick-walled cells. The stems bear helically inserted, elliptical–rhombic, ligulate microphylls. Roots possess an eccentrically positioned monarch vascular strand. *Paurodendron stellatum* is one of a very small number of anatomically preserved lycopsid axes described from the Gondwanan Permian and represents the first post-Carboniferous record of this genus. Based on dispersed vegetative remains, megaspores and microspores, herbaceous lycopsids, such as *P. stellatum*, appear to have been important understorey components of both low- and high-latitude mire forests of the late Palaeozoic.

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1. Introduction

Axis adpressions and casts of subarborescent to arborescent lycopsids are relatively abundant in Permian strata of western Gondwana (South America and southern Africa: Cúneo and Andreis, 1983; Anderson and Anderson, 1985; Cariglino et al., 2012) but are less common in coeval deposits of the eastern sector of the supercontinent. Herbaceous lycopsids, such as *Cyclodendron leslii* (Seward) Kräusel, 1928, have scattered distributions across Gondwana, are sporadically represented through the Permian, and are known mostly from axis impressions and compressions, in some cases with attached microphylls, preserved cuticle, or associated sporangia (Rigby, 1966; Townrow, 1968; Chandra and Rigby, 1981; Rayner, 1985; Beeston, 1990). Permineralized remains of either arborescent or herbaceous lycopsids are very scarce in Permian Gondwanan deposits (Renault, 1890a,b; Archangelsky and de la Sota, 1966; Schwendemann et al., 2010; Ryberg et al., 2012).

The high-latitude Antarctic Permian and Triassic fossil record is particularly sparse with respect to lycopsids compared to the remainder of Gondwana. A review of Antarctic fossil macrofloras by Rigby and Schopf (1969) found no evidence of Permian lycopsids and, although this record has since improved, representatives of this plant group in the late Palaeozoic of Antarctica remain rare. *Lycopodiopsis pedroanus* (Carr.) Edwards, 1952 was reported by Plumstead (1975) from Cisuralian strata of Milorgfjella, Dronning Maud Land, but this material may alternatively represent coniferous remains (McLoughlin et al., 2005). Two herbaceous lycopsid species have been recorded recently from Lopingian strata of the Transantarctic Mountains: compressions and impressions of a leafy axis, *Collinsonites schopfii* (Schwendemann et al., 2010); and siliceous permineralized strobilar remains, *Collinsonostrobus eggertii* (Ryberg et al., 2012). These fossils may represent separate parts and different preservational states of the same whole-plant species.

Antarctic Triassic deposits are also rich in lycopsid spores but only a single macrofossil species, attributed to the Pleuromeiales, has been described (Bomfleur et al., 2011), although dispersed sporangial and microphyll remains have been noted in mesofossil assemblages (McLoughlin et al., 1997; Cantrill and Poole, 2012). Apart from pleuromeians in the Early Triassic, herbaceous or subarborescent lycopsids remained relatively scarce as macrofossils in subsequent austral Mesozoic floras (McLoughlin et al., 2014).

Pigg (1992, 2001) noted several major deficiencies in knowledge of the phylogenetic relationships, anatomy, palaeogeography and palaeoecology of late Palaeozoic and Mesozoic *Isoëtes*-like lycopsids. In particular, the family-level affinities, anatomy and ecological preferences of most Permian Gondwanan lycopsids remain unresolved. Arborescent forms probably have affinities with the lepidodendrids based on gross similarities with Northern Hemisphere Palaeozoic representatives of

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that group (Chaloner et al., 1979). However, herbaceous forms may be confidently affiliated with Isoëtales (Wood and Beeston, 1986), Selaginellales (Townrow, 1968) or Lycopodiales (Ryberg et al., 2012) only where reproductive or specialized vegetative characters are preserved.

Despite the scarcity of lycopsid macrofossils in Gondwanan Permian strata, many deposits yield abundant megaspores and microspores that point towards a significant diversity of these plants in the regional flora. Dispersed cinguli-cavate microspores, generally affiliated with lycopsids (Balme, 1995), are widely distributed in Antarctic Permian palynofloras (Larsson et al., 1990; Farabee et al., 1991; Lindström, 1995a,b; McLoughlin et al., 1997). Megaspores are also abundant in Permian strata of Antarctica and neighbouring regions of Gondwana suggesting that most regions of the supercontinent supported a rich array of heterosporous lycopsids (Archangelsky et al., 1989; Cúneo et al., 1991; Glasspool, 2000, 2003; Ricardi-Branco et al., 2002; Tewari et al., 2009; Slater et al., 2011). The widespread occurrence and diversity of these dispersed palynomorphs suggest that some aspect of taphonomy or ecology selected against the preservation of lycopsid vegetative parts and that this group was potentially an important component of the late Palaeozoic polar herbaceous vegetation.

Here we document the third lycopsid macrofossil taxon confidently recorded from the Permian of Antarctica, thus contributing to evidence for widespread herbaceous lycopsids in the high-latitude glossopterid-dominated mire vegetation of Gondwana. The new fossils extend the macrofossil record of herbaceous heterosporous lycopsids to the Lambert Graben of East Antarctica.

2. Geological setting

The studied fossils comprise anatomically preserved (permineralized) and charcoalified axial and foliar remains from a Guadalupian silicified peat bed in the northern Prince Charles Mountains, Antarctica (Fig. 1). The host deposits accumulated in the Lambert Graben — a meridional intra-continental rift contiguous with the Mahanadi Graben of India (Fedorov et al., 1982; Boger, 2011) that was part of the East Gondwana Rift System (Harrowfield et al., 2005) before continental breakup in the mid-Mesozoic.

The silicified peat bed is up to 40 cm thick and caps a prominent coal seam at the top of the Toploje Member in the lower part of the Bainmedart Coal Measures, within the Permo-Triassic Amery Group (McLoughlin and Drinnan, 1997a, b). The silicified peat (chert) is exposed over a strike length of around 3 km and grades laterally into non-silicified coals and siliceous sandstones. A Wordian (c. 266 Ma) age is ascribed to the peat layer based on palynostratigraphic correlation with the Australian *Didecitriletes ericianus* Zone (= APP4.2 Zone), especially via the presence of the index taxa *Didecitriletes ericianus* (Balme et Hennelly) Venkatachala et Kar, 1965 and *Guttulapollenites hannonicus* Goubin, 1965 (Balme and Playford, 1967; Kemp, 1973; Playford, 1990; McLoughlin et al., 1997; Lindström and McLoughlin, 2007).

The fossiliferous layer represents a siliceous-permineralized autochthonous/parautochthonous accumulation of plant remains from a glossopterid-dominated, mire community (Slater et al., 2015), more narrowly defined as a forested bog in the terminology of Moore (1989). This silicified (chert) layer is overlain by lacustrine sediments of the Dragons Teeth Member (Fielding and Webb, 1996). Siliceous entombment of the organic matter at the base of the lacustrine sequence has been interpreted as a response to seasonally fluctuating alkalinity (and silica solubility) of lake waters that had submerged the peat surface (McLoughlin and Drinnan, 1996; Slater et al., 2015), however, the origin of the high levels of silica remains equivocal. Volcanogenic sediments are not associated with the peat bed in contrast to eastern Gondwanan Permian permineralized peats (Gould and Delevoryas, 1977; Taylor et al., 1989; Pigg and McLoughlin, 1997). Eolian siliceous dust has been proposed as a primary source of silica for bedded cherts deposited in marine settings adjacent to warm arid areas (Cecil, 2004). However, eolian particles are an unlikely source for the large quantity of silica precipitated in the humid high-latitude Lambert Graben, and where intense silicification is restricted to a single massive bed at the base of a lacustrine succession. Deeply circulated groundwaters emerging from springs along adjacent basin-margin faults are another potential source of silica (Ledesma-Vázquez et al., 1997; Sallam et al., 2015) but no definitive origin has been identified in the case of the Toploje Member chert.

3. Associated fossil biota

The studied lycopsid axes are co-fossilized with a moderate diversity of plant macro- and microfossils. The fossil flora is dominated by matted foliage (*Glossopteris* and *Noeggerathiopsis*), stem wood (*Australoxylon*), roots (*Vertebraria*), seeds (*Samaropsis*) and sporangia (*Arberiella*) of glossopterid and cordaitalean gymnosperms (Neish et al., 1993; McLoughlin and Drinnan, 1996; Lindström et al., 1997; Weaver et al., 1997; Holdgate et al., 2005). Macrofossil remains of ferns are rare but this group was clearly common in the local flora based on a diverse array of spores and sporangia co-preserved in the permineralized peat and adjacent strata (McLoughlin et al., 1997; Lindström and McLoughlin, 2007). Sphenophytes have not been recovered from the permineralized peat bed but they are common in the overlying shales of the Dragons Teeth Member. No arborescent lycopsid remains have been found despite extensive sampling of the peat bed and associated strata. However, three megaspore morphotypes have been documented from the peat layer indicating the presence of several heterosporous lycopsids in the local vegetation (Slater et al., 2011).

The silicified peat also preserves a diverse array of fungal hyphae and reproductive structures, and Peronosporomycetes (Oomycetes) fruiting bodies signifying the presence of an extensive saprotrophic community (Slater et al., 2013, 2015). Exoskeleton fragments, together with a range of insect or mite coprolites and other invertebrate traces on plant tissues, attest to a rich arthropod fauna in the peat ecosystem (Weaver et al., 1997; Holdgate et al., 2005; Slater et al., 2012, 2015).

4. Material and methods

About 25 permineralized axes and several isolated roots and microphylls form the basis of this study. Both petrographic thin-sections and cellulose acetate peels were prepared from the silicified peat blocks according to the procedures of Basinger and Rothwell (1977) and Hass and Rowe (1999). Specimens were examined by light microscopy using an Olympus BX-51 microscope and photographed with an Olympus DP-71 digital camera. Scanning electron microscopy (SEM) of charcoalified microphylls and megaspores was undertaken using JEOL JSM-840, Philips XL-30 Field Emission Gun and Hitachi S-4300 Field Emission scanning electron microscopes at the University of Melbourne and the Swedish Museum of Natural History. Isolated megaspores of *Singhisporites hystrix* were also examined using synchrotron X-ray tomographic microscopy (see Slater et al., 2011) at the TOMCAT beamline of the Swiss Light Source, Paul Scherrer Institute, Switzerland, using the techniques described by Donoghue et al. (2006). Specimens are lodged in the Commonwealth Palaeontological Collection (CPC) administered by the Australian Geological Survey Organization, Canberra; Museum Victoria (NMVP), Melbourne; and the Swedish Museum of Natural History, Stockholm (NRM).

5. Systematic palaeobotany

Phylum Tracheophyta
Class Lycopsida
Order Isoëtales (sensu DiMichele et Bateman, 1996)
Parataxon "Ulodendrineae" (sensu DiMichele et Bateman, 1996)

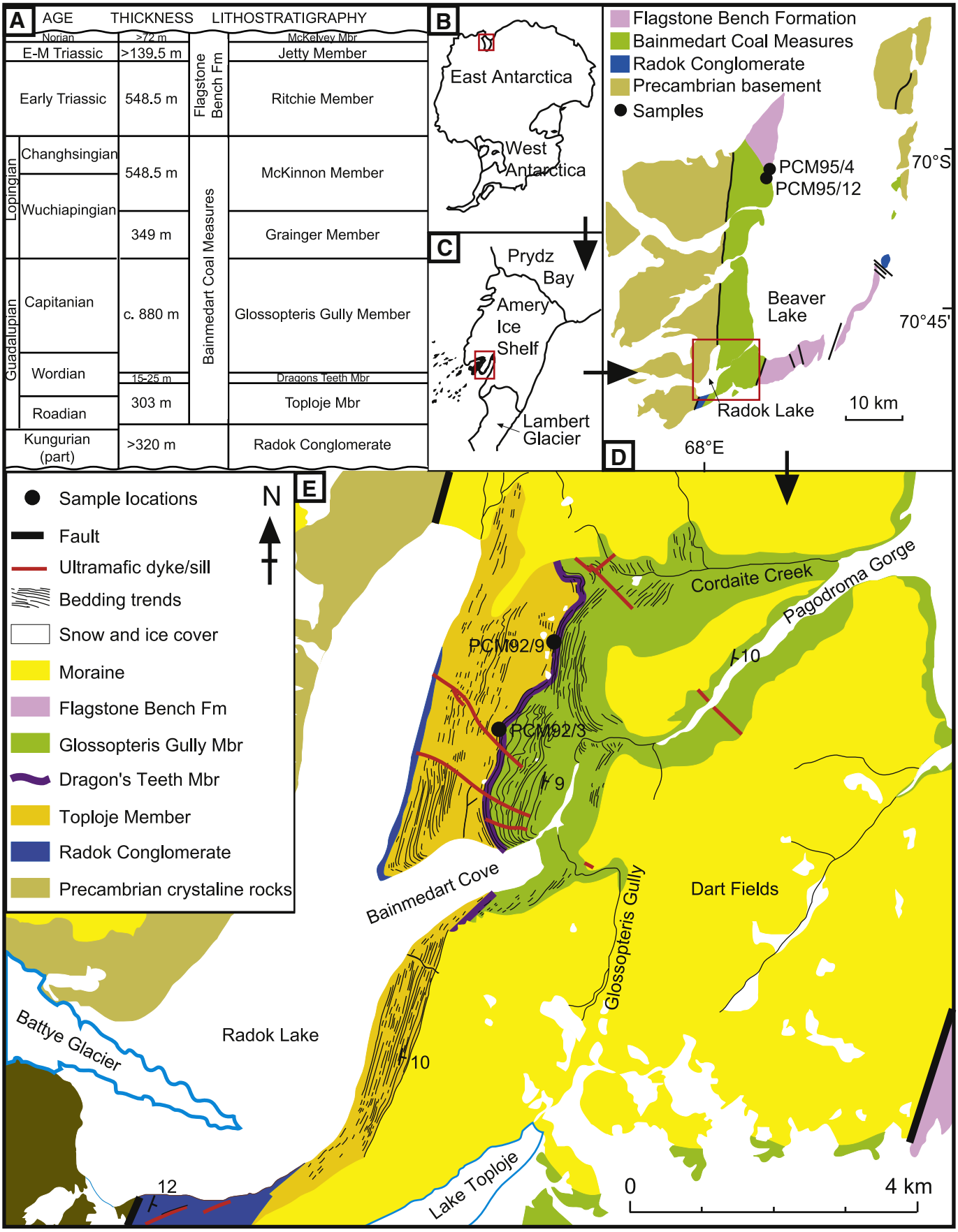

Fig. 1. Map and stratigraphic table of Permian units in the Amery Oasis, Prince Charles Mountains, Antarctica, showing the collecting localities and their stratigraphic position (after McLoughlin and Drinnan, 1997a). A: Amery Group stratigraphy. B: Location of the Lambert Graben. C: Location of the Beaver Lake area. D: Location of the Radok Lake area. E: Detailed geology of the Radok Lake area.

5.1. Genus *Paurodendron* Fry, 1954

Type species: *Paurodendron fraipontii* (Leclercq) Fry, 1954; Mississippian of Arran, Scotland; Pennsylvanian of Belgium, France, Iowa, Illinois, Ohio and Kansas.
Diagnosis: See Fry (1954) and subsequent emendations by Phillips and Leisman (1966) and Schlanker and Leisman (1969).
Remarks: The nomenclatural history of specimens assigned to *Paurodendron* is complex. Stewart and Rothwell (1993) provided a detailed discussion of the changing status of *Paurodendron* and its variably implied affinities to the ferns, Selaginellales, Isoëtales or lepidodendrids. Fry (1954) originally designated *Paurodendron arranense* to be the type species of this genus. However, later authors (Schlanker and Leisman, 1969) considered *P. arranense* to be a junior synonym of *Paurodendron* (*Botryopteris*) *fraipontii* Leclercq, 1924, which is now regarded as the type species.

The earliest studies of *Paurodendron* (Leclercq, 1924; Darrah, 1941) documented slender permineralized axes with actinosteles and robust cortical cells that were interpreted to reflect affinities with ferns. Subsequent studies (Fry, 1954; Hoskins and Abbott, 1956; Leisman, 1961; Phillips and Leisman, 1966; Schlanker and Leisman, 1969) emphasized other characters, such as slender, branched, herbaceous stems with exarch actinosteles, a clavate rhizomorph with limited secondary growth and helically arranged roots, bisporangiate strobili, axillary ligules on leaves, and leaves borne successively in decussate, simple helix, and more complex whorl-like arrangements from the base of the stem to the strobilus (Schlanker and Leisman, 1969). These characters were generally interpreted to reflect similarities to the Selaginellales and particularly to the extant *Selaginella selaginoides* (L.) Beauv. ex Schrank et Mart. Selaginellalean affinities were especially emphasized in relation to possession of features that had been interpreted to represent a central root system arising from a root-producing meristem, secondary growth in the rhizomorph, and a change from centrarch to exarch polyarchy from the rhizomorph to leaf-bearing axes. Based on these apparent gross similarities, Schlanker and Leisman (1969) even transferred the type species of *Paurodendron* to *Selaginella*. However, more recent studies on the structure and development of both fossil and extant lycopsid roots have revealed differences in the supposed homologies in root system development between *Paurodendron fraipontii* and *S. selaginoides* (Karrfalt, 1981; Jennings et al., 1983). Further research on permineralized remains by Rothwell and Erwin (1985) revealed a horizontal embryonic vascular trace in the transition zone between the rhizomorph and leaf-bearing axis of *Paurodendron*. They indicated that the rhizomorph of *Paurodendron* developed, as in other rhizomorphic lycopsids, from the initial geotropic branch of a modified shoot system. Rothwell and Erwin (1985) suggested that *Paurodendron* was most closely affiliated with rhizomorphic lycopsids ranging from herb-like (*Nathorstiana*) to arborescent (lepidodendrid) forms. The eccentrically positioned, monarch vascular bundles of *Paurodendron* rootlets are anatomically similar to those of extant *Isoëtes*, fossil pleuromeian lycopsids and the stigmarian rootlets of lepidodendrids (Cantrill and Webb, 1998) and are interpreted to be leaf-like structures developmentally modified for rooting, hence, fundamentally different in origin from the adventitious roots of extant *Selaginella* and *Lycopodium* (Webster and Steeves, 1964; Rothwell and Erwin, 1985; Stewart and Rothwell, 1993).

Cladistic analyses of extant and fossil lycopsids (Crane, 1990; Bateman, 1992, 1994; Bateman et al., 1992; DiMichele and Bateman, 1996; Kenrick and Crane, 1997; Bateman and Hilton, 2009; Stevens et al., 2010; DiMichele et al., 2013) typically include *Paurodendron* within a rhizomorphic lycopsid clade but its relationship to other members of this clade remains poorly resolved. Crane's (1990) analysis could not resolve the relationships between *Paurodendron* and lepidodendrids on the one hand and an Isoëtaceae-*Nathorstiana* clade on the other, resulting in a topological trichotomy. The preferred phylogenies of Bateman (1992) and Bateman et al. (1992) resolved *Isoëtes* as a sister group to a lepidodendrid clade where *Paurodendron* is the most basally divergent among this group, occurring below *Oxroadia* in some of the most parsimonious trees (e.g., Bateman et al., 1992, Fig. 7); whereas in others it is sister to *Oxroadia* (e.g., Bateman et al., 1992, Fig. 8) in a basal-most position within this group, albeit that the monophyly of this clade is supported only by ornamentation characters of the microspores, which are subject to potential homoplasy. Cantrill and Webb (1998) pointed out that these parts of the cladograms are poorly resolved owing to a large number of parallelisms within *Paurodendron* and the occurrence of a single, poorly constrained reversal (presence of a superficial ligule) segregating *Paurodendron* from the remainder of the lepidodendrids. Nevertheless, Stewart and Rothwell (1993) also identified *Oxroadia* and *Paurodendron* as having a close relationship. DiMichele and Bateman (1996) considered the Ulodendraceae (*Paralycopodites* + *Oxroadia* + *Paurodendron*) as paraphyletic. Kenrick and Crane (1997) supported a relationship between *Isoëtes* and extinct rhizomorphic lycopsids (including lepidodendrids, Pleuromeiales and *Paurodendron*) but their analysis did not investigate the detailed relationships of taxa within the rhizomorphic lycopsids.
Distribution: Representatives of this genus are known principally from the Middle and Upper Pennsylvanian coals of the mid-western United States (Darrah, 1941; Fry, 1954; Hoskins and Abbott, 1956; Leisman, 1961; Phillips and Leisman, 1966; Schlanker and Leisman, 1969; Rothwell and Erwin, 1985). Additional specimens are recorded from the Mississippian of Scotland, the lower part of the Pennsylvanian of Belgium (Leclercq, 1924; Fry, 1954), the Late Pennsylvanian Grand-Croix cherts of France (Galtier, 2008) and the Wordian of East Antarctica (this study). In each case, identification is essentially restricted to permineralized material, so the true range of the genus may be considerably more extensive.

5.2. *Paurodendron stellatum* McLoughlin, Drinnan, B.J. Slater, et J. Hilton sp. nov. (Plates I–V; Fig. 2)

1997 min papillate scale; McLoughlin et al., p. 284, Fig. 3e.
2005 *Paurodendron* axis; Holdgate et al., pp. 172–173, Fig. 14g.
Holotype: CPC34947 (Plate I, 1, 3; Plate II, 3, Plate III, 3).
Type locality: Site 92/9; 2 km east of Radok Lake, Amery Oasis, Prince Charles Mountains, Antarctica (Fig. 1).
Type stratum: Silicified peat bed at the top of the Toploje Member (Wordian), immediately underlying the Dragons Teeth Member, Bainmedart Coal Measures.
Etymology: Latin, *stella* — a star; signifying the shape of the stele in transverse section.
Diagnosis: Sparsely branched, isophyllous, actinostelic axes with 6–20 exarch protoxylem groups separated by deep dissections; metaxylem tracheids variably polygonal, bearing close-spiral or scalariform thickenings. Narrow zone of phloem bounded by endodermis. Narrow inner cortex of thin-walled parenchyma; weakly developed middle cortex; thin outer cortex of thick-walled cells; uniseriate, un-ornamented epidermis. Univeined leaves ovate, elliptical, or rhombic, helically arranged, sessile; margins microcrenulate; apex acute. Roots sparsely dichotomous, circular to transversely elliptical, monarch with eccentrically positioned vascular strand. Extra-vascular tissues of roots consisting of thin-walled inner cortex cells, thick-walled outer cortex cells and uniseriate epidermis.
Description: *Axis structure*: Axes 0.9–2 mm in diameter (Plate I, 1–6), exceeding 11 mm in preserved length (Plate II, 8), unbranched, dichotomous or pseudomonopodially branched (Plate II, 4), bearing helically inserted, univeined microphylls. The axes comprise (in radial order) a central, exarch actinostele of primary xylem, a thin zone of phloem, radially expanded transfusion cells (particularly at zones of branching) and sparse parenchyma, a narrow endodermis and inner cortex, a lacuna representing the position of the middle cortex, a generally thin outer cortex, and a uniseriate unornamented epidermis (Plate I, 1, 4).

Vascular tissues: The actinostele consists of 6–20 wedge-shaped protoxylem arms surrounding a central column of metaxylem cells (Plate I, 3–6). Arms of the stele generally incorporate 5–8 ill-defined ranks of protoxylem tracheids (Plate II, 1; Plate III, 3, 4) that are polygonal to elliptical in transverse section with walls 2–4 μm thick, >160 μm long, and which gradually increase in lumen diameter from the tips of the

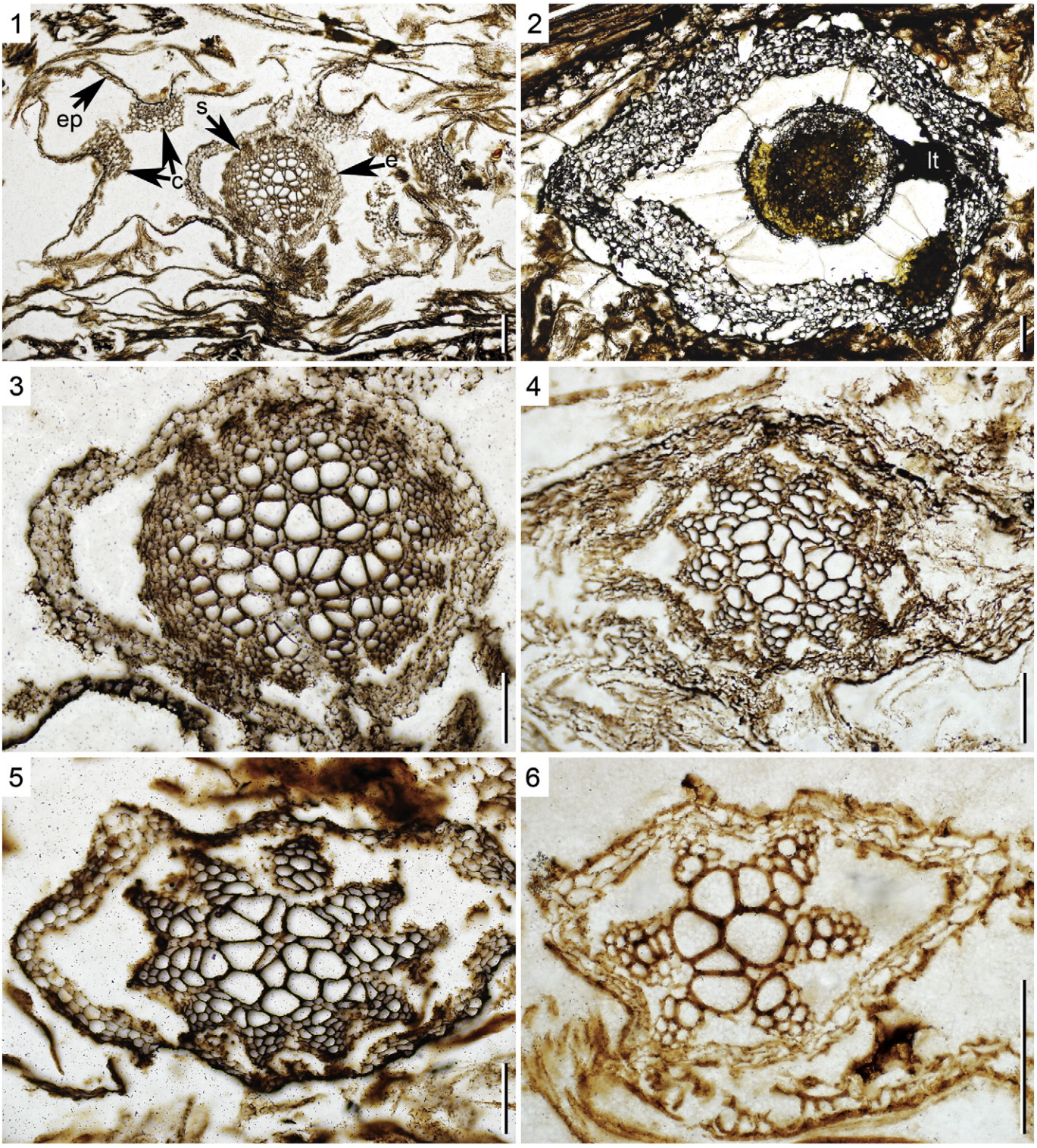

Plate I. *Paurodendron stellatum* sp. nov. Scale bars represent 100 μm.

1 Transverse section of axis showing gross structure; (s) stele, (e) endodermis, (c) degraded and collapsed cortex, (ep) epidermis; CPC34947 (holotype).
2 Transverse section of charcoalified axis showing continuous outer cortex and possible leaf trace (lt) traversing middle cortex lacuna; yellow-tinted areas of stele and portions of the cortex are the result of diagenetic pyrite impregnation; CPC34948a.
3 Stele anatomy of holotype with about 20 protoxylem points; CPC34947.
4 Stele with 11 protoxylem points surrounded by crushed cortex tissues; CPC34949a.
5 Stele with 10 protoxylem points surrounded by a thin detached endodermis; CPC34950.
6 Stele of young/distal axis with six protoxylem points surrounded by thin endodermis layer; CPC34951a.

protoxylem arms (2–4 μm) to the transition with the metaxylem (6–20 μm). Metaxylem tracheids (Plate II, 1; Plate III, 3–6) are typically thick-walled (3–20 μm), variably polygonal (ranging from triangular to nearly elliptical in transverse section), with lumina 16–(32)–72 μm in diameter, and reaching >250 μm long. In proximal portions of the axis, files of small-diameter tracheids occur interspersed with typical large-diameter metaxylem tracheids (Plate III, 3). Metaxylem tracheid walls mostly have close-spiral or scalariform thickenings (c. 1–2 μm wide) separating c. 1–2.5 μm wide slit-like pits (Plate III, 5, 6). The transverse thickenings are rarely joined by vertical to oblique cross-connections. End-walls of xylem tracheids are tapered. In most cases, the xylem is surrounded by a 16–150 μm (generally 20–55 μm) wide lacuna, which is assumed to mark the position of degraded phloem, parenchyma and associated transfusion cells (Plates I, 3–6; III.4). Transfusion tissue is best preserved in regions of axis branching (Plate II, 4, 5) and consists of cells 8–(20)–48 μm in radial diameter, 3–(7)–16 μm wide, with walls 2 μm thick that are pervasively perforated by multiseriate, alternate, simple, circular pits 1–2 μm in diameter (Plate III, 1, 2, 7). These heavily pitted transfusion tissue cells, occurring in radial ranks of up to four, are sparsely associated with non-pitted delicate parenchymatous cells.

Cortex and epidermis: Surrounding the phloem/parenchyma/transfusion tissue (or the lacuna marking their absence) is a band of tissue 2–4 cells thick that is sporadically preserved in the available specimens. It consists of thin- to moderately thick-walled cells considered to represent pericycle or endodermal tissues, in some cases together with incomplete remains of adjoining inner cortex parenchyma (Plate I, 3–6; Plate II, 1; Plate III, 3). Cell walls in this band are 0.5–2 μm thick and lumina are generally small [2–(6)–14 μm in radial diameter, 4–10 μm in tangential diameter] and circular to broadly polygonal in cross-section. The outer margin of this band of tissues is commonly irregular suggesting that it marks the boundary of a zone of degraded tissues. External to this is a lacuna up to 160 μm wide representing the position of the degraded middle cortex (Plate I, 1, 2; Plate II, 2). The surrounding outer cortex constitutes a layer around 6–14 cells wide (120–270 μm wide) composed of circular, elliptical or polygonal cells 5–40 μm in diameter with wall thicknesses increasing from c. 1 μm in the inner cells to 12 μm in the outer cells (Plates I, 2; II, 2, 3). In poorly preserved specimens, the outer cortex may be strongly degraded or absent. The single-layered epidermis consists of rectangular cells 6–(10)–24 μm in tangential width, 6.5–(8)–12 μm in radial width, with walls c. 3–4 μm thick (Plate II, 3), lacking obvious inflation or ornamentation.

Roots: The arrangement of roots on the axis is uncertain. Roots are circular to elliptical in transverse section, 300–580 μm in maximum dimensions, 140–440 μm in minimum dimensions, with lengths exceeding several mm. Roots are monarch with an eccentrically positioned vascular strand (Plate IV, 1). Protoxylem tracheids are small (4–10 μm

Plate II. *Paurodendron stellatum* sp. nov. Scale bars represent 100 μm except for fig. 8 where scale bar represents 1 mm.

1 Details of protoxylem and metaxylem tracheids in transverse section; remnants of phloem and parenchyma occur between protoxylem arms; CPC34950.
2 Portion of axis showing strong compression of cortical tissues around stele, which has essentially retained its cylindrical shape; mc = relict middle cortex cells; CPC34952a.
3 Details of outer cortex and degraded epidermis (dark line arrowed at top) in transverse section; CPC34947 (holotype).
4 Transverse section of stele showing branching; NMVP200003.
5 Details of stele adjacent to incipient branch showing strong development of heavily pitted, radially expanded, transfusion cells (t) around protoxylem arms; NMVP200003.
6 Charcoalified stele with contracted rim of endodermis; NRMS089700.
7 Fungal hyphae (arrowed) penetrating axis metaxylem tracheids; CPC34950.
8 Longitudinal section of microphyll-bearing axis preserved parallel to bedding and bracketed by *Glossopteris* leaves; CPC34949b.

Plate III. *Paurodendron stellatum* sp. nov. Scale bars represent 10 μm for 1–4, 100 μm for 5–7. (See on page 8)

1 Oblique section through transfusion tissue flanking stele at base of departing branch showing heavily pitted cell walls; CPC34951b.
2 Details of pitting in transfusion tissue cells; CPC34951b.
3 Details of a proximal portion of an axis (holotype) in transverse section showing development of small-diameter tracheids between typical large metaxylem tracheids, and degraded endodermal/inner cortex tissues surrounding stele; CPC34947 (holotype).
4 Transverse section of a distal portion of an axis showing preferential preservation of robust tissues; (m) metaxylem, (p) protoxylem, (ph) cavity representing the position of phloem and associated parenchyma, (e) endodermis/inner cortex, (m) cavity representing the position of degraded middle cortex; CPC34951a.
5 Longitudinal section of large metaxylem tracheids showing mostly annular or close-spiral thickenings; CPC34953.
6 Longitudinal section of smaller tracheids showing annular to close-spiral thickenings with sporadic development of vertical to oblique cross-connections resulting in a tendency towards reticulate thickenings; CPC34952b.
7 Longitudinal sections through transfusion tissue between protoxylem arms showing cell walls with pervasive simple pitting; CPC34949b.

Plate IV. *Paurodendron stellatum* sp. nov. Scale bars represent 100 μm. (See on page 9)

1 Transverse section of root showing incipient branching and eccentric position of vascular strands within cavities left by degradation of inner to middle cortex and surrounded by thick-walled outer cortex; CPC34948b.
2 Transverse section of charcoalified microphyll showing uniseriate epidermis of inflated cells and single, poorly preserved vascular strand (s); adaxial surface at top of figure; CPC34948c.
3 Transverse section through a flattened microphyll consisting of a uniseriate epidermis, mostly degraded mesophyll and a central vein of one or two tracheids; CPC34952c.
4 Longitudinal section of axis (left) attached to a distally arched microphyll (right); CPC34949b.
5 Transverse section of microphyll base at emergence from axis showing continuity of cortical and mesophyll tissues, and lack of lacunae; CPC34951b.
6 Longitudinal section of attached, distally arched microphyll with ligular pit (arrowed) on adaxial surface; CPC34949b.
7 Longitudinal section through attached microphyll showing adaxial ligule (arrowed); CPC34949b.
8 Enlargement of ligule on adaxial surface of microphyll; CPC34949b.

Plate V. Scanning electron micrographs of isolated charcoalified microphylls attributed to *Paurodendron stellatum* sp. nov. and affiliated megaspores. Scale bars represent 100 μm for 1–6, 9; 10 μm for 7, 8, 10. (See on page 10)

1 Isolated elliptical microphyll, abaxial surface; CPC34970.
2 Isolated fragmentary microphyll, adaxial surface; CPC24966.
3 Enlargement of CPC24966 showing inflated epidermal cells along distal margin of microphyll.
4 Isolated fragmentary microphyll, adaxial surface; NRMS089724.
5 Enlargement of the mid-portion of a partially enrolled microphyll showing inflated epidermal cells distally (top) and sunken cells proximally (bottom); CPC34968.
6 Details of inflated epidermal cells in distal half of microphyll; CPC34968.
7 Details of sunken epidermal cells in proximal half of microphyll; CPC34968.
8 Details of epidermal cells in proximal half of microphyll showing sunken and wrinkled texture with a prominent central raised circular feature (possible trichome/papilla base); CPC34968.
9 SEM of *Singhisporites hystrix* Slater et al., 2011 (proximal surface), co-preserved with remains of *Paurodendron stellatum*; NRMS089705.
10 Scabrate trilete microspore entrapped between lacerate sculptural elements of a *Singhisporites hystrix* megaspore NRMS089726.

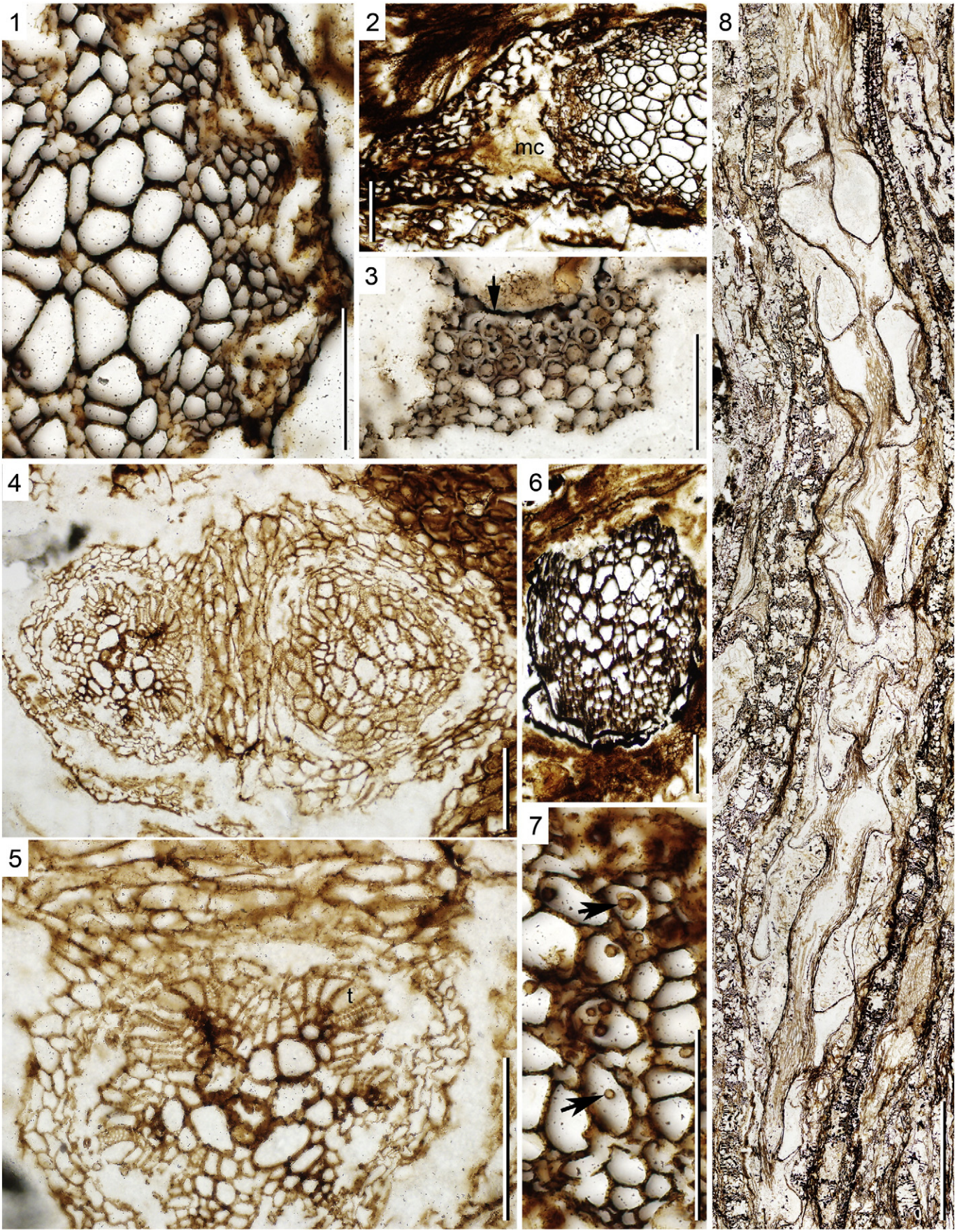

Plate II.

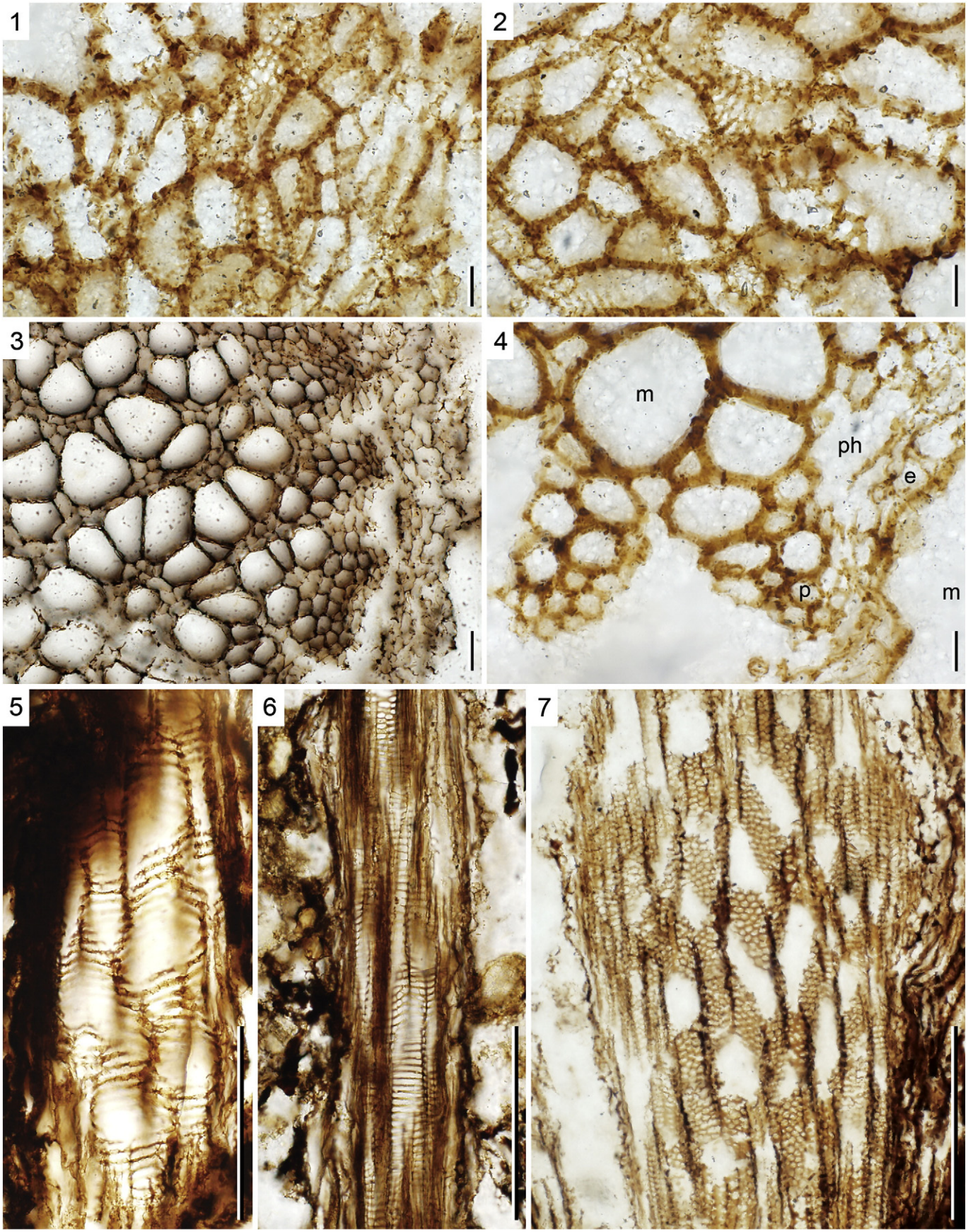

Plate III. (*Caption on page 6*).

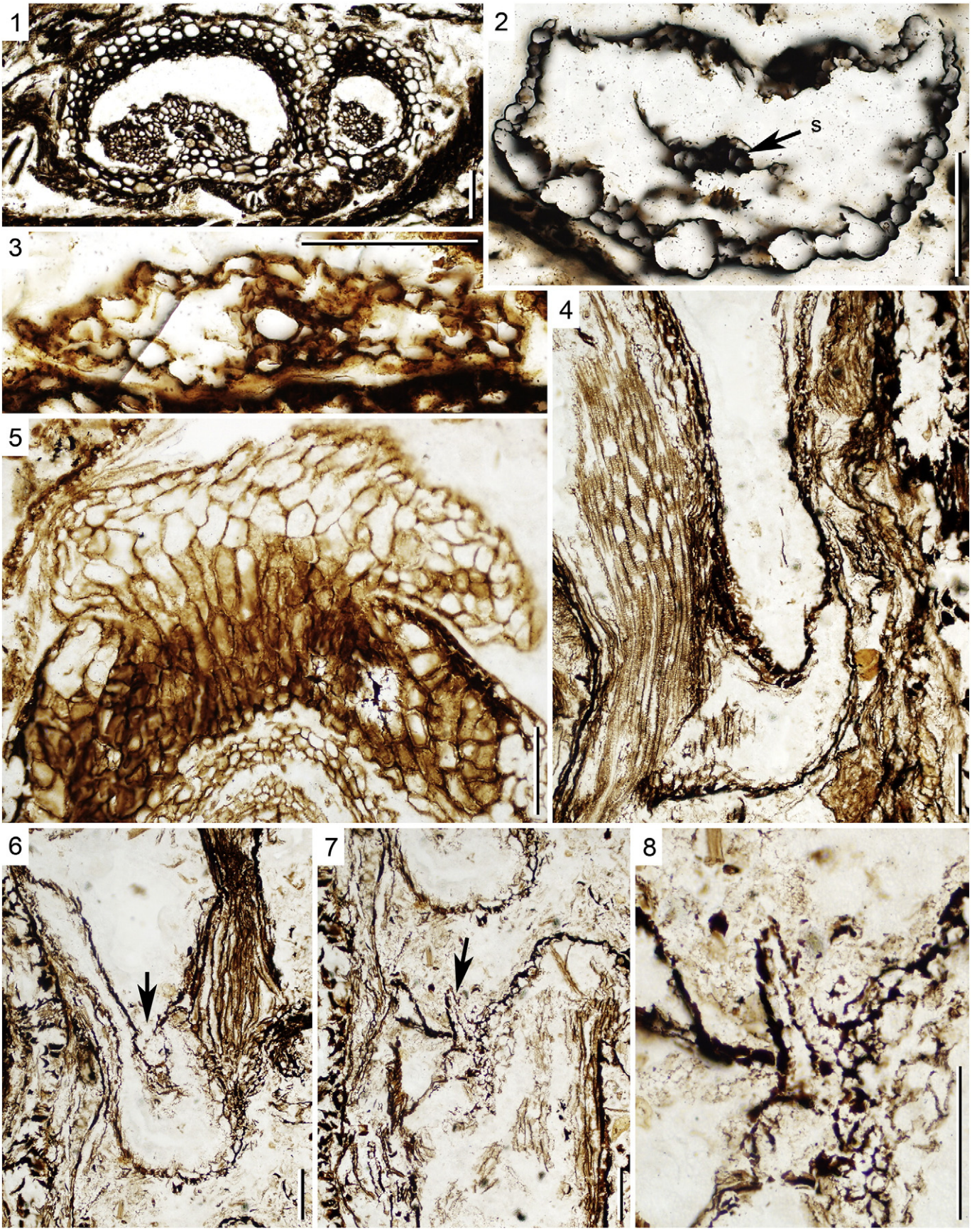

Plate IV. (*Caption on page 6*).

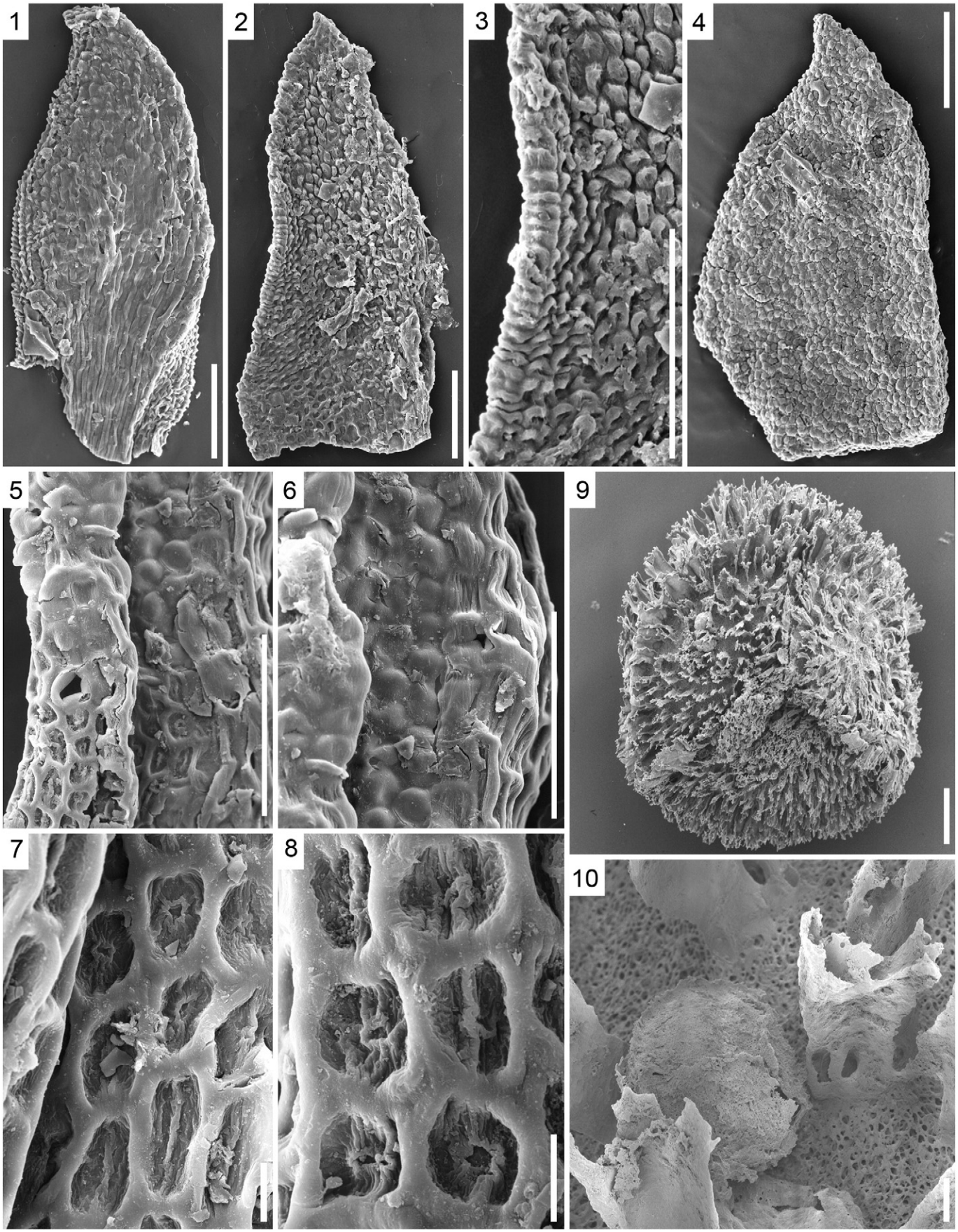

Plate V. (*Caption on page 6*).

Fig. 2. Reconstruction of the morphology and anatomy of the aerial portion of *Paurodendendron stellatum*. Scale: 1 mm.

diameter) with 1 μm thick dark walls, typically positioned against the tip of a spur of middle–outer cortical cells projecting towards the centre of the root. The protoxylem is surrounded by an elliptical–reniform column of metaxylem up to 350 μm wide and 160 μm deep. Metaxylem tracheids are 6–(12)–24 μm in diameter, generally broadest towards the margin of the vascular cylinder. Phloem and inner to middle cortical tissues are not preserved leaving a reniform lacuna (Plate IV, 1). The outer cortex consists of dark, very thick walled (c. 8 μm) cells with small lumina (typically <14.5 μm in diameter; Plate IV, 1). Cells of the outer cortex gradually increase in diameter radially, with lumina reaching 52 μm in diameter and cell walls reducing to <2 μm thick. The epidermis is generally degraded but in some places it is marked by a dark uniseriate rim of crushed cells <12 μm thick. In some cases, two root traces are enclosed by a single band of cortex tissues suggesting an incipient dichotomy (Plate IV, 1).

Microphylls: Numerous charcoalified microphylls are dispersed throughout the type formation. They are typically ovate, elliptical, or rhombic (Plate V, 1–4), 300–1500 μm long, 200–650 μm wide, with an acute or, in some cases, weakly mucronate apex, and a slightly contracted base. In rare cases, microphylls are preserved attached to slender (>150 μm long, 60 μm wide) axes in a helical arrangement (Plate II, 8) and each is inserted by a broad or slightly contracted base. Longitudinal sections of the axes show attached microphylls having little overlap with microphylls in the succeeding helix (Plate II, 8). Microphyll margins are entire or minutely crenulate (but not spinose), whereby crenulations are produced by a marginal row of inflated epidermal cells (Plate V, 3). Both abaxial and adaxial epidermal cells of microphylls are arranged in longitudinal ranks; they are square to longitudinally rectangular at the base and centre of the microphylls and become transversely rectangular towards the margins (Plate V, 1–3). Central cells (over the midvein) are typically 5–50 μm long and 5–25 μm wide, whereas marginal cells are typically 5–10 μm long and 10–20 μm wide. Epidermal cells in the proximal half of one microphyll have periclinal walls collapsed below the level of the anticlinal walls, which form ridges 4–5 μm wide and 3–10 μm high. Epidermal cells in the proximal and central parts of this microphyll typically show striae arranged longitudinally or radiating from a distorted, central, circular, elevation (<4 μm diameter) — possibly representing a trichome/papilla base at the centre of the cell (Plate V, 7, 8). Distal and marginal epidermal cells are typically bulbous and lack micro-ornamentation (Plate V, 5, 6). No stomata are evident on the microphylls. In transverse section, microphylls are spindle-shaped, semicircular or crescentic, and are c. 75–225 μm thick, depending on the degree of compression, and show no evidence of aerenchyma or natural lacunae (Plate IV, 3). Transverse sections of charcoalified microphylls (Plate IV, 2) reveal a single layer of bulbous epidermal cells 10–25 μm thick and a single, central, degraded, dorsiventrally flattened, vascular strand <100 μm in diameter; mesophyll tissues are poorly preserved. Non-charcoalified microphyll bases attached to *Paurodendron stellatum* axes show a mesophyll consisting of thin-walled, polygonal cells, <60 μm in diameter, which are poorly ordered except at the point of insertion on the stem where they are elongate, sub-parallel and continuous with the outer cortex (Plate IV, 5). In longitudinal section, microphylls are flexed adaxially (Plate IV, 4). A ligular pit is preserved on the adaxial surface near the base of microphylls (Plate IV, 6). In rare cases, a short (100 μm long), slender ligule is preserved within the pit (Plate IV, 7, 8).

6. Discussion

6.1. Antarctic herbaceous lycopsids

Despite their long fossil record in Antarctica, extending from at least the Givetian (Rigby and Schopf, 1969; Grindley et al., 1980; McLoughlin and Long, 1994; Xu and Berry, 2008) to Neogene (Jiang and Harwood, 1992; Warny et al., 2009), lycopsids have not dominated the vegetation of that region since the Devonian. They appear to have been consistent subsidiary elements of the vegetation through the late Palaeozoic and Mesozoic (Cantrill and Poole, 2012).

Paurodendron stellatum is the first macrofossil record of Antarctic Permian heterosporous lycopsids and adds to the generally poor record of high-latitude Permian lycopsids. The new species is established on several incomplete specimens that collectively allow a partial reconstruction of the vegetative morphology of this herbaceous plant (Fig. 2). Two recently described taxa from the Lopingian of the Transantarctic Mountains also appear to represent herbaceous lycopsids. *Collinsonites schopfii* Schwendemann et al., 2010 is based on branched, leafy axes up to 4 mm wide and 98 mm long. The material is based on impressions and compressions in which anatomical details are unavailable. However, *C. schopfii* can be readily distinguished from *P. stellatum* by its eligulate

microphylls that, in some cases, bear distinct spinules along the margins. Further, *C. schopfii* is slightly larger than *P. stellatum* in almost all its axial and foliar dimensions. *Collinsonostrobus eggertii* (Ryberg et al., 2012) is known only from permineralized microsporophylls. The sporophylls bear marginal teeth and consistently small (<30 μm diameter) spores suggesting a homosporous condition and potential affiliation with the eligulate *Collinsonites*. No anatomical details of the *Collinsonostrobus* axis are available for comparison with *Paurodendron*.

Although not yet recorded from Antarctica and only known from compressions, *Selaginella harrisiana* from the Lopingian of Australia (Townrow, 1968) is similar in habit to *Paurodendron stellatum*. Although few morphological features of *S. harrisiana* leaves were described by Townrow (1968), they are slightly larger (1–4 mm long, 1–3 mm wide) and more triangular than those of *P. stellatum*.

6.2. Associated spores

The fertile organs of *Paurodendron stellatum* remain unknown. However, the Toploje Member chert hosting this species, has yielded three types of megaspores described by Slater et al. (2011) that are plausibly associated with this lycopsid: *Singhisporites hystrix*, *Duosporites lambertensis* and *Banksisporites antarcticus*. *Singhisporites hystrix* (Plate V, 9) is the most likely affiliated megaspore based both on its much greater abundance than the other two forms, and its regular co-occurrence with *Paurodendron* axes in the same laminae within the peat profile. *Singhisporites hystrix* bears elaborate lacerate flange-like sculptural elements (Plate V, 9, 10; Slater et al., 2011) in contrast to the megaspores of *Paurodendron fraipontii*, which have either an ill-defined (Leisman, 1961) or a reticulate (Hoskins and Abbott, 1956) ornament. Megaspores recovered from *Selaginella harrisiana* strobili from the Lopingian of eastern Australia differ in having spinose, pilate or weakly conate ornamentation (Townrow, 1968).

Microspores associated with *Singhisporites hystrix* are known from specimens entrapped in the complex ornamentation of that megaspore, which has been studied via SEM and synchrotron X-ray microtomography (Slater et al., 2011). The microspores are similar to representatives of *Lundbladispora* (Foster, 1979; Visscher et al., 2004; Looy et al., 2005) in being cinguli-cavate with scabrate to sparsely spinose ornamentation (Slater et al., 2011, pl. V.1–4; Plate V, 10 herein). The in situ permineralized microspores of *Collinsonostrobus eggertii* from the Lopingian of the Transantarctic Mountains, by contrast, bear reticulate ornamentation (Ryberg et al., 2012). The microspores of *Selaginella harrisiana* differ in having a spinulose (distal) to verrucate (proximal) ornamentation.

6.3. Comparison with the type species

The only previously recognized representative of *Paurodendron* is the type species [*Paurodendron fraipontii* (Leclercq) Fry, 1954; here regarded as synonymous with *Paurodendron arranense* Fry, 1954 and *P. radiatum* Fry, 1954], which is exclusively known from the Carboniferous of the Northern Hemisphere (Euramerica). *Paurodendron stellatum* is distinguished from *P. fraipontii* principally by its proportionately thinner outer cortex, more irregularly shaped metaxylem tracheids, and the absence of spine-like appendages on the axis and leaves.

Both *Paurodendron* species have a lacuna in the position of the middle cortex. This zone may have been traversed by loose trabeculae forming an aerenchymatous zone similar to that of the early lycophyte *Asteroxylon* (Kidston and Lang, 1920). This interpretation is supported by the presence, in some crushed specimens, of a sparse network of cells in this region (Plates I, 4, II, 2). Alternatively, the middle cortex may have been entirely composed of very thin-walled cells that degraded soon after death, as suggested by several axes entirely lacking cells in this region (Plate I, 2). In either case, this tissue layer is poorly preserved in the available fossils and the zone is traversed only by sporadic patches of dense cells that may represent departing leaf traces (Plate I, 2).

The smaller diameter and fewer protoxylem points in *Paurodendron stellatum* axes compared to many *Paurodendron fraipontii* axes illustrated by Fry (1954) probably indicate only that the sections of the Antarctic specimens derive from more distal parts of the axes, because the number of protoxylem points has been shown to decrease distally in the stems (Schlanker and Leisman, 1969). Metaxylem tracheids of *P. stellatum* have only very sparse filamentous vertical thickenings connecting adjacent scalariform/spiral bars, compared to their more common occurrence in *P. fraipontii* (Fry, 1954), but this may be a consequence of incomplete preservation of these delicate structures. No information is yet available on the base of the *P. stellatum* axis, and whether the root-bearing portion was a clavate, corm-like rhizomorph as in *P. fraipontii* (Phillips and Leisman, 1966; Rothwell and Erwin, 1985) is unclear. No evidence of secondary growth, either within the vascular tissue or cortex, was found in *P. stellatum* axes. However, the small diameter of the axes (<2 mm) and sparse branching suggests that the plant was herbaceous, or pseudoherbaceous sensu Bateman and DiMichele (1991) and Bateman (1992). A prominent endodermis is developed in the axes of *P. stellatum*. An equivalent band of tissue in *P. fraipontii* has been variably described as remnants of the phloem, inner parenchymous cortex, pericycle, or aerenchymatous cortex (Fry, 1954; Phillips and Leisman, 1966; Rothwell and Erwin, 1985).

The isolated, minute, charcoalified, scale-like leaves co-preserved with *Paurodendron stellatum* axes were initially considered to be possible coniferous scales (McLoughlin et al., 1997) but their diminutive size, simple vasculature, association with other lycopsid remains, the presence of similar-sized microphyll bases attached to permineralized axes, and the absence of other convincing coniferous remains in the host strata suggest that these scales are microphylls of the *P. stellatum* plant. Microphylls of *Paurodendron fraipontii* are similar to those of *P. stellatum* in size (300–1000 μm wide, 200–500 μm thick), in hemispherical cross-section, and in possession of undifferentiated, irregularly polygonal, mesophyll cells (Fry, 1954; Phillips and Leisman, 1966; Schlanker and Leisman, 1969). Unlike *P. fraipontii*, however, *P. stellatum* microphylls appear to be incurved rather than recurved, at least during early stages of development, and broaden slightly from the point of insertion before tapering, rather than tapering throughout. *Paurodendron stellatum* microphylls also differ from those of *P. fraipontii* in lacking multicellular spine-like enations on the abaxial surface and minutely cusped margins.

Paurodendron stellatum is characterized by the development of transfusion tissue surrounding the protoxylem arms, at least in regions of axis branching (Plate II, 5, Plate III, 1, 2, 7). This tissue is broadly similar to the zone of radially expanded and strongly pitted transfusion cells developed between the vascular strand and endodermis in gymnosperm leaves (Hu and Yao, 1981). Tissues between the protoxylem and the endodermis are typically not preserved in published examples of *Paurodendron fraipontii*. However, Pigg and Rothwell (1983) identified transfusion tissue flanking the basal part of the leaf trace in the related *Chaloneria cormosa* Pigg and Rothwell, and DiMichele et al. (1979) noted transfusion tissue on the adaxial side of the midvein in sporophyll bases of *C. periodica* Pigg and Rothwell.

The characters described for *Paurodendron stellatum* highlight its close similarity to *Paurodendron fraipontii* and confirm most of the character states applied to the genus in previous phylogenetic analyses. Few additional characters are available from *P. stellatum* to better resolve relationships among rhizomorphic lycopsid taxa in future cladistic analyses. However, if *P. stellatum* axes are associated with *Singhisporites*, as inferred herein, then megaspore morphology within *Paurodendron* extends to lacerate, ribbon-like sculptural elements beyond the reticulate ornamentation evident in *P. fraipontii* megaspores.

6.4. Growth habit and habitat

Paurodendron fraipontii has been reconstructed as a small scrambling or prostrate, *Selaginella*-like, plant (Schlanker and Leisman, 1969; Bateman et al., 1992), although a more upright dichotomous or

pseudomonopodially branched axis arising from a clavate rhizomorph is also possible (Phillips and Leisman, 1966). The Antarctic specimens provide few further clues to the growth habit of the genus because only incomplete material is available. With foliage-bearing axes of <2 mm diameter, *P. stellatum* is interpreted to be a very small lycopsid (pseudoherbaceous sensu Bateman, 1992) with well-spaced, helically arranged, dorsiventrally flattened microphylls (Fig. 2). The isophyllous character and helical leaf arrangement argue against a prostrate growth habit.

Paurodendron roots occur within densely matted, parautochthonous leaf litter at the type locality suggesting that the fossils have not been transported significantly. This bed is also penetrated by abundant *Vertebraria* (glossopterid) roots that have commonly been interpreted to reflect an adaptation for growth in dysaerobic waterlogged peat and subaquatic environments (Neish et al., 1993). Several *P. stellatum* axes bear fungal hyphae ramifying through the xylem tissues (Plate II, 7), which together with widespread loss of thin-walled tissues, signify moderate aerobic decay before entombment in silica. The Toploje Member peat is interpreted to represent an ombrotrophic glossopterid-dominated mire deposit (Slater et al., 2015), i.e., a forested bog sensu Moore (1989). We interpret *P. stellatum* to have been a diminutive, sparsely branched, upright plant living on the subaerially exposed peat surface of glossopterid-dominated raised mires. The presence of charcoalified axes and microphylls of *Paurodendron* and charred woody tissues of other plants in this deposit indicates that the environment was sufficiently dry at times to permit extensive burning of the vegetation and peat surface (Slater et al., 2015). Recognizable herbaceous lycopsid remains form 0.85–1.2% of the peat volume in the lower Baimedart Coal Measures, Antarctica (Slater et al., 2015). Moreover, megaspores and charcoalified microphylls are relatively common among the phytodebris extracted from associated floodbasin facies via bulk maceration (McLoughlin et al., 1997). Herbaceous lycopsids apparently formed an important subsidiary component of the southern high-latitude glossopterid-dominated Permian mire and alluvial plain vegetation. Herbaceous lycopsids also appear to have been locally abundant in Northern Hemisphere Carboniferous palaeotropical peat-forming ecosystems (DiMichele and Phillips, 1995).

Modern (semi)aquatic *Isoetes* lack stomata and use a specialized Lycopsid Photosynthetic Pathway (LPP: Green, 2010), whereby CO_2 is taken up by the roots from the substrate and stored in internal canals and aerenchyma, and O_2 is conversely passed downwards through the roots into the soil. Aquatic *Isoetes* species employ a form of Crassulacean Acid Metabolism (CAM), whereby carbon is fixed as organic acids at night and stored in large vacuoles (Keeley, 1998; Pedersen et al., 2011). The apparent absence of stomata in the leaves of various *Isoetes* species (Keeley et al., 1994) is a character shared with *Paurodendron stellatum* and with Triassic pleuromeian lycophytes (Bomfleur et al., 2011). This character combined with other specialized anatomical features of *P. stellatum* including the presence of large air chambers in the stem and root cortex, relatively spongy leaf mesophyll, and extensive transfusion tissue around the stele suggests that *Paurodendron stellatum* may also have employed LPP and/or CAM in its periodically submerged mire habitat. Moreover, Green (2010) has pointed out that related arborescent lepidodendrids, having similar anatomical features, probably also utilized these metabolic systems. This suggests that LPP/CAM may have played a widespread and important role in carbon cycling in the extensive mire ecosystems of the late Palaeozoic.

6.5. Distribution

The geographic range of *Paurodendron* is now extended to the Southern Hemisphere, at a locality situated at c. 70° south palaeolatitude (Scotese and Langford, 1995). The occurrence of *Paurodendron* in Wordian strata extends the stratigraphic range of the genus by approximately 35 million years beyond the Northern Hemisphere records. The geographic and stratigraphic disjunctions between the Northern and Southern hemisphere records may seem problematic for inclusion of *P. stellatum* and *Paurodendron fraipontii* in the same genus. However, strong preservational biases may explain the sparse records of this genus.

Scheihing (1980) and Spicer (1981) noted that understorey plants in general are under-represented in lacustrine and fluvio-deltaic fossil assemblages. Other authors have emphasized that preservational biases related to slower decay of robust plant tissues (e.g., lignin and thick cuticles) play a strong role in defining the composition of plant assemblages and favour the preservation of woody plants over herbaceous forms (Gastaldo, 1988; Spicer, 1989). Further, there may be a strong bias in the published macrofossil record against the identification of diminutive plant taxa lacking strongly distinctive morphological characters, especially when preserved as adpressions (Burnham, 2008).

The recognition of herbaceous *Paurodendron* remains only in siliceous permineralized peat deposits and coal balls suggests that these plants may have been geographically widespread and long-ranging through the late Palaeozoic but that their diminutive size and delicate anatomy has resulted in rare preservation and poor recognition in adpression assemblages. Moreover, the age difference between the Antarctic *P. stellatum* and the youngest examples of *Paurodendron fraipontii* is less than that of the total temporal range of the latter species in the Northern Hemisphere. Further, numerous plant taxa have stratigraphic ranges characterized by temporally remote representatives (known as precocious taxa when appearing well before the group's typical range, and Lazarus taxa when appearing long after the characteristic range: Looy et al., 2014). With respect to plants, Lazarus taxa are perhaps best known among gymnosperms. For example, rare representatives of Corystospermales, Bennettitales and cheirolepidiaceous conifers have been reported in Paleogene strata, up to tens of millions of years younger than the typical Mesozoic representatives of these clades (McLoughlin et al., 2008, 2011; Barreda et al., 2012). Bateman and DiMichele (1991) noted that several lepidodendrid genera (e.g., *Anabathra, Sigillaria, Diaphorodendron* s.l., *Lepidodendron* and *Lepidophloios*) have long stratigraphic ranges through the late Palaeozoic, so a similarly long range for related coeval herbaceous heterosporous lycopsids is not unexpected.

The broad spectrum of lycophytic megaspores identified in Gondwanan Permian strata (Bharadwaj and Tiwari, 1970; Dijkstra, 1972; Pant and Mishra, 1986; Tewari and Maheshwari, 1992; McLoughlin et al., 1997; Glasspool, 2000, 2003; Tewari et al., 2009; Slater et al., 2011), attests to a great diversity of heterosporous lycopsids in this region that is not yet matched by macrofossils. Diminutive herbaceous lycopsids with low preservational potential, such as *Paurodendron stellatum*, are strong candidates for the parent plants of some of these dispersed megaspores.

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