

Revision and biostratigraphic implications of Thore Halle's Permian plant fossils from the Falkland (Malvinas) Islands

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Received 19 December 2023, Accepted 19 June 2024

The Permian fossil plant assemblages from the Lafonia Group on the Falkland (Malvinas) Islands collected by Thore Gustav Halle on the 1907–1909 Swedish Expedition to Patagonia and Tierra del Fuego are re-described and their systematic placement revised. Two species of sphenophytes based on foliage and one on axial remains are recognized. Eight morphotypes of *Glossopteris* are differentiated using more rigorously defined criteria than Halle's original character sets. A single species each of cordaitaleans and conifers are recognized. The absence of ferns and lycophytes may indicate significant taphonomic filters on the composition of the plant assemblages. Re-assessment of the characters of the fossil woods and their nomenclatural and taxonomic problems suggests that only a single species is recognizable in the assemblage. Several of the wood and leaf species bear evidence of fungal degradation along with a broad array of arthropod herbivory and oviposition damage that add to the diversity of biotic interactions documented in the middle–high southern latitude Glossopterid Biome of the late Paleozoic. The ages of the various fossiliferous units on the Falkland (Malvinas) Islands remain equivocal, but similarities with chronostratigraphically constrained leaf assemblages from the Karoo Basin, South Africa, suggest that the Bay of Harbours Formation (uppermost unit of the Lafonia Group) is referable to the upper Guadalupian to lowermost Lopingian.

Keywords: *Glossopteris*, sphenopsids, conifers, Lopingian, Lafonia Group, Karoo Basin.

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INTRODUCTION

Thore Gustaf Halle's (1911) original paper on the Permian flora of the Falkland Islands, recognized by Argentina as the 'Islas Malvinas', was the fourth in the series of geological publications on the results of the Swedish Expedition to Patagonia and Tierra del Fuego, 1907–1909, led by botanist and explorer Dr Carl Skottsberg. Halle (at age 23) participated in Skottsberg's expedition, collected the fossil material, carried out additional extensive geological investigations on the Falkland (Malvinas) Islands, and published the results for his doctoral dissertation at Uppsala University under the supervision of Professor Arvid-Gustaf Högbom. The geology of the Falkland (Malvinas) Islands had received little attention between Charles Darwin's visits of 1833 and 1834 (Armstrong 1992) and the Swedish South Polar Expedition of 1901–1902. Andersson (1907) and Halle (1911) provided the first serious attempts to clarify the geology of the islands and provided age constraints on the stratigraphic succession using marine and continental fossils. Halle spent a little under four months on the Islands (26 October 1907 to 12 February 1908). He described elements of the Devonian,

Permian and Quaternary fossil floras, of which only the Permian material is revised here.

Nathorst (1904) published possibly the earliest report of pre-Quaternary fossil plants from the Falklands, based on material collected by Johan Gunnar Andersson from the southern end of East Falkland (Soledad) Island during the 1901–1902 Swedish South Polar Expedition. His identification of *Asterocalamites* was later revised to *Phyllothea* (Nathorst 1906), suggesting a Permian age for these strata. Halle (1908, 1911) confirmed a Permian age for these plant-bearing beds and documented two species of sphenopsids, five *Glossopteris* leaf types, a glossopterid scale leaf, spine-leaved conifer branches, strap-shaped leaves attributed to *Desmiophyllum*, and two species of permineralized wood.

Several subsequent studies have mentioned, described or illustrated Permian plant remains from the Falkland (Malvinas) Islands (Table 1). Key studies include those of Seward & Walton (1923) who described four morphotypes of *Glossopteris* and a new species of permineralized wood (*Dadoxylon bakeri*) from George Island, Speedwell Island and North Arm, near the southern tip of East Falkland (Isla Soledad). Baker (1924) recorded additional silicified

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Table 1. Principal published records of Permian plant fossils (original published identifications) from the Falkland Islands with their location and stratigraphic assignment.

Author/year	Taxon	Location	Stratigraphic unit
Nathorst (1906)	<i>Phyllothea</i> sp.	Seal Cove, Bull Cove, Speedwell Island	Egg Harbour Mbr, Bay of Harbours Fm
Halle (1911)	(1) <i>Phyllothea australis</i> Brongniart (leaves and associated ribbed axes)	(1) Speedwell Island + most Permian plant localities except Darwin Harbour and Dos Lomas	See Materials and Methods
	(2) <i>Phyllothea deliquescens</i> (Goeppert)	(2) Same localities as (1) + Dos Lomas.	
	(3) <i>Glossopteris browniana</i> Brongniart	(3) South of Dos Lomas on Falkland Sound, south of Goose Green, and Speedwell Island	
	(4) <i>Glossopteris indica</i> Schimper	(4) Darwin Harbour, Goose Green, Bodie Creek Head, Dos Lomas, Low Bay, Speedwell Island	
	(5) <i>Glossopteris angustifolia</i> Brongniart	(5) Southernmost point of Speedwell Island and at Bodie Creek Head	
	(6) <i>Glossopteris damudica</i> Feistmantel	(6) Dos Lomas	
	(7) <i>Gangamopteris cyclopteroides</i> Feistmantel var. <i>major</i> (Feistmantel)	(7) South of Dos Lomas	
	(8) Scale-frond of <i>Glossopteris</i> sp. (?)	(8) Dos Lomas	
	(9) Coniferous branches	(9) Speedwell Island, north of the Halfway Cove settlement	
	(10) <i>Desmiophyllum</i> sp.	(10) South coast of East Falkland opposite Speedwell Island	
	(11) <i>Dadoxylon lafoniense</i>	(11, 12) See Table 2	
	(12) <i>Dadoxylon</i> cf. <i>angustum</i> Felix		
Seward & Walton (1923)	(1) Equisetaceous stems (possibly <i>Phyllothea</i> sp.)	(1) Unspecified	Speedwell Island, George Island, Cygnet Harbour and Dos Lomas = Egg Harbour Mbr, Bay of Harbours Fm. North Arm = Praltos Mbr, Bay of Harbours Fm. Walker Creek and Fanny Cove = Saladero Mbr, Brenton Loch Fm. Goose Green = Possibly Saladero Mbr or Praltos Mbr
	(2) Equisetaceous stems cf. <i>Phyllothea australis</i> Brongniart and <i>P. deliquescens</i> (Goeppert)	(2) Speedwell Island, George Island, North Arm (Bay of Harbours), Dos Lomas	
	(3) Equisetaceous stems cf. <i>Neocalamites carrerei</i> (Zeiller)	(3) Cygnet Harbour, Egg Harbour	
	(4) <i>Glossopteris indica</i> Schimper	(4) Speedwell Island, George Island, North Arm (Bay of Harbours), Dos Lomas, Goose Green	
	(5) <i>Glossopteris indica</i> Schimper, cf. var. <i>wilsoni</i> Seward	(5) North Arm (Bay of Harbours)	
	(6) <i>Glossopteris indica</i> Schimper, cf. var. <i>decipiens</i> Feistmantel	(6) George Island and Bay of Harbours	
	(7) <i>Glossopteris browniana</i> Brongniart	(7) George Island, North Arm (Bay of Harbours), Goose Green	
	(8) <i>Dadoxylon bakeri</i>	(8) Walker Creek and Fanny Cove, on the southern side of Choiseul Sound, East Falkland	
Trewin <i>et al.</i> (2002)	(1) Plant debris	(1) Unspecified	(1) Cantera and Saladero members, Brenton Loch Formation
	(2) <i>Glossopteris</i> sp.	(2) Unspecified	(2) Praltos Member, Bay of Harbours Formation
Stone (2010)	Silicified wood	Bleaker Island, SE of Lafonia, East Falkland	Praltos Member, Bay of Harbours Formation
Simões <i>et al.</i> (2012)	<i>Glossopteris</i> sp. cf. <i>G. communis</i> Feistmantel	Rorys Creek, East Falkland	Saladero Member, Brenton Loch Formation
Stone & Rushton (reviewing collections of Baker 1924)	<i>Calamites</i> -type plant stems; <i>Glossopteris</i> spp.	Lafonia (possibly George and Speedwell islands)	Probably Egg Harbour Mbr, Bay of Harbours Fm

wood at Walker Creek. Aldiss & Edwards (1999) summarized the occurrences of fossil plants on the Falkland (Malvinas) Islands and noted anecdotal reports of permineralized wood up to 40 cm in diameter and 4 m long in the southern part of East Falkland (Isla Soledad) and its adjacent islands. Trewin *et al.* (2002) noted that *Glossopteris* leaf fossils were abundant in certain beds of the Bay of Harbours Formation (Lopingian), exposed primarily in the central and southern portions of East Falkland (Isla Soledad) and its offshore islands, but no specimens were illustrated. Stone (2010) illustrated an unidentified permineralized wood with prominent growth rings from the same unit. Simões *et al.* (2012) illustrated two leaf specimens attributed to *Glossopteris* sp. cf. *G. communis* from the Saladero Member (Capitanian) of the Brenton Loch Formation at Rorys Creek, East Falkland (Isla Soledad). Stone (2012) mentioned that the Brenton Loch and Bay of Harbours formations host abundant plant fossils including *Glossopteris*, but no additional material was described or illustrated.

The only other non-aquatic body fossil recovered from the *Glossopteris*-bearing beds is a single insect wing illustrated by Halle (1911) and tentatively assigned to the Palaeodictyoptera, but later interpreted to derive from a damselfly by Tillyard (1928) or a basal group of damselfly-like Odonatoptera by Nel *et al.* (2012). The three fossil insect wings reported to have been recovered from the Permian of the islands by Schlüter (2003) apparently all represent the single specimen collected by Halle (1911). A sparse fauna of non-marine bivalves was documented by Simões *et al.* (2012) from the Saladero Member, Brenton Loch Formation. Various non-marine invertebrate grazing traces, trackways, and burrows, together with fish trails (*Undichna*) have also been reported from this unit (Trewin 2000; Trewin *et al.* 2002; Stone 2016).

Seward & Walton (1923) wrote, in evaluating Dr Herbert Arthur Baker's collection of Permian fossil plants from the Falkland (Malvinas) Islands, 'A thoroughly satisfactory determination and specific separation of the numerous and, nearly always, incomplete leaves obtained from the different Permo-Carboniferous localities in the Falkland Islands is, we feel, a hopeless task'. We are less pessimistic about the demarcation of Permian leaf forms than those authors and we apply rigorous morphological and anatomical criteria to distinguish multiple fossil species and morphotypes from that region.

Since Halle's identifications of Permian plant impressions were supported mainly by sketches with limited or inaccurate morphological details, we aim to illustrate the principal components of the flora using colour photography. In doing so, we present additional observations on the fossils and confirm or revise various identifications presented in Halle's (1911) report. We provide comparisons primarily with fossils from South Africa and Argentina – the regions that were geographically closest to the Falklands (Malvinas) Block during the Permian (Trewin *et al.* 2002). Included in this analysis are the first Permian plant–insect interactions to be recognized on leaf and stem impressions from the Islands. We also provide a new anatomical analysis of the permineralized wood using

modern transmitted-light microscopy techniques. We use these results to assess the taxonomic placement of the woods and to document the first record of permineralized fungus- and oribatid mite-interactions with probable glossopterid axes from the region.

GEOLOGICAL SETTING

Following the work of Adie (1952), the Falkland (Malvinas) Islands (and adjacent continental crust of the Falklands/Malvinas Plateau and Maurice Ewing Bank) were generally interpreted to have been contiguous with the southeastern margin of the Karoo Basin before Gondwanan breakup and rotation of the Falklands block in the Mesozoic (Mitchell *et al.* 1986; Marshall 1994; Aldiss & Edwards 1999; Stone 2016; and references therein). More recent work by Ramos *et al.* (2017, 2019), Lovecchio *et al.* (2019, 2020) and Bonifacio *et al.* (2023) has favoured a more southerly (south of the Cape Fold Belt) position of the Falklands (Malvinas) (and a fixed relationship to Patagonia) prior to continental breakup. Regardless of which reconstruction is correct, the Falkland (Malvinas) Islands would have been located at about 60–65°S during the Lopingian, with a cool- to cold-temperate climate (Torsvik & Cocks 2012; Prevec *et al.* 2022). Faulting and sediment accumulation in the Falklands (Malvinas) region may even have been linked to the western extent of a broad band of pan-Gondwanan rifting that formed in the Permian and provided structural weaknesses that were later reactivated during Gondwanan breakup (Harrowfield *et al.* 2005).

Several studies have documented the geology of the Falkland (Malvinas) Islands in recent decades (Aldiss & Edwards 1999; Trewin *et al.* 2002; Simões *et al.* 2012; Stone 2016). Carboniferous–Permian strata are confined primarily to the southern part of East Falkland (Isla Soledad) and adjacent islands (Fig. 1), together with a few isolated exposures near Byron Sound on the west coast and along Falkland Sound on the east coast of West Falkland (Isla Gran Malvina) (Greenway 1972). Permian strata also probably occur in the subsurface of the South Falkland (Malvinas) Basin and in the Malvinas Basin to the south and west of the Falkland (Malvinas) Islands, respectively (Stone 2016; Lovecchio *et al.* 2019).

Carboniferous and Permian strata on the Falkland (Malvinas) Islands are assigned to the Lafonia Group (Aldiss & Edwards 1999), which is synonymous with the Grupo Isla Soledad (East Falkland Group) of Borrello (1963, 1972). Distinct lithic, feldspathic and volcanigenic components of sedimentary strata in the Lafonia Group indicate that an orogenic belt (possibly the Cape Fold Belt) supplied sediments to the area (Aldiss & Edwards 1999). The Lafonia Group is up to 7 km thick and is generally divided into five formations (Fig. 2): The Bluff Cove Formation, Fitzroy Tillite, Port Sussex Formation, Brenton Loch Formation and Bay of Harbours Formation, in ascending stratigraphic order. Several of these have been further subdivided into members (Aldiss & Edwards 1999), which Trewin *et al.* (2002) compared in detail to the lithostratigraphic succession in the Karoo Basin.

The Bluff Cove Formation consists primarily of fine-

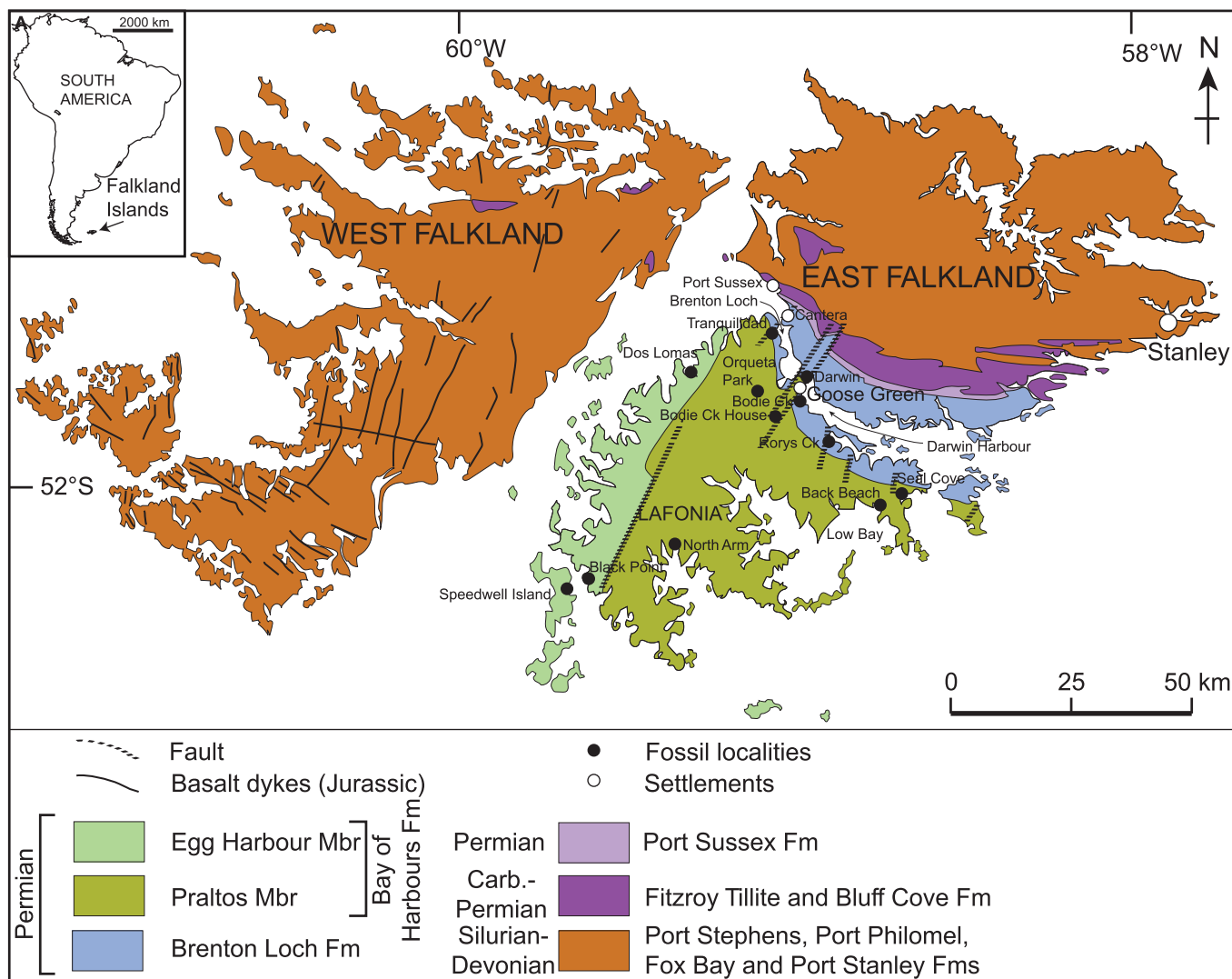


Figure 1. Geological map of the Falkland (Malvinas) Islands highlighting the distribution of Permian units and localities from which Halle's plant fossils were recovered (adapted from Halle 1911; Aldiss & Edwards 1999; Trewin 2002; Simões *et al.* 2012).

grained sandstones with interbedded siltstones and shales that lack identifiable body fossils but contain small indeterminate trace fossils and some disseminated unidentifiable plant debris (Aldiss & Edwards 1999). Sedimentary facies relationships suggest that the unit was deposited in shallow marine or deltaic settings prior to the Cisuralian (early Permian) glaciation of the region (Aldiss & Edwards 1999; Trewin *et al.* 2002).

The Fitzroy Tillite consists predominantly of clast-poor diamictite with a sandy mudstone matrix. Deposition occurred in subaqueous to continental glacial settings (Trewin *et al.* 2002). Examples of the trace fossil *Umfolozia* Savage provide the only evidence of biological activity in the unit, and the formation is tentatively assigned a Stephanian–Asselian or Sakmarian age (Isbell *et al.* 2003), based primarily on correlation with the Dwyka Group in South Africa where it is relatively common in Dwyka and lowermost Eccia Group deposits (Anderson 1981; Aldiss & Edwards 1999).

The Port Sussex Formation (Frakes & Crowell 1967) is divided into three subunits: the Hells Kitchen, Black Rock and Shepherds Brook members in ascending stratigraphic order (Aldiss & Edwards 1999). The Port Sussex Formation contains post-glacial, shallow-water, lami-

nated, fine- to medium-grained sandstones, dark grey and purple, siliceous, locally bentonitic, marine mudstones, and heterolithic facies containing sparse horizontal burrows (*Planolites*). Frakes & Crowell (1967) noted the presence of plant fossils in a claystone near the top of the Shepherds Brook Member at Port Sussex, and Aldiss & Edwards (1999) also reported plant debris from the lower half of this unit in the same area but no remains were identifiable. Age constraints on this unit are poor but lithological correlations with the Karoo Basin suggest an Artinskian–Roadian age (Aldiss & Edwards 1999; Trewin *et al.* 2002).

The Brenton Loch Formation is also divided into three subunits: the Terra Motas, Cantera and Saladero members (Aldiss & Edwards 1999). Collectively, this formation is composed of variable associations of sandstones, mud-dominated rhythmites, and massive mudstones and siltstones. A rich ichnofauna dominated by arthropod trackways is preserved in the Cantera Member and, together with sedimentological features ranging from wave and current-rippled tops of sandstone beds to turbiditic facies, suggest deposition in shallow bay to marine slope settings possibly representing a prograding delta front (Trewin *et al.* 2002). Poorly preserved fossils of

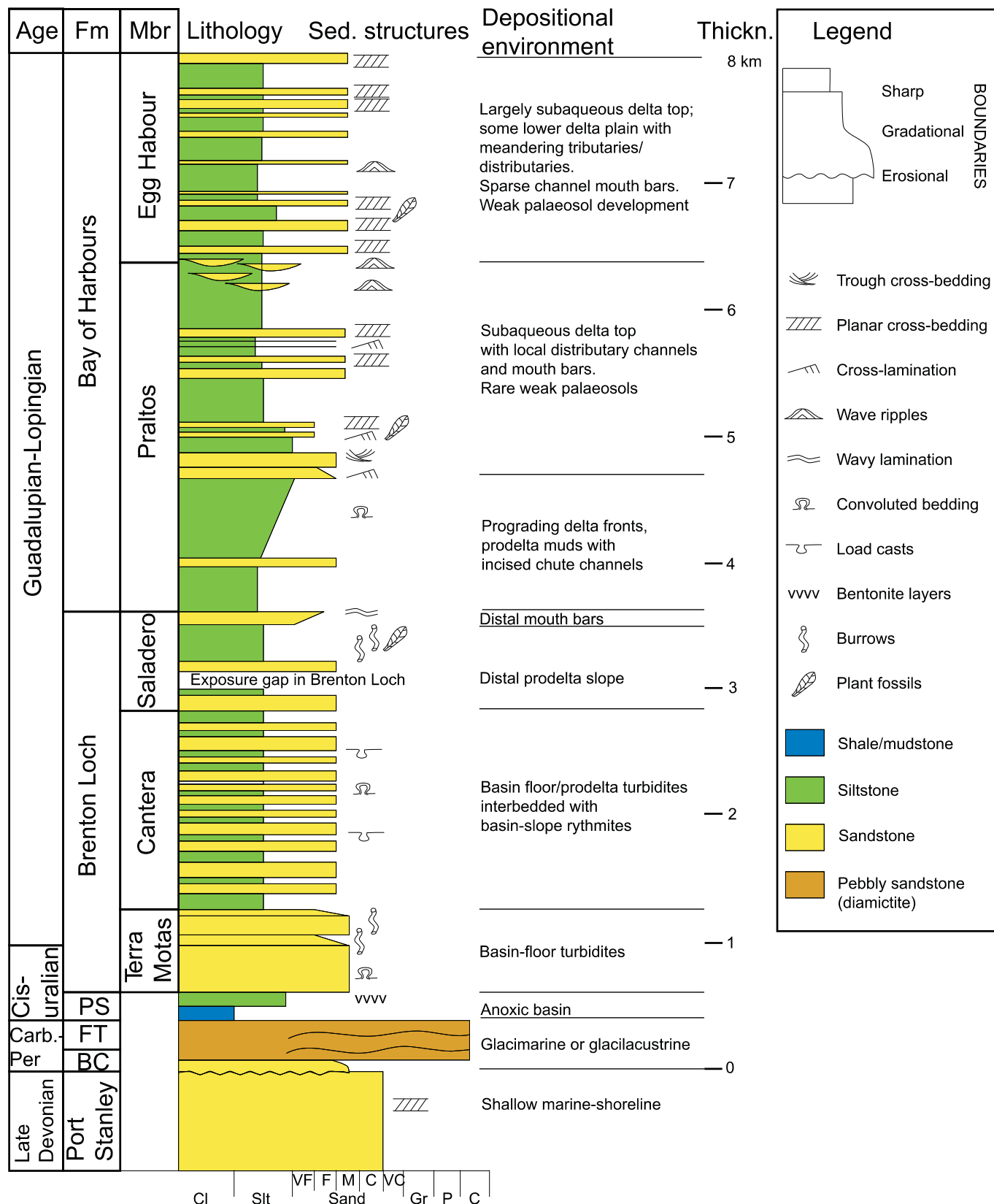


Figure 2. Simplified composite stratigraphic log of the Permian sedimentary succession on the Falkland (Malvinas) Islands (after Trewin *et al.*, 2002). C. = Carboniferous; G.-As. = Gzhelian-Asselian; A.-R. = Artinskian-Roadian; BC = Bluff Cove Formation; FT = Fitzroy Tillite; PS = Port Sussex Formation.

sphenopsid stems and glossopterid leaves occur in sandstones of the Brenton Loch Formation on the east coast of West Falkland (Isla Gran Malvina) (Scasso & Mendiola 1985), and Simões *et al.* (2012) illustrated *Glossopteris* leaves from the Saladero Member at Rorys Creek on East Falkland (Isla Soledad). Based on its stratigraphic position, the

unit has been inferred to be predominantly Guadalupian (middle Permian) in age (Simões *et al.* 2012).

The Bay of Harbours Formation has a gradational lower contact with the Brenton Loch Formation and consists primarily of coarse- to fine-grained sandstones, intercalated with siltstones and minor mudstones. The formation

is generally divided into the mudstone-dominated but coarsening-upward Praltos Member and an overlying succession of channel sandstones, intercalated massive sandstone–mudstone couplets, and sparse conglomerate beds constituting the Egg Harbour Member. The formation is interpreted to have been deposited in a mix of delta slope to lower delta plain environments from subaqueous to exposed floodplain settings with weak palaeosol development (Aldiss & Edwards 1999; Trewin *et al.* 2002). This formation represents the uppermost unit of the Permian succession in the onshore part of Falkland (Malvinas) Islands and is overlain only by minor Cenozoic deposits. Bioturbation is common in siltstones of the Bay of Harbours Formation, but discrete identifiable traces are sparse (Aldiss & Edwards 1999). Plant fossils are relatively common in this unit and the vast majority of Halle's Permian fossil plant specimens probably derive from this formation (see Materials and Methods). The age of the Bay of Harbours Formation is poorly resolved but has been considered Guadalupian–Lopingian based on its stratigraphic position and tentative correlations with the Karoo Basin (Trewin *et al.* 2002; this study).

MATERIALS AND METHODS

Over 300 specimens were examined in this study; all are registered in the collections of the Department of Palaeobiology at the Swedish Museum of Natural History (Naturhistoriska riksmuseet: prefixed NRM), Stockholm, under the numbers: NRM S047751–S047955 (all impression fossils); and S04005, S004024, S004034, S004038, S004040, S004042, S004047, S004048, and S081825 (thin sections of permineralized wood). When more than one *Glossopteris* leaf was present on a slab, a numerical epithet was assigned, e.g. S0047795–01. Halle (1911) collected plant impressions and permineralized woods from 13 principal localities and received, from local residents, some donations of fossils from unspecified sources. Placed in the context of current stratigraphic resolution of the Lafonia Group (Trewin *et al.* 2002; Stone 2016), we assign the lithostratigraphic sources of his sampled beds as follows:

1. Localities on east coast of Speedwell Island near Halfway Cove: Egg Harbour Member, Bay of Harbours Formation.
2. Southwest coast of Lafonia near Black Point (opposite Speedwell Island): Egg Harbour Member, Bay of Harbours Formation.
3. North Arm, Bay of Harbours: Praltos Member, Bay of Harbours Formation.
4. Dos Lomas, Kelp Harbour, west coast of East Falkland (Isla Soledad): Egg Harbour Member, Bay of Harbours Formation.
5. Orqueta Park area, c. 10 km west of Goose Green: Praltos Member, Bay of Harbours Formation.
6. Bodie Creek House area, c. 7 km southwest of Goose Green: Praltos Member, Bay of Harbours Formation.
7. Bodie Creek Inlet (both banks), c. 2 km south of Goose Green: either Saladero Member, Brenton Loch Formation or Praltos Member, Bay of Harbours Formation.
8. Darwin settlement area: either Saladero Member,

Brenton Loch Formation or Praltos Member, Bay of Harbours Formation.

9. East of Tranquilidad (ruins): probably Praltos Member, Bay of Harbours Formation, less likely Saladero Member, Brenton Loch Formation.
10. The Back Beach, Low Bay: Praltos Member, Bay of Harbours Formation.
11. Arrow Harbour (not indicated on Halle's map, but mentioned in his text): Saladero Member, Brenton Loch Formation.
12. Between Port Sussex and Cantera (not indicated on Halle's map, but mentioned in his text): Saladero Member, Brenton Loch Formation.
13. Seal Cove: Praltos Member, Bay of Harbours Formation.

Plant macrofossils were photographed using either a Canon EOS 40D digital camera or an Olympus SZX10 stereomicroscope equipped with a Sony Exmoor E3CMOS digital camera. In some cases, multiple photographs were taken at different focal planes and a composite image was obtained using the auto-stacking and alignment features available in Adobe Photoshop. ImageJ was used to measure *Glossopteris* leaves. Only leaves that showed minimal distortion, with a portion of medial lamina with midrib, leaf margin and a clear venation pattern visible, were included in the analysis. All leaves are preserved as impressions, and preservation is generally poor, with very few complete leaves, many leaves torn and distorted prior to and during preservation, and venation of highly variable quality. Descriptions focused on the medial portion of the leaves, as defined by Prevec (2011). This represents the largest section of the leaf (and is, therefore, most commonly preserved in fragmented leaves), and venation characteristics are most consistent in this region. In the base and apex, venation varies markedly over a short distance, making standardization of measurements, such as vein angle and mesh characteristics, more challenging to define. As per the schema used by Prevec (2011), three zones were delimited within each half of the medial portion of a leaf, to either side of the midrib: (1) proximal, for the region close to the midrib; (2) mid-laminar, for the region halfway between midrib and margin and (3) marginal, for the zone close to the leaf margin. Changes in leaf characters between these regions are key to the identification of morphospecies, and here the degree of change between vein angle and mesh width across the zones was quantified using two new size-independent ratios Change in Vein Angle (CVA) and Change in Mesh Width (CMW). CVA values define vein course. CVA1 represents the ratio of the angle between the midrib and the secondary veins at the midpoint of the lamina-half *versus* the equivalent angle at secondary vein emergence from the midrib. In other words, this ratio is a measure of the change in secondary vein angle from adjacent to the midrib to the mid-laminar region, as defined by Prevec (2011). CVA2 represents the ratio of the angle between the midrib and secondary veins at the leaf margin *versus* the equivalent angle at the midpoint of the lamina half. This quantifies the degree of curvature of the veins from the mid-laminar portion of the leaf to the

margin. These ratios, therefore, reflect the strength or degree of arching of the veins across the three leaf sectors of the lamina-half; a value of 1 reflects an absolutely straight vein path, and the higher the value, the sharper the curve. CMW values allow for rapid assessment of the change in mesh width across the lamina. CMW1 reflects the change in mesh width from those adjacent to the midrib to the mid-laminar part of the lamina-half, in other words the ratio of proximal mesh width to mid-laminar mesh width as defined by Prevec (2011). A value greater than 1 reflects a decrease in mesh width from those adjacent to the midrib to the mid-laminar region. Similarly, CMW2 reflects the change in mesh width from those in the mid-laminar region to those at the margin of the leaf.

The most readily preserved and consistently observable features were used in the comparative analysis, viz. leaf width, leaf shape, form and width of midrib, mesh shape and size across the lamina, venation course across the lamina, tangential angle of the venation adjacent to the midrib, in the mid-lamina, and at the margin, and marginal vein density. Where possible, size class of the leaf morphotypes has been allocated, as per the schemes of Raunkiaer (1934) and Webb (1959). The designation ‘n’ refers to the number of leaves assessed for any particular character, even though multiple measurements may have been taken per leaf; averages are of all measurements taken for a particular character, across multiple leaves.

Photo-micrographs of thin sections of fossil wood were taken using an Olympus BX51 microscope with an Olympus DP71 digital camera. Nine sets of thin-sections of fossil wood were identified in Halle’s collection at NRM (Table 2). Among these samples, S004040 was identified as the specimen described by Halle (1911) as *Dadoxylon* cf. *angustum*; specimen S081825 was identified as the first sample described by Halle (1911) as *Dadoxylon lafoniense*, with well-preserved pith and poorly preserved secondary xylem, and S004042 as the second specimen described by Halle (1911) as *Dadoxylon lafoniense*, lacking pith but with well-preserved secondary xylem. The six other samples are only alluded to in Halle’s contribution (1911). Museum labels provide locality information that is partly missing from Halle’s (1911) paper (see Table 2).

A key goal of this study is to clarify the definitions of the

wood taxa described by Halle as *Dadoxylon lafoniense* and *D. cf. angustum*, hence, we focused primarily on anatomical information relating to the secondary xylem. Wood descriptions follow the template proposed by Boura *et al.* (2021). Biogenic traces on leaves are attributed to the Damage Type (DT) categories of Labandeira *et al.* (2007) where possible.

Since the higher-level taxonomy of plants is in a state of flux, we organize the identified taxa only below order-level in the systematic section. Synonymy lists encompass only fossils previously illustrated from the Falkland (Malvinas) Islands. Some fossils were unidentifiable or could only be assigned to a genus; a full catalogue of the registered fossils and their geographic and stratigraphic sources is provided in Supplementary Table 1.

SYSTEMATIC PALAEOBOTANY

Order Equisetales

Genus *Paracalamites* Zalessky, 1932

Paracalamites sp., Fig. 3A–D, K, L

- 1906 *Phyllothea* sp.; Nathorst, pp. 74–76, pl. 7, figs 1–4.
- 1906 *Phyllothea* or *Schizoneura* sp.; Nathorst, p. 75, pl. 7, fig. 7.
- 1911 *Phyllothea australis* Brongniart; Halle, pp. 51–54, pl. 1, figs 12–16 (non figs 17–19).
- 1911 *Phyllothea* cf. *deliquescent* Goeppert; Halle, pp. 54–55, pl. 1, fig. 26 (non figs 21–25).
- 1923 Equisetaceous stems cf. *Phyllothea australis* Brongniart; Seward & Walton, pp. 318–319, text-fig. 2, pl. 19, figs 3, 4, 6, pl. 21, fig. 16.
- 1923 Equisetaceous stems cf. *Neocalamites carrerei* (Zeiller); Seward & Walton, pp. 319–321, text-fig. 3, pl. 20, figs 8, 10, 12.

Material. NRM S047751 (Fig. 3A), S047752a-01, S047752a-02 (Fig. 3K), S047752b, S047753 (Fig. 3B), S047754-03, S047756, S047757, S047758, S047760a, S047760b, S047761a, S047761b, S047767 (Fig. 3C, D), S047768, S047769, S047770, S047792a, S047792b, S047798, S047823, S047825, S047837, S047858, S047885, S047914, S047915, S047925, S047926, S047927, S047952-01 (Fig. 3L).

Description. Impressions of jointed axes, the largest exceeding 150 mm long and up to 20 mm wide (e.g. S047753, S047823), with longitudinal ribbing varying from pronounced (Fig. 3A) to indistinct (Fig. 3K), in almost every case crossing the nodes oppositely. Nodes thick, in some cases wider than internode width. Internodes generally longer than wide. Branching, where present, occurring from the node, where circular scars also indicate sporadic branch detachment.

Remarks. *Paracalamites* accommodates isolated, large, articulated, leafless sphenopsid stems and pith casts, differing from the similar northern hemisphere *Calamites* in that the ribs remain mostly opposite and do not alternate as they cross the node. As noted by Rigby (1966), multiple sphenopsid genera, such as *Phyllothea*, *Schizoneura* and *Raniganjia*, among others, produce stems of indistinguishable morphology, with generic attribution dependent on the morphology and arrangement of attached leaves. He suggested using the fossil-genus *Paracalamites* for leafless sphenopsid stems found widely

Table 2. Locality details for Permian fossil wood specimens (and associated thin sections) from the Falkland Islands studied by Halle (1911).

Specimens	Slides	Locality on label	Name on label	Material: figs in pl. 4 of Halle (1911)
S004005	3	Bodie Creek House	<i>Dadoxylon</i>	
S004024	3	Tranquilidad	<i>Dadoxylon</i>	
S004034	3	Tranquilidad	<i>Dadoxylon</i>	
S004038	3	Port Sussex	None	
S004040	3	Bodie Creek House	<i>D. cf. angustum</i>	8 and 9
S004042	3	Tranquilidad	<i>D. lafoniense</i>	5, 6 and 7
S004047	3	None stated	None	
S004048	3	None stated	None	
S081825	4	Arrow Harbour	<i>D. lafoniense</i>	1, 2, 3 and 4

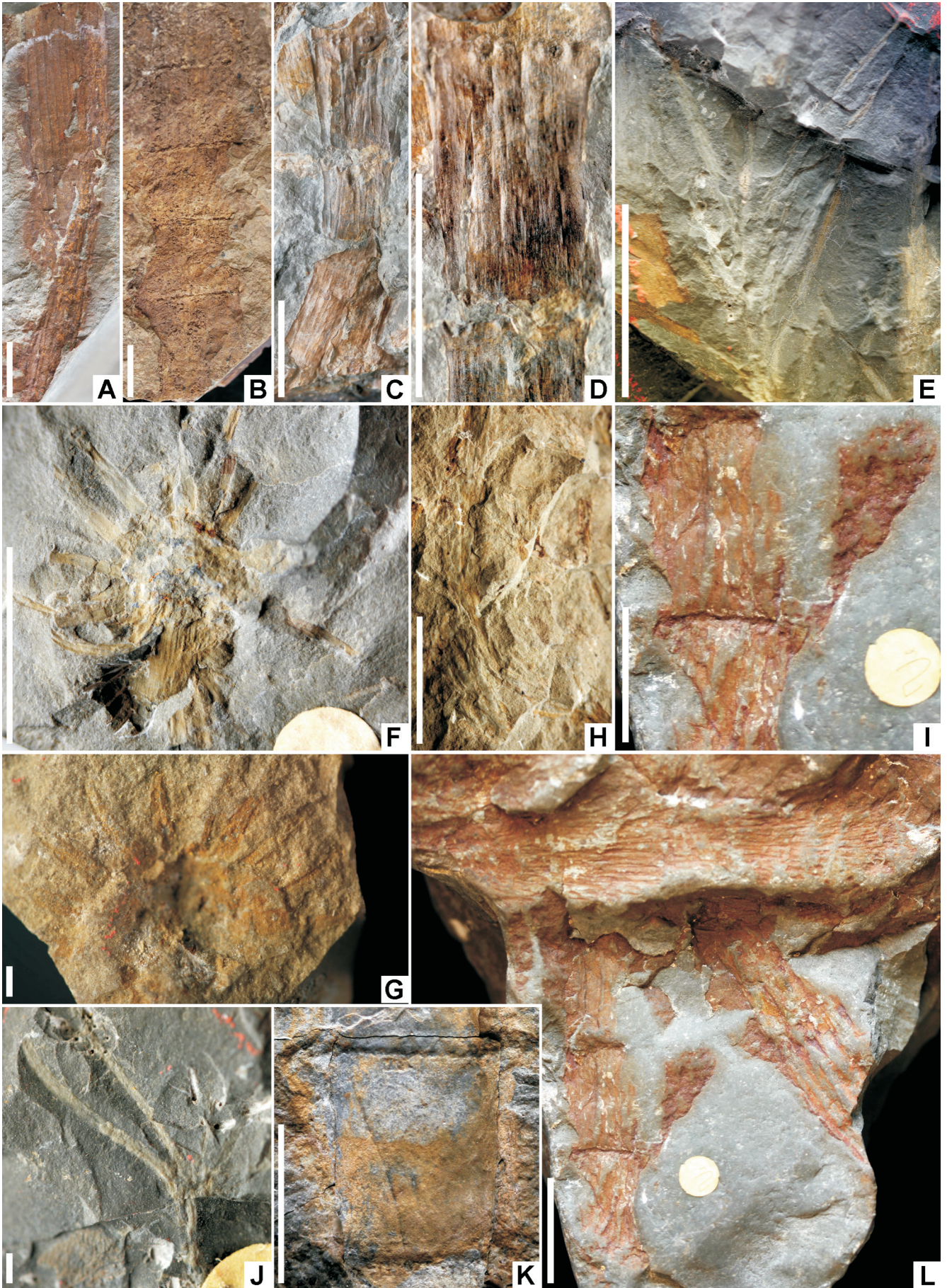


Figure 3. Permian sphenophytes from the Falkland (Malvinas) Islands. A–D, K, *Paracalamites* sp.; E, H, J, *Phyllothea deliquescens* (Göppert) Schmalhausen, 1879; F, G, *Phyllothea australis* Brongniart, 1828; I, L, possible strobilus attached to *Paracalamites* sp. All scale bars = 10 mm, except G and J (= 1 mm). A, S047751; B, S047753; C, D, S047767; E, S047776-01; F, S047754-01; G, S047771-02; H, S047932; I, L, S047952-01; J, S047776-02; K, S047752a-02.

across Gondwana in upper Paleozoic strata. Accordingly, Rigby (1966) erected *Paracalamites australis* and assigned to this species various specimens from the Falklands (Malvinas) that had been assigned to *Phyllothea australis* and *P. cf. deliquescens* by Halle (1911, pl. 1, figs 12–14 and 26, respectively).

We agree with Rigby's diagnosis of *Paracalamites* and, therefore, place all of the specimens represented by articulated leafless stems with (usually) opposite ribbing at the nodes under this taxon (Fig. 3A–D, K, L). However, as Rigby's diagnosis for *Paracalamites australis* indicated that branch tubercles were absent, we leave the specific assignation open, since several specimens from the Falklands (Malvinas) are poorly preserved and lack evidence of branching (e.g. S047792) or branch tubercles adjacent to the nodes (Fig. 3D).

Seward & Walton (1923) described plant material recovered from the Falklands (Malvinas) collected by H.A. Baker in 1922, among which were equisetaceous stems that differed from the others in their narrower, more crowded ribbing, and which they assigned to *cf. Neocalamites carrerei* (Zeiller) Halle, 1908. Given the variation in ribbing expression evident in axes within Halle's (1911) collection, we argue that these forms with slightly more dense ribbing are also better attributable to *Paracalamites*.

Possible strobilus attached to *Paracalamites* sp., Fig. 3I, L

Material. NMR S047952-01 (Fig. 3I, L)

Description. Articulated stems with ribs that are opposite across the node. One of the stems (Fig. 3L: marked with a yellow dot) incorporates three internodes 1.7 cm long and 0.8 cm wide; nodes wider than internode width, with circular marks indicating branch bases. A stalk 0.9 cm long and 0.2 cm wide bearing an oval structure, 1.1 cm long and 0.6 cm wide, emerges from one of the nodes, indicating the possible presence of a strobilus.

Remarks. Compared to the northern hemisphere, there are few records of sphenophytes with attached strobili in upper Paleozoic strata of Gondwana. Apart from a few reports of sphenophyllalean cones (Cúneo *et al.* 1993; Prevec *et al.* 2010, 2012; Cariglino & Prevec 2018), only strobili attributed to *Schizoneura gondwanensis* from the uppermost Permian of the Sydney Basin, Australia (Etheridge 1903), and *Neocalamites* sp. from the Permian La Golondrina Formation, Santa Cruz Province, Argentina (Escapa & Cúneo 2006), have been described to date. *Neocalamites* is typically employed for Mesozoic leafless ribbed, rarely branched axes, with continuous ribbing through the well-defined nodes, and linear leaves with acute apices and free bases. Such Mesozoic axes are otherwise indistinguishable from Permian *Paracalamites* (Brown 1977). Argentinean strobili affiliated with *Neocalamites* are stalked, compact, bractless and consist of peltate sporangiophores. Although the Falkland (Malvinas) specimen is too poorly preserved to resolve fine details, such as the leaves and sporangiophores, the presence of a stalked, apparently bractless strobilus, reveals similarities to *Neocalamites*. However, owing to the absence of leaves, the fragmentary nature, and poor preservational quality of this specimen, we provisionally retain this material

under *Paracalamites*, axes of which are abundant elsewhere in the same beds.

Genus *Phyllothea* Brongniart, 1828

Phyllothea australis Brongniart, 1828, Fig. 3F, G

1906 *Phyllothea* sp.; Nathorst, pp. 74–76, pl. 7, figs 5, 6.

1911 *Phyllothea australis* Brongniart; Halle, pp. 51–54, pl. 1, figs 17–19 (non figs 12–16).

Material. NMR S047754-01 (Fig. 3F), S047766, S047771-01 (Fig. 3G), S047771-02, S047772, S047773.

Description. Impressions of leaf-bearing stems or isolated leaf whorls. Largest axis (S047773) c. 70 mm long and 8 mm wide, incorporating five internodes of equal length (1.2 cm long); leaves c. 5 mm long emerging from the nodes. Isolated whorls incorporate 3–11 leaves (Fig. 3F, G), basally fused, with indistinct median vein and acute to slightly rounded apices (e.g. S047754-01, S047772).

Remarks. *Phyllothea* was established by Brongniart (1828) for upper Paleozoic plants resembling extant *Equisetum*. Brongniart noted that the articulated stems could be unbranched or monopodially branched, and grooves and ridges did not alternate through the nodes; leaves were basally fused into sheaths to varying degrees, but remained free for most of their extent, tapering distally.

Much later, Townrow (1955) emended Brongniart's diagnosis to include cuticle-bearing and fertile material, and described *P. australis*, the type species, in detail to better delimit and define the genus. Townrow (1955) defined *Phyllothea* as plants with stems up to 20 mm wide, bearing branches and leafy shoots. The leaves had a single, commonly indistinct midrib, and were basally fused in a sheath. The cuticle revealed epidermal cells and stomata similar to those of other equisetitaleans. The associated (but not attached) cones consisted of alternating whorls of sterile leaf-like bracts and sporangiophores, abaxially bearing from few to numerous sporangia. When referring specifically to *P. australis*, he stated there were 18–23 leaves per whorl, usually 20 (Townrow 1955), although numbers ranging from 8–33 have been mentioned by other authors for this species (Maheshwari 1967; Rayner 1992).

A very similar species, *P. indica* Bunbury 1861, has been an issue of discussion since many authors have argued that this species should be synonymized with *P. australis* (e.g. Seward, 1898; Du Toit 1932; Maheshwari 1967). Townrow (1955) also stated that the characters used to separate these species were probably inadequate; however, he regarded the slightly longer leaves in *P. indica* and the fact that they taper only very close to the apex as sufficient to distinguish them. We do not agree that these characters are adequately diagnostic or consistent and, therefore, also consider *P. indica* to be a junior synonym of *P. australis*.

Although no cuticle can be recovered from the Falkland (Malvinas) specimens, and there is no evidence of fertile structures closely associated with the leaf-bearing specimens, those sphenophytes from the Falklands (Malvinas) that have linear leaves with an indistinct median vein,

either borne on an axis or preserved in detached leaf whorls, are consistent in morphology with the widespread *P. australis*.

***Phyllothea deliquescens* (Göppert) Schmalhausen, 1879**
Fig. 3E, H, J

1911 *Phyllothea* cf. *deliquescens* Göppert; Halle, pp. 54–55, pl. 1, figs 21–25 (non fig. 26).

Material. NMR S047776-01 (Fig. 3E), S047776-02 (Fig. 3J), S047776-03, S047776-04, S047932 (Fig. 3H).

Description. Small, fragmentary articulated stems bearing c. 12–14 leaves per whorl (estimated from S047776-02). Leaves 8–11 mm long, 0.5 mm wide, fused at the base to form a funnel-shaped, 1-mm-long sheath; free segments longer than internode. Median vein visible (S047776-01).

Remarks. *Phyllothea deliquescens* is generally characterized by robust articulated stems, with well-defined ribs and whorls of branches, typically arising from the nodes. Leaf bases are fused to form a well-developed, funnel-shaped sheath, splitting into linear free segments with a median vein.

Although it was first described from Siberia, Townrow (1955) considered *P. deliquescens* to be part of the ‘australis group’, in which he grouped the southern hemisphere Permian species of *Phyllothea* commonly associated with *Glossopteris*. The main difference from *Phyllothea australis* is that the free, slender leaf segments radiating from the sheath of *P. deliquescens* are traversed by a more prominent median vein, and tend to be upwardly curved near their apex (Arber 1905; Halle 1911). We agree and consider these characters sufficiently robust to separate *P. deliquescens* from *P. australis*. The Falkland (Malvinas) specimens of *P. deliquescens* (Fig. 3E, H, J) also tend to have longer free parts of their leaves compared to *P. australis*. *Phyllothea lawleyensis* Anderson & Anderson also has strong similarities in its slender, univeined leaves united into a small basal cup, but the individual leaves on that species reach in excess of 35 mm long, and they are possibly associated with *Giridia*-like strobili (Anderson & Anderson 1985, pl. 41).

Order Glossopteridales (= Dictyopteridiales)

Genus *Glossopteris* Brongniart 1828 ex Brongniart 1831

General remarks on the classification of *Glossopteris*. Halle (1911) recognized four species of *Glossopteris* and one of *Gangamopteris* in the small collections he recovered from multiple fossil localities in the Falkland (Malvinas) Islands. We found that it is not possible to unequivocally assign the Falkland (Malvinas) glossopterid leaves to established species (particularly so where cuticular details are required for confident identification), hence we have described the various forms under eight informal morphotypes (MF), some of which are distinctive and easily differentiated, whereas others encompass a significant degree of variation. There is also some overlap in individual character ranges between morphotypes. The overlapping ranges of quantitative variables and subtle qualitative features used to distinguish morphotypes forms a data matrix that is difficult to represent graphi-

cally with any clarity. Additionally, we recognize that, given the small number of leaves considered here, it is impossible to capture the full range of morphological variation within a taxon. With more comprehensive sampling, it is possible that some of these morphotypes will constitute end-members of more broadly circumscribed species.

Sampling bias is also heightened in small collections, where collectors may specifically target specimens that have an unusual appearance, in an attempt to represent the greatest range of leaf morphotypes. Ironically, in the case of *Glossopteris*, this approach does not work towards accurate representation of diversity, as there is great difficulty in demarcating fossil-species within the morphological continua for which this group of plants is renowned. For example, it is possible that MF01 and MF02, distinguished primarily by the angle of the secondary venation to the midrib, lie on a morphological spectrum of a single species. But other morphotypes, such as MF05, are clearly distinct, even where based on a single leaf.

Large collections can assist greatly in recognizing morphological continua, contributing to a far more robust taxonomic framework. In the Falkland (Malvinas) collections, morphospecies MF03, MF05 and MF08 were represented by only single specimens. This, in combination with the overall poor quality of preservation of the leaves and the absence of attached or associated fertile organs, has limited the precision of our identifications and, consequently, our biostratigraphic interpretations. Further exploration of the islands, and collection of larger numbers of (better preserved) plants, within a more detailed stratigraphic and sedimentological context, is critical to better understand the palaeoenvironmental, biostratigraphic and biogeographic implications of these floras, and particularly how the Falklands (Malvinas) Block related to Argentina and southern Africa during the Permian.

Quantifying *Glossopteris* leaves at the level of detail presented here is vexatious and time-consuming, but a necessary step if this field of palaeobotany is to progress. Even if consensus is never reached on the names used for different fossil-species, detailed descriptions at least facilitate accurate comparisons of these plants across Gondwana. We compare the glossopterid leaf morphotypes described below, with fossil leaves documented primarily from southern Africa and Argentina – the two regions likely juxtaposed with the Falklands (Malvinas) Block during the Permian.

***Glossopteris* morphotype MF01, Fig. 4A–D; Suppl. Fig. 1D**

1911 *Glossopteris indica* Schimper; Halle, pl. 2, fig. 4, 4a.

1923 *Glossopteris browniana* Brongniart; Seward & Walton, p. 325, pl. 20, fig. 11.

1923 *Glossopteris indica* Schimper; Seward & Walton, pp. 321–322, pl. 21, figs 14, 15, 17.

Material. S047780 (identified by Halle as *Glossopteris indica* in NRM database: Fig. 4 A, B); S047867, S047840 (Fig. 4C, D; Suppl. Fig. 1D) (identified by Halle as *Glossopteris* sp.); S047953-1; S047953-2 (*G. sp. cf. G. browniana*).

Localities. Bodie Creek Head Site 1; Low Bay; Speedwell Island (southern point).

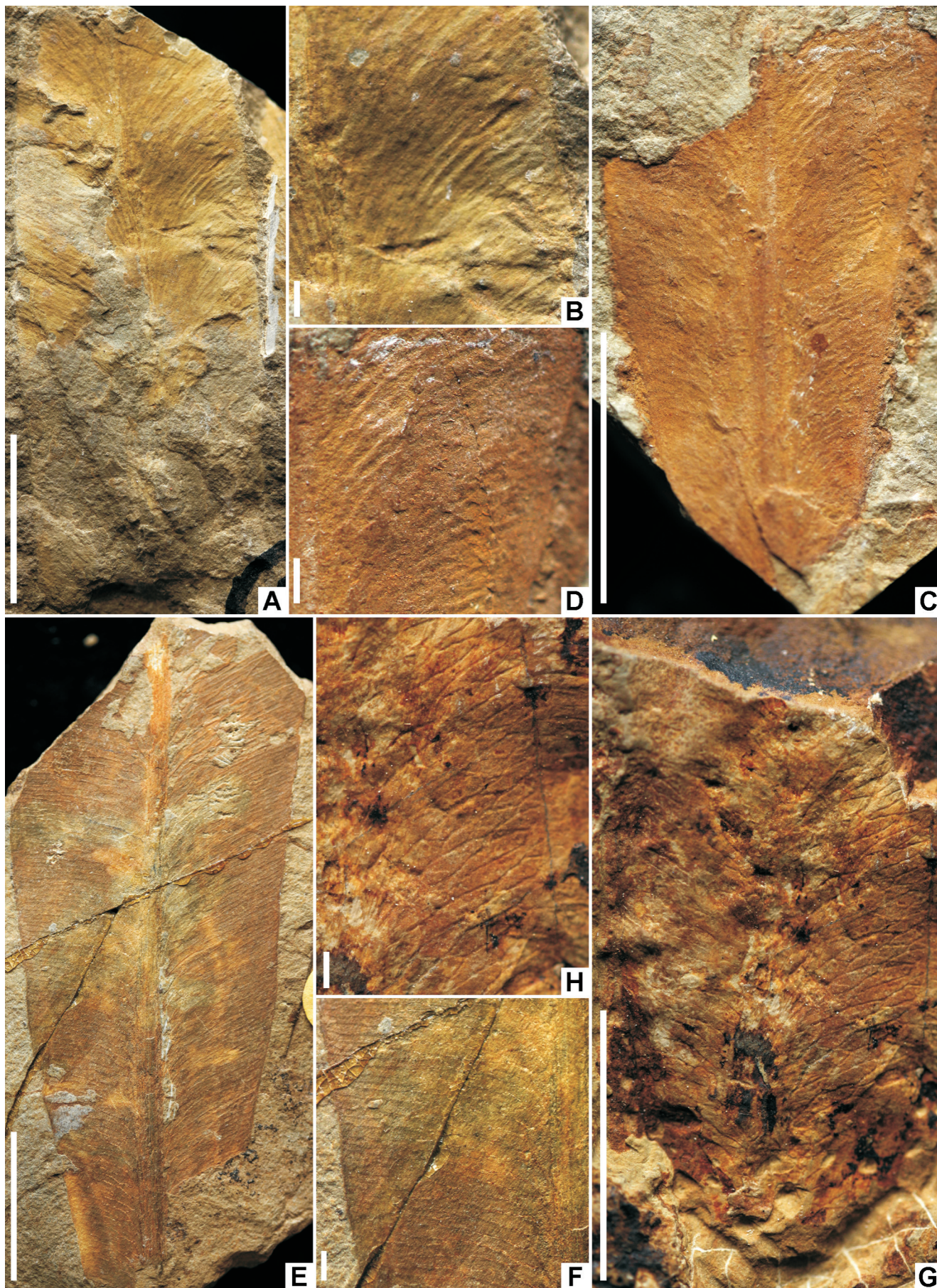


Figure 4. A, B, *Glossopteris* morphotype MF01; C–H, *Glossopteris* morphotype MF04. A, central portion of leaf; B, details of venation; S047780; C, proximal portion of leaf tentatively assigned to this taxon; D, details of venation S047840; E, central portion of leaf; F, details of venation showing relatively straight course of veins in outer lamina; S047775; G, central portion of relatively broad-meshed leaf; H, details of venation; S047835-01. Scale bars = 10 mm for A, C, E, G; 1 mm for B, D, F, H.

Description. Oblong to elongate-elliptical or lanceolate microphyll-sized leaves (Fig. 4A); estimated leaf area 810–1198 mm² ($n = 3$), with acute apex; 52 mm long ($n = 1$), 14–(15.8)–16.2 mm wide ($n = 4$). Midrib indistinct, weak parallel veins evident in some specimens, unknown if persistent to apex; medial width 0.38–(0.58)–0.88 mm ($n = 4$). In medial portion of leaf, lateral veins arise sub-parallel to midrib, arch across lamina at a narrow angle of 13.8°–(22.3°)–31.4° ($n = 4$), flexing slightly from proximal one third of lamina to 30°–(47.7°)–62.1° ($n = 4$), intercepting the margin at 48°–(57.4°)–66° ($n = 4$) to midrib (Fig. 4B; Suppl. Fig. 1D). In medial portion of leaf, veins anastomose 2–5 times and bifurcate 3–5 times from midrib to margin; meshes proximal to midrib are elongate-elliptical to elongate-trullate; becoming linear, elongate-polygonal to elongate-elliptical in mid-laminar region and towards the margin. Proximal mesh width is 0.28–(0.35)–0.42 mm ($n = 3$), becoming slightly broader in the mid-laminar region 0.39–(0.43)–0.56 ($n = 4$), narrowing again at margin 0.29–(0.35)–0.46 mm ($n = 4$). Marginal meshes are similar in width to proximal meshes, with marginal vein density of 12–(15.6)–18 veins per 5 mm ($n = 4$).

Remarks. Four leaves were identified and analysed. These are long, narrow microphyll-sized, with steeply angled, gently curving venation. The curvature from midrib to mid-lamina is sharper, with a CVA1 of 1.7–(2.3)–2.5 ($n = 4$), becoming gentler from mid-lamina to margin, with a CVA2 of 1–(1.3)–1.7 ($n = 4$). Meshes are narrow and elongate, of fairly consistent width across lamina, but broadening slightly in the mid-laminar region as reflected by a CMW1 of 0.73–(0.84)–0.91 ($n = 3$), and CMW2 of 1.04–(1.29)–1.63 ($n = 4$). The midrib is poorly defined.

Comparisons with South African and Argentinean leaves. Long, narrow *Glossopteris* leaves with subparallel margins, a midrib reaching the apex and gently arching secondary venation with fairly sparse anastomoses and elongate meshes are common in the middle to upper Permian of South Africa (Anderson & Anderson 1985; Bordy & Prevec 2008; Prevec *et al.* 2009, 2010; Botha *et al.* 2020) and Argentina (e.g. Menéndez 1966), and are strongly associated with various species of the ovuliferous fructification *Lidgettonia*. Those leaves most similar to MF01 include upper Permian examples from the Karoo Basin within the concept of '*Lidgettonia lidgettonioides*' proposed by Anderson & Anderson (1985, pl. 127, figs 1, 4, 6, p. 302, Mooi River; pl. 128, figs 13–14, p. 303, Bulwer), *Glossopteris loskopensis* (Anderson & Anderson 1985, pl. 132, p. 307, Loskop quarry); Clouston Farm morphotypes C2b, c (Prevec *et al.* 2009, pl. IV, figs 6–8; pl. VII, C2b, c); Wapadsberg Pass morphotypes WP1 and WP2 (Prevec *et al.* 2010; fig. 9, E–L, p. 399) and leaves figured from Kwa Yaya (Bordy & Prevec 2008; pl. II, figs D, G, H).

MF01 also has similarities with several leaves from older, probably middle Permian fossil assemblages, from Somkhele Mine (Bordy & Prevec 2008, pl. 3, fig. A, p. 450); Lawley ('*Lidgettonia lawleyensis*' leaves, Anderson & Anderson 1985, pl. 124, p. 299) and Hammanskraal ('*Ottokaria hammanskraalensis*' leaves of Anderson & Anderson

1985, pl. 60, fig. 9, p. 235; *Glossopteris leptoneura* of Kovács-Endrödy 1991, pl. 5.3, figs 1–4, pp. 24–26).

Specimens from the Bonete Formation that were assigned to *Glossopteris angustifolia* by Menéndez (1966, pl. 2, figs. 5–7; and previously by Harrington 1934) were described as long, narrow leaves with subparallel margins, a midrib reaching the apex and smoothly arched secondary venation, rarely anastomosing and forming elongated meshes. This description corresponds well with MF01 in its slightly curved secondary venation, as opposed to MF02, which has markedly straight venation.

MF01 also resembles some leaves attributed to *Glossopteris browniana* Brongniart from the Bonete Formation (i.e. FCEN 6501, 6510) and the Carapacha Formation (i.e. GHUNLPam 3134) (Menéndez 1966; Melchor & Césari 1997). These leaves have secondary veins that initiate almost parallel to the midrib then curve gently at c. 20°, to intercept the margin at c. 55°, with few anastomoses and forming fine, elongated meshes.

Of particular interest are some leaves formerly assigned to *G. indica* from the Bajo de Véliz, Arroyo Totoral, Tasa Cuna and the Rio Genoa formations, which were later reclassified as *Glossopteris wilsonii* (Seward) Archangelsky *et al.*, 1981 (Archangelsky *et al.* 1981; Césari 2014). *Glossopteris wilsonii* includes long, narrow leaves, with subparallel secondary venation, and very few (if any) anastomoses. In their revision, Archangelsky *et al.* (1981) proposed that *Glossopteris indica* leaves from South Africa, Antarctica and the Falklands (Malvinas) be transferred to *G. wilsonii*, including Halle's (1911, pl. 2, figs 4, 4a) specimen from the Bodie Creek Head site (S047780). We consider that a more rigorous morphometric analysis of the Argentinian and South African material is needed before the Falkland (Malvinas) specimens can be confidently attributed to this species.

***Glossopteris* morphotype MF02, Fig. 5A–J; Suppl. Fig. 1A, C**

1911 *Glossopteris indica* Schimper; Halle, pp. 56–58, pl. 2, fig. 3.

1911 *Glossopteris angustifolia* Brongniart; Halle, pp. 58–60, pl. 3, figs 1–4.

1923 *Glossopteris indica* Schimper; Seward & Walton, pp. 321–322, pl. 19, figs 5, 7, pl. 20, fig. 9.

Material. S047779-01 (Fig. 5C) S047877, S047894 (Fig. 5G, H; Suppl. Fig. 1A), S047950a, b (all identified by Halle as *Glossopteris indica* in NRM database); S047782-01, S047783-01, S047783-02, S047795 (Fig. 5I, J; Suppl. Fig. 1C), S047801 (Fig. 5A, D) (all identified by Halle as *G. angustifolia*); S047779-02, S047782-02, S047797-02, S047832, S047861-01 (Fig. 5B, F), S047870, S047902, S047907 (all identified by Halle as *Glossopteris* sp.); S047800 (Fig. 5E) (identified by Halle as *cf. Gangamopteris* sp.); S047862 (identified by Halle as *Glossopteris browniana*).

Localities. Bodie Creek/Bodie Creek Head Site 1; Speedwell Island Southern Point; between Darwin and Goose Green; Brenton Loch (Site 1); Speedwell Island (south of settlement); Low Bay; Darwin (south of Goose Green).

Description. Leaves oblong, elongate-elliptical, or elongate-lanceolate, of large microphyll size with estimated leaf area of 823–(1528)–2000 mm² ($n = 3$); 52 mm long

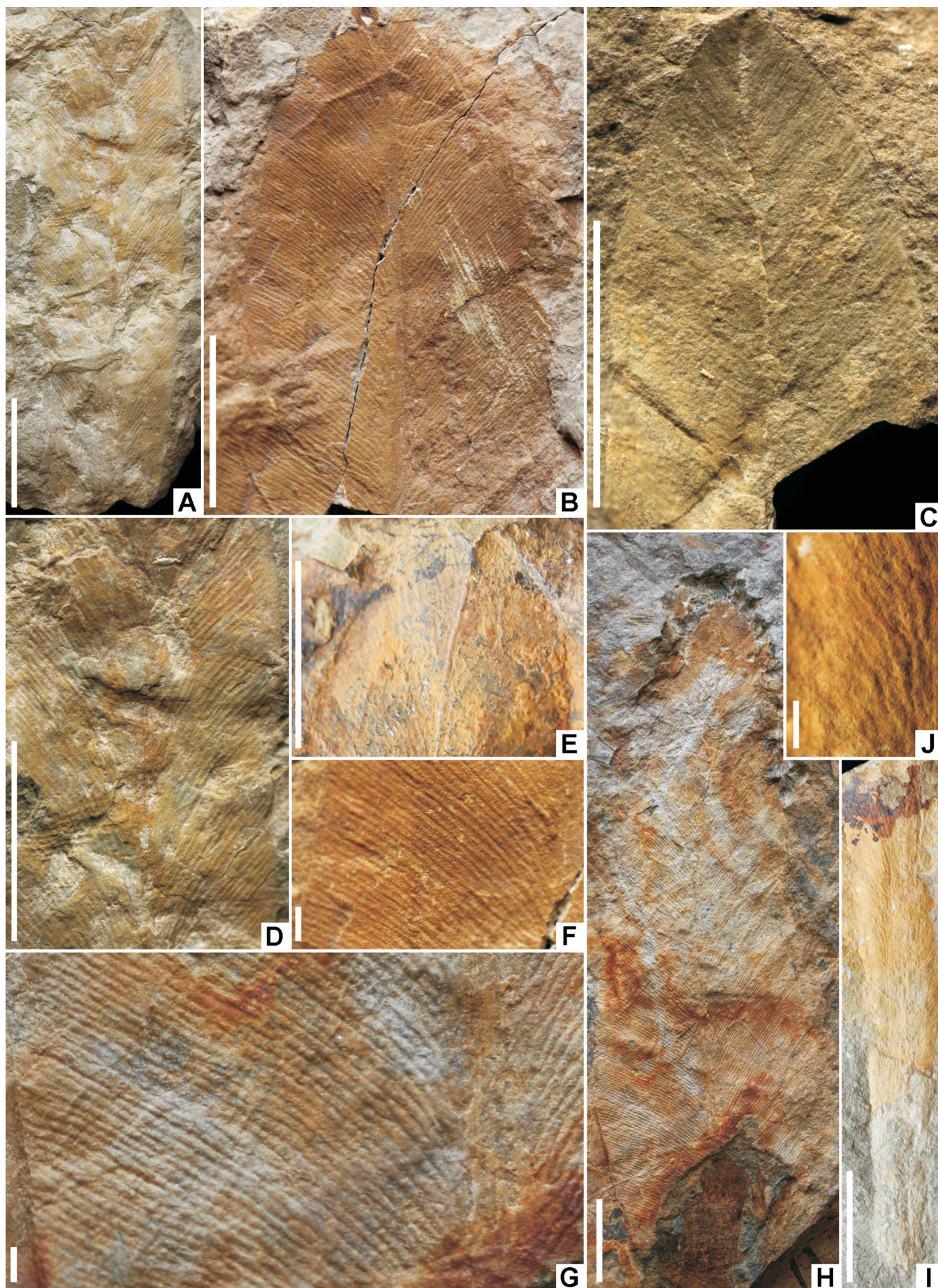


Figure 5. A–J, *Glossopteris* morphotype MF02. **A**, complete leaf; **D**, enlargement of venation; S047801. **B**, distal portion of leaf, **F**, details of venation; S047861-01; **C**, distal portion of leaf; S047779-01. **E**, distal portion of leaf with notched apex; S047800. **G**, details of venation; **H**, whole leaf; S047894; **I**, atypical narrow leaf; **J**, details of venation; S047795. Scale bars = 10 mm for A–E, H, I; 1 mm for F, G, J.

($n = 1$), 14–(15.8)–16.2 mm wide ($n = 4$) (Fig. 5A, H). Apex acute with rounded or pointed tip (Fig. 5B, C, H), base narrowly cuneate. Midrib well-defined but narrow, flat, becoming indistinct and very narrow apically (Fig. 5E); individual veins are visible in some specimens; width ranges from 1.2 mm at base ($n = 1$), 0.57–(0.89)–1.4 mm in medial part of leaf ($n = 9$), to 0.17–(0.4)–0.8 mm at apex ($n = 6$). In medial portion of leaf, lateral veins arise from midrib and traverse the lamina at a fairly constant angle between 27.6° and 60.4° (av. 41.3°) ($n = 10$), following a notably straight path to intersect the margin at 34.4°–(49.5°)–67.2° to the midrib ($n = 9$) (Fig. 5D, F, G; Suppl. Fig. 1A, C). In the medial portion of leaf, veins typically anastomose 3–4 times and bifurcate three times from midrib to margin; most meshes adjacent to midrib are strongly linear, but some are elongate-elliptical to narrowly trullate, becoming consistently and strongly linear in mid-laminal region and towards the margin. Proximal mesh width is 0.23–(0.37)–0.57 mm ($n = 10$), becoming progressively narrower across the mid-laminal region 0.19–(0.33)–0.47 mm ($n = 9$) to the margin 0.19–(0.26)–0.35 mm ($n = 10$). Marginal vein density variable, 14–(16.9)–21 mm per 5 mm of margin ($n = 10$).

Remarks. The ten measured leaves are distinguished by their long and narrow lamina with a narrow midrib that is well-defined in the basal and medial portions of the leaf, becoming less distinct apically. The venation is distinguished from other forms by curving slightly from midrib to mid-lamina with a CVA1 of 1.3–(1.9)–2 ($n = 9$), but is markedly straight from mid-lamina to margin, with a CVA2 of 1.1–(1.2)–1.7 ($n = 10$). This produces meshes that are narrow and of fairly consistent width across the lamina, with a CMW1 of 0.94–(1.18)–1.79 ($n = 10$), and a CMW2 of 1.01–(1.2)–1.48 ($n = 10$). A few leaves are especially slender (e.g. S047862) but they are here deemed to be variants (possibly early-season leaves) of MF02 based on their similar venation course. Leaf S047795 (Fig. 5I, J) is atypical, with a particularly broad, flat midrib, and disproportionately narrow lamina. MF01 and MF02 are very similar, and the latter may represent a morphological variant of the former. The main distinctions between the two, are the greater vein angles (on average) and more intense curvature of the veins from midrib to mid-lamina in MF01, and the more prominent midrib in MF02.

Comparison with South African and Argentinean leaves. Leaves from several South African upper Permian floras figured by Anderson & Anderson (1985), resemble MF02, including some placed within '*Lidgettonia africana*' (their pl. 114, p. 289; Lidgetton), '*L. mooiriverensis*' (pl. 117, figs 8–11, p. 292, pl. 118, p. 293, Mooi River), '*L. lidgettonioides*' (pl. 126, figs 10, 11–13, p. 301, Mooi River; pl. 130, figs 1, 4, p. 305, Bergville), although these leaves are larger than MF02 and are elongate-obovate. Leaves associated with '*L. inhluzanensis*' of Anderson & Anderson (1985; pl. 120, p. 295, Inhluzani; pl. 121, figs 18–31, p. 296, Bulwer; pl. 122, figs 15–17, p. 297, Loskop quarry) are also similar, but the venation in MF02 is denser, and the leaves larger. The anomalous leaf in Fig. 5I, J, is somewhat reminiscent of the glossopterid ovuliferous fructification *Dictyopteridium flabellatum* known from the upper Permian of

South Africa (Anderson & Anderson 1985). This species of seed-bearing organ has a very high length to width ratio, and is particularly leaf-like in appearance, with prominent and steeply inclined venation visible across both the seed-bearing and opposing surfaces. The specimen figured here is, unfortunately, too poorly preserved to make a conclusive identification, although some of the tubercle-like features present on the surface of the organ are reminiscent of seed scars. Prevec *et al.* (2022, p. 7, fig. 4g,) figured undescribed leaves from the middle Permian flora at the Onder Karoo locality that bear a close resemblance to MF02. These narrowly oblanceolate leaves have a well-defined midrib and linear venation following a steep, straight path across the lamina, and may be conspecific with the Falklands (Malvinas) specimens.

Although much larger than MF02, some long, slender leaves from the (probably late middle to early late Permian) Lawley flora have a similar venation pattern (e.g. '*Arberia allweyensis*' leaf figured by Anderson & Anderson 1985, pl. 110, fig. 3, p. 285). Similar leaves from the lower Permian, include those placed within the concept of '*Hirsutum dutoitides*' proposed by Anderson & Anderson (1985) (a fructification now assigned to *Gladiopomum dutoitides*; Adendorff *et al.* 2002), from Vereeniging. These leaves are generally larger than those of MF02, and have a more pronounced midrib, particularly in the proximal parts of the leaf, but they share the very narrowly lanceolate shape and the fine venation that follows a very steep, straight path from midrib to margin (e.g. Anderson & Anderson 1985, pl. 75, figs 1–6, 14, p. 250, pl. 76, p. 251; Adendorff *et al.* 2002, p. 6, figs 3–5).

Almost straight, linear secondary venation is evident in a fragmentary leaf attributed to *Glossopteris decipiens* Feistmantel from the Bonete Formation (i.e. BA-PB 3504); however, the angle at which the secondary veins depart from the midrib is steeper (c. 10–15°), and the midrib is not well-defined (Menéndez 1966). Straight secondary venation is also evident in a *Glossopteris argentina* Archangelsky leaf, figured from the Carapacha Formation (GHUNLPam 3130; Melchor & Césari 1997), but this is the only specimen with secondary venation similar to MF02. Other specimens assigned to *G. argentina* (Melchor & Césari 1997, fig. 9.1–7) have more curved secondary venation, similar to the type specimens from the La Golondrina Formation (Archangelsky 1958).

***Glossopteris* morphotype MF03**, Fig. 6F, G; Suppl. Fig. 1F

Material. S047799 (identified by Halle as *cf. Gangamopteris* sp. in the NRM database).

Locality. Bodie Creek Head Site 1.

Description. Leaf incomplete, but probably oblong to elongate-elliptical, of large microphyll size; at least 23 mm wide (Fig. 6F). Midrib narrow, poorly preserved, details not distinct, medial width 1.26 mm. The meshes in the first row adjacent to the midrib are oriented at a steep angle to midrib 12.5°–(15.4°)–18.9° ($n = 1$); veins curve slightly to mid-lamina 23.3°–(27.2°)–29.9° ($n = 1$), and follow a straight course to the margin at 26.8°–(27.4°)–27.7° to the midrib ($n = 1$) (Fig. 6G; Suppl. Fig. 1F). In the median part of the leaf, veins anastomose and bifurcate multiple times

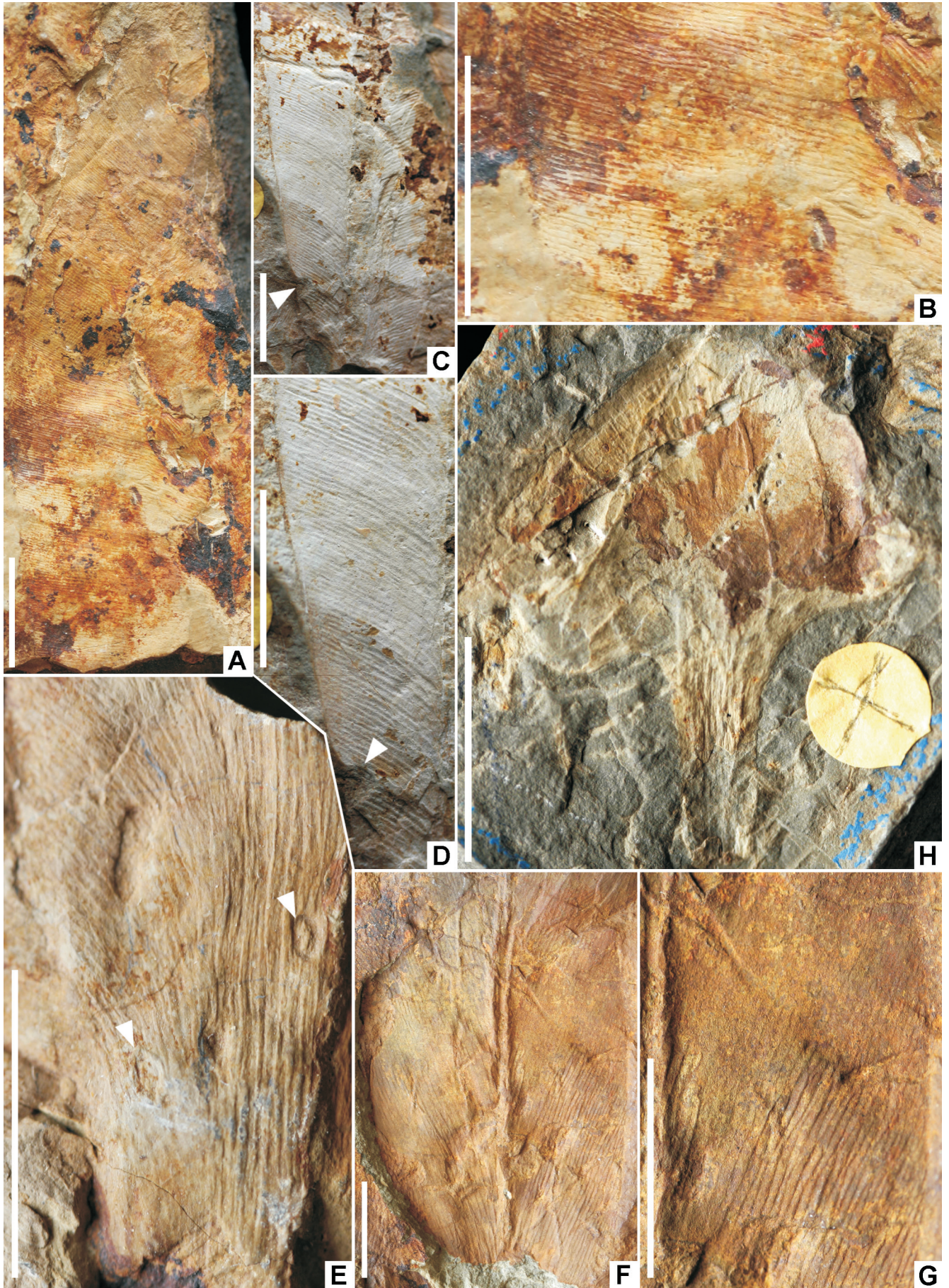


Figure 6. A–D, *Glossopteris* morphotype MF07; E, *Glossopteris* morphotype MF08; F, G, *Glossopteris* morphotype MF03; A, half lamina; B, details of venation; S047835-02. C, proximal lamina; D, details of venation and simple scalloped margin-feeding damage (arrowed); S047777-01. E, proximal portion of lamina with prominent midrib and elliptical oviposition scars (arrowed); S047785. F, central portion of lamina; G, details of venation; S047799. H, glossopterid scale leaf (cf. *Eretmonia* sp.) showing details of petiole and triangular lamina; S047786. All scale bars = 10 mm.

across the lamina, forming an elongate-trullate row of meshes proximally, becoming linear, elongate-polygonal to elongate-elliptical in the mid-laminar region, and parallel towards the margin. Proximal mesh widths are 0.25–(0.26)–0.27 mm ($n = 1$), becoming slightly narrower in mid-laminar region 0.15–(0.2)–0.27 mm ($n = 1$) and near the margins 0.13–(0.14)–0.15 ($n = 1$), with a marginal vein density of 10 veins per 5 mm ($n = 1$), reflecting the strongly oblique angle of vein intersection with the margin.

Remarks. One medial to sub-medial portion of a leaf corresponding to this morphotype was identified in the collection. This large microphyll-classed leaf is characterized by venation that is steeply inclined with veins intersecting the margin at a narrowly oblique angle. Veins are distinctive in curving slightly after leaving the midrib, with a CVA1 of 1.8, but then following a straight path to the margin (CVA2 of 1). The vein angle also decreases towards the apex, which is unusual, since vein angle is generally consistent in the medial portion of glossopterid leaves, with a decrease in angle only occurring close to the apex, converging on the leaf tip.

Comparison with South African and Argentinean leaves. This leaf fragment is reminiscent of *Palaeovittaria* with its very steeply angled veins that follow an unusually straight path across the lamina, e.g. *Palaeovittaria kurtzii* from Vereeniging (Anderson & Anderson 1985, p. 229, pl. 54, figs 4, 6, 7, 9). Further, the venation appears to radiate slightly from the base of the specimen, a feature typical of this taxon. However, upon close inspection, the veins in MF03 anastomose regularly, the meshes are elongate-elliptical to linear, and the midrib appears to have been disrupted/distorted, which might account for the peculiar decrease in vein angle away from the base.

A poorly preserved leaf on the underside of slab BA-PB 7708 from the Bonete Formation (Menéndez 1966, unfigured; B.C. pers. obs.) has notably low-angled secondary venation emerging from a poorly defined midrib, and follows a straight path to the margin, in a similar manner to that of MF03. This is the only example of a leaf similar to morphotype MF03 recognized in the Argentinean fossil floras.

Glossopteris morphotype MF04, Fig. 4E–H; Suppl. Fig. 1G, J

1911 *Glossopteris browniana* Brongniart; Halle, pp. 55–56, pl. 1, fig. 28, 28a, pl. 1, fig. 27. (non pl. 1, fig. 29)

1923 *Glossopteris indica* Schimper; Seward & Walton, pp. 321–322, pl. 21, fig. 18.

2012 *Glossopteris* sp. cf. *G. communis* Feistmantel; Simões *et al.*, p. 544, fig. 4A, B.

Material. S047775 (Fig. 4E, F; Suppl. Fig. 1G), S047781-01, S047835-01 (Fig. 4G, H; Suppl. Fig. 1J), S047836-01 (all identified by Halle as *Glossopteris browniana* in NRM database), S047838, S047884-01 (identified by Halle as *Glossopteris* sp.).

Localities. Darwin Harbour Site 1; Dos Lomos Site 1; North Arm Site 1.

Description. Large microphyll-class leaf (Fig. 4C, E, G), 12.4–(18.25)–24 mm wide ($n = 4$), oblanceolate, oblong or obovate, with cuneate base, apex acute. Midrib well defined, flat, with individual veins visible in some cases,

persistent to apex; basal width 1.6 mm ($n = 1$), medial width 0.6–(0.81)–1.24 mm ($n = 5$), narrowing to 0.36 mm ($n = 1$). First row of meshes adjacent to midrib broader and at a steep (narrow–moderate) angle to midrib 20.3°–(36.1°)–58.5° ($n = 4$), veins arching strongly in second row of meshes, with medial meshes at a wider angle 61.6°–(64.4°)–69.4° ($n = 4$), curving gently to follow an almost straight path at 63.1°–(71.3°)–80.1° ($n = 3$) to margin (Fig. 4D, F, H; Suppl. Figs 1G, J). In the medial portion of the leaf, veins anastomose and bifurcate 3–4 times ($n = 4$) across lamina; first row of meshes rhombic, trullate, polygonal, broadly falcate, with a width of 0.5–(0.61)–0.74 mm ($n = 3$) becoming falcate, trullate to linear in second row, with medial meshes becoming elliptical, to linear, 0.37–(0.55)–0.8 ($n = 6$), and becoming progressively narrower towards margin 0.25–(0.4)–0.72 ($n = 5$). Marginal meshes similar in shape to mid-laminar meshes, with a marginal vein density of 9–(15)–19 veins per 5 mm ($n = 5$).

Remarks. Six leaves were identified and analysed. This large microphyll-class leaf type is distinguished by a well-defined midrib from base to apex, with veins arising from the midrib at a narrow angle, then arching (CVA1 of 1.5–(1.9)–2.4, $n = 4$) and following an almost straight path to the margin (CVA2 of 1–(1.1)–1.2, $n = 3$) at a moderate angle. Mesh widths decrease consistently across the lamina from midrib to margin at (CMW1 of 1.09–(1.33)–1.71, $n = 3$; CMW2 of 1.12–(1.33)–1.74, $n = 5$), but the first few rows of meshes adjacent to the midrib are shorter and more angular in shape, becoming more elongate-elliptical to elongate-polygonal across the midlamina and towards the margin.

There is a large range in leaf size, and in mesh width (and consequently in marginal vein density) in this morphotype, but these do not appear to be correlated – the two largest leaves fall at opposing ends of the spectra for both vein density and mesh size. The meshes of MF04 are less linear in appearance than in MF01 and MF02, the leaf is shorter and broader. These leaves are smaller than those of MF07, and the venation is more consistent (with broader areolae) across the lamina.

Comparison with South African and Argentinean leaves. Halle (1911) placed these leaves in *G. browniana*. Of all glossopterid leaf species, this is possibly the most misrepresented in the literature. The type material of *G. browniana* derives from the upper Permian Newcastle Coal Measures in the Sydney Basin (Rigby *et al.* 1980), and the species is widely represented in the Sydney-Gunnedah-Bowen foreland basin complex of eastern Australia (McLoughlin 1994a), but beyond this province, its recognition is equivocal. This species is commonly used as a catchall for leaves with no particularly outstanding diagnostic features, and could be called the ‘wastebasket’ of glossopterid taxonomy, a sentiment shared by Kovács-Endrödy (1991, p. 32). The general concept for this species is: a leaf that is oblanceolate, of small to medium size, with venation arising at a narrow angle and curving gently across the lamina to intersect the margin at a moderate angle; meshes are generally slightly broader near the midrib, polygonal to elongate-trullate, becoming more

elongate-polygonal to elongate-elliptical across the lamina, retaining a linear pattern and there is no dramatic decrease in mesh width towards the margin. In this broad sense of '*G. browniana*', MF04 accords well. However, Rigby *et al.* (1980), in a study of topotype material, noted that this species is defined by very few (<3) anastomoses across the lamina in contrast to >3 in MF04. Moreover, Australian upper Permian examples (including the neotype) of *G. browniana* have vein marginal angles of 40–50° (Rigby *et al.* 1980; McLoughlin 1994a), i.e. much less than the >60° evident in the Falkland (Malvinas) specimens.

The fragmentary nature of the studied specimens means that we do not have a full appreciation of the size and shape of these leaves. Although they would fall within the upper size ranges, they nevertheless bear a strong resemblance to some of the South African upper Permian leaves linked to *Lidgettonia* species by Anderson & Anderson (1985). For example, among the leaves grouped under '*L. lidgettonioides*', are forms in which the venation pattern is very similar to that evident in MF04 (e.g. their p. 301, pl. 126, figs 4–6, from Mooi River).

Kovács-Endrödy (1991, pp. 33–34, pl. 5.6, figs 3–6) figured several diminutive leaves from Hammanskraal, Karoo Basin outlier, that she attributed to *G. browniana*. These have very similar venation to MF04 and might be conspecific pending a reappraisal of the taxonomy of that leaf assemblage. Leaves associated with, or attached to, *Scutum leslii* fructifications from Vereeniging, South Africa (Anderson & Anderson 1985, p. 242, pl. 67, figs 22–23; p. 243, pl. 68; Prevec 2011, p. 11, figs 24–26, p. 14, figs 44–47) are also similar, although the meshes in these forms are generally narrower than in MF04, and the leaves are much larger.

Despite the wide variation in shape and size that characterizes *Glossopteris browniana* leaves, the well-defined polygonal meshes separate it from other species. Notably, when compared to the Falklands (Malvinas) fossils, some Bonete Formation (Argentina) fossil leaves show strong similarities with MF04 (S047884-01, not figured by Halle 1911), and specimens attributed to *G. browniana* by Halle (1911, pl. 1, figs 27–28), particularly in the angle of secondary vein departure from the midrib, ranging from acute to almost perpendicular in some cases, distinguishing them from similar leaves with elongate-polygonal meshes across the lamina. The Falklands (Malvinas) specimens, however, differ slightly in that the relatively broader elongate-polygonal to elongate-elliptical meshes continue to the margins in some cases (e.g. S047835-01 [Fig. 4G, H], S047781-01), whereas in leaves attributed to '*G. browniana*' from the Bonete Formation, the meshes tend to reduce in width and become more elongate. A similar pattern is evident in leaves assigned to '*G. browniana*' from the La Golondrina Formation (Archangelsky 1958; Cariglino 2011).

In specimen GHUNLPam 3243 from the Carapacha Formation (Argentina), assigned to *Glossopteris tortuosa* Zeiller, the meshes in the row adjacent to the midrib are polygonal to trapezoid, and arise from a thick, well-defined midrib (Melchor & Césari 1997, fig. 6.5). This

species, however, differs from MF04 in that the secondary veins emerge almost perpendicular to the midrib with little curvature towards the margin, and the meshes retain constant width across the lamina. The length-width ratio of the meshes is also considerably smaller than in MF04.

***Glossopteris* morphotype MF05**, Fig. 7A–C; Suppl. Fig. 1I
1911 *Glossopteris damudica* Feistmantel; Halle, pp. 60–61, pl. 3, figs 5–7.

Material. S047784.

Localities. Dos Lomas Site 1.

Description. Large microphyll to small mesophyll-class leaf, probably elongate-elliptical (Fig. 7A), with a width of 34.8 ($n = 1$); base and apex unknown. Midrib narrow but well defined, individual veins not resolved; observed width of 0.84 mm ($n = 1$). Secondary veins arise from midrib at very wide angle 51.4°–(71.1°)–81.3° ($n = 1$), and abruptly curve to run almost perpendicular to midrib 80.6°–(83.7°)–86.1° ($n = 1$) following an almost straight course to intersect the margin at 82.3°–(85.6°)–89.1° ($n = 1$) (Fig. 7B, C; Suppl. Fig. 1I). In medial portion of leaf, meshes adjacent to midrib are broadly triangular, 0.46–(0.54)–0.6 mm wide ($n = 1$), becoming strongly linear, narrowly elongate-elliptical, 0.26–(0.29)–0.36 mm wide ($n = 1$) in mid-lamina, and progressively narrowing towards margin 0.12–(0.18)–0.22 mm ($n = 1$), with a marginal vein density of 15–(26)–27 veins per 5 mm ($n = 1$).

Remarks. This morphotype is represented by only a single leaf yet it is possibly the most distinctive form in the collections. It is relatively large (large microphyll/small mesophyll-class), with secondary venation following a straight course to the margin (CVA1: 1.2, $n = 1$; CVA2: 1, $n = 1$) at a very large angle (virtually perpendicular) to the midrib. Meshes are also distinctive in being polygonal and broad in the row adjacent to the midrib, but becoming abruptly more linear to narrowly elliptical, and steadily decreasing in width across the lamina (CMW1: 1.84, $n = 1$; CMW2: 1.67, $n = 1$). Among other leaf types in the collection, it is most similar to MF07, but the vein angle in the latter is at a lesser angle, and the meshes are broader.

Comparison with South African and Argentinean leaves. Among South African fossil leaves, MF05 is strongly reminiscent of forms from Hammanskraal described by Kovács-Endrödy (1991, pp. 48–49, pl. 5.11, figs 7, 9) as *Glossopteris divergens* and (p. 65, pl. 5.15, fig. 7) *Glossopteris* cf. *damudica*. The Falklands (Malvinas) specimen (34.8 cm wide) is slightly smaller than the Hammanskraal leaves (c. 5 cm wide), but is much smaller than the very large *G.* cf. *damudica* leaves (c. 14 cm wide) from Lawley figured by Anderson & Anderson (1985, pl. 135, figs 1–3, pl. 136, figs 1–2). The latter leaves have veins that form several polygonal meshes at a low angle to the midrib, and then recurve at a very broad angle across the lamina to the margin. This recurved venation pattern was not observed in MF05, but it is otherwise similar. Other leaves figured by Anderson & Anderson (1985, pl. 100, figs 5–7), from the Cedara locality, are larger than M05 but have similar venation. Lacey *et al.* (1975, p. 371, NM 1775b) figured one small section of leaf from Mooi River (Normandien Formation), which they compared to *G. damudica* Feistmantel, with

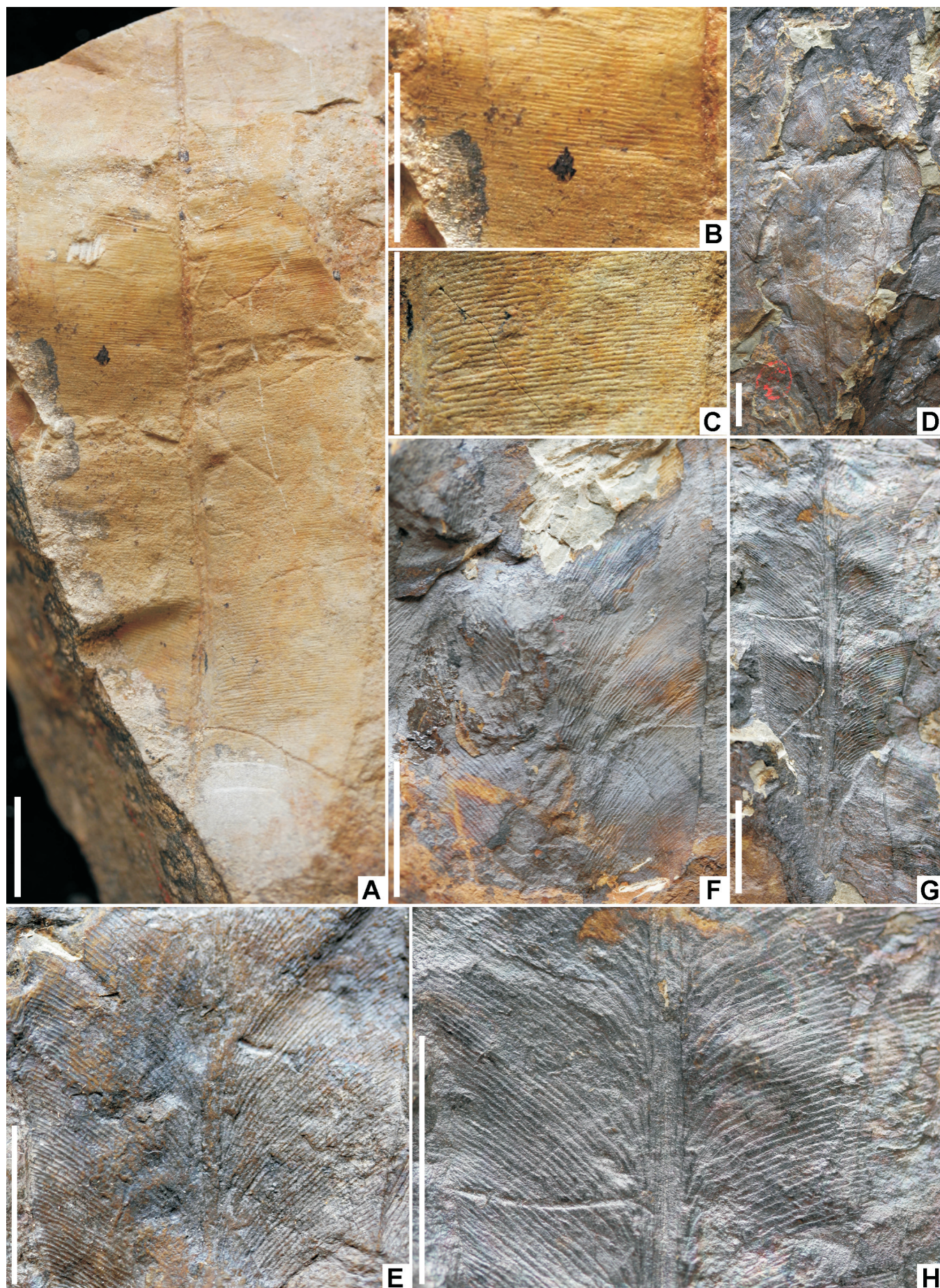


Figure 7. A–C, *Glossopteris* morphotype MF05; S047784; A, large leaf with secondary venation almost perpendicular to the midrib; B, C, details of venation. D–H, *Glossopteris* morphotype MF06. D, elliptical leaf; E, details of venation; S04778a-01; F, central portion of leaf showing dense venation; S047872-01-02. G, obovate leaf; H, details of dense venation; S04778b-02. All scale bars = 10 mm.

venation perpendicular to the midrib, including the first row of meshes adjacent to the midrib. Meshes in this leaf then appear to become narrower and more elongate-elliptical away from the midrib. This fragment is within the size range, and closely similar in morphology to M05 and might be conspecific.

Leaves similar to MF05 with a narrow but well-defined midrib and secondary veins arising almost perpendicular to the midrib, following a straight, (sub)parallel course to the margin, and forming narrow, linear meshes have been described from the Carapacha Formation of Argentina and were assigned to *Glossopteris damudica* (Melchor & Césari 1997). The latter species has also been confirmed from the La Golondrina Formation (Archangelsky 1958; Cariglino 2011). Both of these leaves are very similar to MF05 and might indicate a *Glossopteris* species shared between South Africa, the Falklands (Malvinas) and Argentina.

***Glossopteris* morphotype MF06**, Fig. 7D–H; Suppl. Fig. 1B

Material. S047778a-01 (Fig. 7D, E; Suppl. Fig. 1B), S047778a-02, S047778b-02 (Fig. 7G, H) (all identified by Halle as *Glossopteris indica* in NRM database), S047872-01-02 (Fig. 7F; identified by Halle as *Glossopteris browniana* in NRM database).

Localities. Low Bay.

Description. Leaves lanceolate to oblanceolate, microphyll-class, 100 mm long ($n = 1$), 22.89–25.39 mm wide ($n = 2$), with estimated leaf area of 1781.2 mm² ($n = 1$), apex acute and base cuneate (Fig. 7D, E, G). Midrib narrow, well-defined in basal and medial portion of leaf, persistent to apex; basal width up to 1.43 mm ($n = 2$), medial width 0.78–(0.99)–1.19 mm ($n = 3$) tapering to 0.65–0.31 mm ($n = 2$) near apex; individual veins weakly defined, depending on preservational quality. Secondary veins arise from midrib at steep (low) to moderate angle of 21.9°–(28.9°)–39.8° ($n = 2$), arch gently to mid-lamina where they follow an almost straight path at 54.6°–(62.7°)–70.6° ($n = 2$) across the lamina, intersecting the margin at 65.3°–(72.1°)–78.6° ($n = 2$) (Fig. 7E, H; Suppl. Fig. 1B). Veins anastomose 3–4 times and bifurcate four times from midrib to margin in medial part of leaf; meshes adjacent to midrib are elongate-trullate, polygonal to triangular, 0.27–(0.41)–0.72 mm wide ($n = 3$), becoming strongly linear and elongate-elliptical across mid-lamina 0.29–(0.33)–0.38 mm ($n = 3$), becoming narrower progressively towards margin 0.17–(0.22)–0.27 mm ($n = 3$), with a marginal vein density of 18–(20)–22 veins per 5 mm ($n = 3$).

Remarks. Leaves attributed to this morphotype are in the large microphyll size-class with an acute apex and a narrow, well-defined midrib. This morphotype is distinguished by the secondary veins emerging at a narrow to moderate angle from the midrib, initially arching strongly with a CVA1 of 2.2 ($n = 2$) into the mid-lamina, then following an almost straight path to the margin, with a CVA2 of 1.2 ($n = 2$). The meshes in the first few rows adjacent to the midrib are slightly broader, but then mesh size decreases gradually into the mid-laminar region with a CMW1 of 0.95–(1.23)–1.69 ($n = 3$), and then decreasing more intensely towards the margin with a CMW2 of

1.40–(1.53)–1.78 ($n = 3$). Marginal vein density is high. The relatively straight path of the venation in some specimens of this morphotype is reminiscent of MF07 but the vein angles are much steeper (lower), and the venation more gently curved and denser in the former. The prominent midrib and leaf shape of MF06, which appears to be oblanceolate with a sharply cuneate base, separates it from MF01 and MF02, which are narrower, more linear leaves.

Comparison with South African and Argentinean leaves. This form of *Glossopteris* has generalized features and is potentially common in South African floras, depending on how the morphotypes are categorized. Some of the leaves attributed to various ‘*Arberia*’ associations by Anderson & Anderson (1985) have similar shape and venation, although they are all much larger, e.g. ‘*A. madagascariensis*’ from Hammanskraal (their pp. 280–281 pl. 105, figs 1, 2; pl. 106, figs 1–4); ‘*A. leeuukuilensis*’ from Vereeniging (their p. 283, pl. 108); ‘*A. allweyensis*’ from Lawley (their p. 285, pl. 110, figs 1–3). There are also similarities in venation between MF06 and some leaf taxa attributed to the ‘*Lidgettonia*’ associations of Anderson & Anderson (1985), e.g. ‘*Lidgettonia africana*’ from Lidgetton (their p. 289, pl. 114, figs 3–10); ‘*Lidgettonia mooiriverensis*’ from Mooi River (their pp. 292–293, pls 117–118), also figured by Lacey *et al.* (1975) and attributed to *G. indica* (p. 366, NM 1774). Leaves figured by Anderson & Anderson (1985, pl. 142, figs 1–4) from Zwartskraal and included within their concept of *Glossopteris symmetrifolia*, are larger than MF06, but have very similar venation.

Among the leaf forms represented in Argentina and the Falklands (Malvinas), Menéndez (1966) found close similarities between his *Glossopteris indica* and those described by Halle (1911, pl. 2) and here attributed to MF06, although he stated that in some, the secondary veins tended to follow a straighter course than those from the Bonete Formation. Menéndez (1966) also regarded specimens that Seward & Walton (1923, pl. XX, fig. 9, pl. XIX, fig. 7) attributed to *G. indica* from the islands also coincided with his view. Based on the morphotypes proposed herein, the Bonete Formation *G. indica* shares an oblanceolate to lanceolate shape, a well-defined midrib that is persistent to the apex, and secondary venation with few meshes, curving slightly across the lamina to reach the leaf margin at 50–70°.

Glossopteris indica described from the La Golondrina Formation could also be conspecific with material assigned to MF06, based on the presence of a well-defined persistent midrib, and secondary venation that moderately arches away from the midrib, taking a straight path to the margin at c. 60–70°, and forming long, narrow, parallel meshes (Archangelsky 1958).

***Glossopteris* morphotype MF07**, Fig. 6A–D;

Suppl. Fig. 1E, H

1911 *Glossopteris indica* Schimper; Halle, pp. 56–58, pl. 2, fig. 1, pl. 2, fig. 6, 6a.

1923 *cf. Glossopteris indica* var. *wilsoni* Seward; Seward & Walton, p. 322, pl. 21, fig. 13.

Material. S047777-01 (Fig. 6C, D; Suppl. Fig. 1E),

S047781-02, S047811, S047835-02 (Fig. 6A, B; Suppl. Fig. 1H) (all identified by Halle as *Glossopteris indica* in NRM database).

Localities. Dos Lomos Site 1; Speedwell Island Site 2; Bodie Creek Head Site 1.

Description. Leaf large, mesophyll-class, probably elongate-lanceolate with a width of 30–43 mm (Fig. 6A, C); base narrowly cuneate, truncated/sessile. Midrib wide (>3.2 mm) and prominent in leaf base, becoming narrow (0.67 mm) but well-defined in medial part of leaf; individual veins distinct. In medial portion of leaf, veins depart from midrib at a moderate angle 47.3° –(48.9°)– 50.7° ($n = 1$), curve immediately to follow a straight path across lamina at 73.5° –(74.3°)– 74.8° ($n = 1$) to intersect margin at 73.9° –(74.6°)– 75.6° ($n = 1$) (Fig. 6B, D; Suppl. Fig. 1E, H); venation very linear in pattern, first two rows of meshes markedly broader, then decreasing gradually in width across lamina to margin. In medial portion of leaf, veins anastomose and bifurcate four times from midrib to margin, forming meshes that are falcate, triangular and elongate-polygonal, 0.37 –(0.54)– 0.75 ($n = 2$) mm wide, adjacent to midrib, gradually narrowing to 0.3 –(0.4)– 0.5 ($n = 2$) in mid-lamina, and becoming abruptly and strongly linear or narrowly elongate-elliptical, 0.14 –(0.23)– 0.3 mm wide ($n = 1$) towards margin. Marginal vein density of 21 veins per 5 mm.

Remarks. Four incomplete leaves were identified and two of the larger fragments were analysed. This relatively large leaf (small mesophyll-size class) is also distinguished by its prominent midrib, and broader, triangular/polygonal meshes adjacent to the midrib, and the abrupt curvature of the venation from these proximal meshes (CVA1: 1.5, $n = 1$), forming strongly linear meshes that follow a straight path at a moderate angle (CVA2: 1, $n = 1$) to the margin. Meshes are longer near the midrib and in the mid-lamina, than evident in MF05, and the vein angle is slightly steeper (lesser). MF07 differs from MF04, in being much larger, and there is a greater decrease in mesh width from midrib to margin in the former.

Comparison with South African and Argentinean leaves. There are similarities between MF07 and leaves from the South African Hammanskraal flora assigned by Anderson & Anderson (1985) to '*Hirsutum leslii*' (pp. 257–258, pl. 82–83), some attached to *Elatra leslii* fructifications. Kovács-Endrödy (1991 p. 64, pl. 5.15, fig. 6) assigned these leaves to *Glossopteris taeniopteroides*. Both the Falkland (Malvinas) and South African forms are linear, very elongate-obovate leaves with a long, cuneate base, although some of the Hammanskraal leaves have an expanded base associated with attached *E. leslii* fructifications. The midrib is very prominent, particularly at the base. Both MF07 and leaves assigned by Kovács-Endrödy (1991) to *G. taeniopteroides* have very linear venation with slightly broader, trullate meshes near the midrib, becoming finer towards the margin and crossing the lamina at a wide angle to the midrib. Lacey *et al.* (1975; NM1761, p. 371) figured a leaf with similar venation, but possibly a more broadly lanceolate lamina, that they compared with *G. ampla*. As in MF07, the venation is steeply angled at the midrib, curves fairly sharply and then crosses the

lamina on a straight path to the margin, the linear meshes becoming progressively narrower.

A characteristically strong, thick midrib has been observed in very few leaves from the Permian of Argentina. Specimen GHUNLPam 3224 from the Carapacha Formation (Melchor & Césari 1997, fig. 4.9) is characterized by a 3-mm-wide midrib with secondary veins forming long, linear meshes throughout the lamina, reaching the margin at *c.* 50° . The leaf was assigned to *Glossopteris browniana*, but it is very similar to MF07. Another specimen with a thick midrib and also previously assigned to *G. browniana*, is BA-PB 13832 from the La Golondrina Formation (Cariglino & Gutiérrez 2011). This specimen in particular, closely resembles S047777-01 (Halle 1911, pl. 2, fig. 1) in the moderate arching of the secondary veins near the midrib and the linear, straight path to the margin, forming few, elongated meshes.

***Glossopteris* morphotype MF08, Fig. 6E**

1911 *Gangamopteris cyclopteroides* var *major* Feistmantel; Halle, pp. 61–62, pl. 3, figs 8, 9.

Material. S047785 (Fig. 6E).

Localities. Dos Lomos Site 1.

Description. Relatively large mesophyll-class leaf, leaf base broadly cuneate, truncated at width of 8 mm; proximal margins of lamina diverge at a moderate angle to form broad leaf (>40 mm wide). Midrib very broad and flat basally, 4.7 mm wide; individual veins anastomose and bifurcate (Fig. 6E). In basal portion of leaf, secondary veins run parallel to midrib, depart at a very narrow angle of 10.3 – 17° ($n = 1$), arch strongly and consistently across mid-lamina to 38.5° –(42.5°)– 47.3° ($n = 1$), before curving more gently to intersect margin at 52° –(54.8°)– 58° ($n = 1$) to the midrib. In medial portion of leaf, meshes adjacent to midrib are elliptical, falcate to linear and 0.3 –(0.34)– 0.38 mm wide ($n = 1$), becoming more linear and narrowly elongate-elliptical across the lamina, narrowing slightly towards the mid-lamina to 0.28 –(0.31)– 0.34 mm wide ($n = 1$), then remaining consistent with a width of 0.27 –(0.3)– 0.32 mm ($n = 1$) at margin. Marginal vein density is 17 veins per 5 mm ($n = 1$).

Remarks. Only the lowermost medial portion of a single leaf base, with one half torn and distorted, is present in the collection. Experience has shown that leaf bases tend to have convergent or conservative morphology across glossopterid species that are otherwise quite distinct. Hence, the available features alone are not reliable for species recognition. However, this leaf base is clearly distinct from other morphotypes available in Halle's collection. The shape of the base, extremely broad midrib incorporating clearly anastomosing and bifurcating veins, the venation that arches strongly from midrib to mid-lamina, with a CVA1 of 3.1, flattening slightly from the mid-lamina towards the margin with a CVA2 of 1.3, are all distinctive features of this morphotype.

Glossopterid scale leaf: cf. *Eretmonia* sp., Fig. 6H

1911 Scale-frond of *Glossopteris* sp. (?) Halle, p. 62, pl. 3, fig. 10.

Material. S047786.

Locality. Dos Lomas Site 1.

Description. Bract consisting of a 10-mm-long robust (6-mm-wide) petiole and 13-mm-long, 20-mm-wide rounded triangular lamina (Fig. 6H). Margin entire. Petiole containing multiple dense reticulate veins. Lamina lacking an obvious midrib, veins indistinct, reticulate, forming elongate-polygonal to elliptical meshes typically 2 mm long and 0.4 mm wide. Veins in mid-lamina departing from midline at 30°–40° then passing relatively straight to margin.

Remarks and comparison. Bracts of this type are fairly common in Permian strata across Gondwana and are generally assigned to *Eretmonia* where a pair of sporangiophores is inserted on the midline. No sporangiophores were detected on the Falkland (Malvinas) specimen, but these may have detached before burial. The specimen from the Falklands (Malvinas) is similar in size and shape to microsporophylls of *Lidgettonia inluzanensis* Anderson & Anderson 1985 (otherwise referable to *Eretmonia* du Toit 1932) from the Lopingian Normandien Formation of the northeastern Karoo Basin, although examples of the latter tend to have slightly more pointed apices.

Order Cordaitales

Genus *Noeggerathiopsis* Feistmantel, 1879

Noeggerathiopsis sp., Fig. 8A–K

1911 *Desmiophyllum* sp.; Halle, pp. 63–64, pl. 4, figs 1–7.

Material. NRM S047789 (Fig. 8A), S047790 (Fig. 8B, G), S047910 (Fig. 8C, H), S047911 (Fig. 8D, I), S047914 (Fig. 8E, J), S047930-02, S047934-01 (Fig. 8E, K), S047935.

Description. Oblanceolate to linear leaves (possibly falcate in one case), up to 107 mm long and 11 mm wide (possibly reaching 18 mm in one case); margin entire, apex rounded, base narrowly tapered (Fig. 8A–C); venation parallel to slightly divergent proximally, slightly convergent distally; c. 10 veins or grooves per 5 mm across the mid-region of leaf (Fig. 8D–F).

Remarks. Halle (1911) assigned these leaves to *Desmiophyllum*, a heterogeneous fossil-genus of parallel-veined, strap-shaped leaves, normally recognized from Mesozoic strata and possibly having czekanowskialeen, ginkgoaleen or pinaleen affinities (van Konijnenburg-van Cittert *et al.* 2019). However, *Desmiophyllum* tends to be represented by leaves that are more slender (narrowly linear) with numerous interveinal striae (Miller & Hickey 2010; van Konijnenburg-van Cittert *et al.* 2019). We consider the Falklands (Malvinas) examples to be of cordaitaleen affinity, given the wide distribution of morphologically similar parallel-veined oblanceolate leaves in Permian strata across Gondwana (Pant & Verma 1965; Rigby *et al.* 1980).

The type specimen of *Noeggerathiopsis hislopianii* (Bunbury) Feistmantel, 1879 (the type of the genus) lacks cuticle and is difficult to differentiate from species of the predominantly northern hemisphere *Cordaites* Unger, 1850 on macro-morphological grounds. On this basis, several researchers have proposed that all such cordaitaleen leaves should be assigned to *Cordaites* (Meyen 1969; Maheshwari & Meyen 1975; Rigby *et al.* 1980). However, both cuticular and

anatomical studies of Gondwanan cordaitaleen leaves show them to differ significantly from northern hemisphere *Cordaites* (Pant & Verma 1965; McLoughlin & Drinnan 1996; Degani-Schmidt & Guerra-Sommer 2019). Consequently, Rigby (1984) erected *Pantophyllum* for Gondwanan cordaitaleen leaves retaining cuticular details but this name has generally not been used by later workers and *Noeggerathiopsis* continues to be employed, collectively, for impressions, cuticle-bearing compressions, and petrifications (Pant & Verma 1964; McLoughlin & Drinnan 1996; Srivastava & Tewari 2004).

Noeggerathiopsis leaves vary in their micromorphology, hence Pant & Verma (1965) erected *N. bunburyana*, *N. papillosa* and *N. fibrosa*, and Lele & Maithy (1964) established *N. indica*, *N. gondwanensis* and *N. zeilleri* for leaves with a gross form equivalent to the type species, *N. hislopianii* (Bunbury) Feistmantel, 1879, but having distinctive suites of cuticular characters. In some cases, the differences are very subtle and several or all of these species may be synonyms (Srivastava & Tewari 2004). Further, *Cordaites dumanii* was erected by Chandra & Srivastava (1991) for *Noeggerathiopsis*-type leaves with major veins separated by apparent minor veins. However, the latter features probably represent stomatiferous grooves that, typically, are indistinct on impressions, but have been well-characterized in permineralized specimens (McLoughlin & Drinnan 1996).

Leaf form is variable within individual populations of *Noeggerathiopsis* leaves. Even within a single cluster of attached leaves, lamina shape and dimensions can vary significantly as part of a seasonal growth series (Etheridge 1918). Leaves from the Falkland (Malvinas) Islands lack preserved cuticle, and the preservational quality is insufficient to resolve whether the linear features on the leaf represent veins or interveinal stomatiferous grooves in most cases (Fig. 8D–K). Some leaves appear to have a wrinkled texture that might be the result of desiccation before burial (Fig. 8H, I). The linear features dichotomize in one case (Fig. 8I), but in other cases appear to initiate between adjacent lineations (Fig. 8J), hence these features probably represent a combination of both veins and stomatiferous grooves. Owing to their indistinct features, we can not definitively assign these leaves to any established species, although we note close similarities to the narrowly oblanceolate, densely veined leaves of *Cordaites* (= *Noeggerathiopsis*) *dumanii* from the Karharbari Formation (upper Cisuralian) of India (Chandra & Srivastava 1991) and *Noeggerathiopsis elongata* from the Vryheid Formation (Artinskian) of the northeast Karoo Basin, South Africa (Anderson & Anderson 1985). The two slightly stronger veins in the long, tapering base of S047790, are also strongly reminiscent of *Sphenobaiera eccanensis* Anderson & Anderson from Vereeniging, Karoo Basin (Anderson & Anderson 1985, p. 323). That South African species also possesses apparent stomatiferous grooves between veins, lacks lamina divisions typical of *Sphenobaiera*, and might better be placed in *Noeggerathiopsis*. The very gently tapered base of the Falkland (Malvinas) specimens and their slightly convergent venation in the distal portion of the lamina is also similar to that of

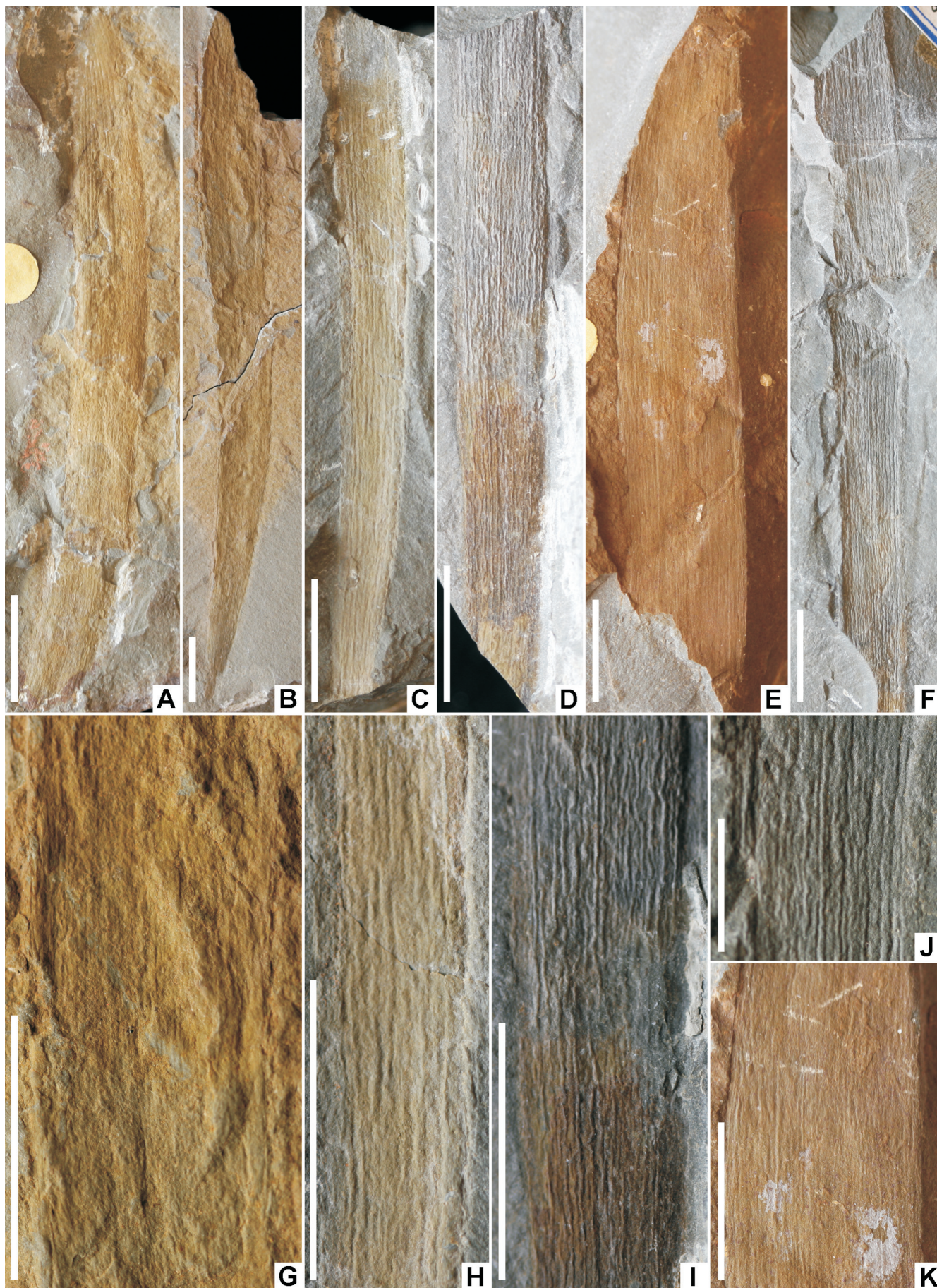


Figure 8. *Noeggerathiopsis* sp. (Cordaitales) leaves. A–F, leaves showing gently tapered base with slightly divergent venation, rounded apex with slightly convergent venation, and entire margins. G–K, enlargements of leaf mid-regions showing the variable prominence of sparsely dichotomizing veins and interveinal ridges and wrinkles. A, S047789; B, G, S047790; C, H, S047910; D, I, S047911; E, K, S047934-01; F, J, S047914. All scale bars = 10 mm except for J (= 5 mm).

Metreophyllum lerouxii Anderson & Anderson, 1985 from the Vryheid Formation of South Africa except that the vein density of the Falkland (Malvinas) specimens is greater than in *N. elongata* and *M. lerouxii*.

Order Buriadiales

Family uncertain

Genus *Brasiliocladus* Yoshida (in Bernades de Oliveira & Yoshida 1982)

Brasiliocladus* sp. cf. *B. acicularis Yoshida (in Bernades de Oliveira & Yoshida 1982), Fig. 9A–F

1911 Coniferous branches Halle, p. 63, pl. 3, figs 11–15.

Material. S047754-02 (Fig. 9C), S047787 (Fig. 9A, B), S047921 (two specimens), S047924 (listed as *Phyllothea australis* on museum labels by Halle 1911).

Localities. Speedwell Island (Site 1); Speedwell Island (north of settlement); Black Point (Site 1).

Description. Fragments of leaf-bearing axes, sparsely branched, up to 38 mm long, 0.5 mm wide (Fig. 9A). Leaves attached at variable orientations (10–70°) to axis, linear, straight, univeined, typically 3–5 mm but rarely up to 8 mm long, and 0.5 mm wide, with blunt to pointed apices and broadly clasping bases (Fig. 9B–F). Leaves inserted in apparent helical arrangement (Fig. 9C).

Remarks. Several of the specimens illustrated by Halle (1911, pl. 3, figs 11–15) are not readily recognizable in the collections and it appears that the lithograph illustrations of the conifers prepared for his publication include some degree of artistic license. The short, spirally arranged, stiff, spine-like leaves of these fossils suggest affiliation with the voltzialean conifers. Fossils of this group are widely distributed but are relatively uncommon in Permian strata of Gondwana. Nevertheless, multiple genera have been established and some (e.g. *Walkomiella*) can be distinguished from the Falkland (Malvinas) specimens based on their triangular to rhombic foliage (White 1981). Others (e.g. *Paranocladus*, *Ugartecladus* and *Ferugliocladus*) generally have narrowly ovate to triangular leaves, in many cases appressed to the axis, and are typically differentiated on cuticular or reproductive characters (Fittipaldi & Rösler 1978; Bernades de Oliveira & Yoshida 1982; Archangelsky & Cúneo 1987; Ricardi-Branco *et al.* 2013; Mune *et al.* 2016) that, unfortunately, are not available for the Falkland (Malvinas) specimens. Leaves of *Buriadia* differ in being polymorphic, incorporating forms with bifid and multifid apices (Pant & Nautiyal 1967; Ricardi-Branco *et al.* 2013; Serbet *et al.* 2010). *Searsolia* differs by both its bifid leaf tips and decussate leaf arrangement (Pant & Bhatnagar 1975). *Krauselcladus* has robust needle-like leaves, some of which have bifid apices (Fantón *et al.* 2006). *Coricladus* is characterized by well-spaced, high-angled, small, univeined leaves with acute apices (Jasper *et al.* 2005). The Falkland (Malvinas) specimens are most similar to *Brasiliocladus acicularis* Yoshida described from the Rio Bonito Formation (?Sakmarian–Roadian) of Brazil, based on the acutely orientated, univeined, needle-like, <12-mm-long, homomorphic leaves, lacking bifid apices

(Yoshida 1968; Bernades de Oliveira & Yoshida 1982), although the Brazilian specimens tend to have slightly denser leaf helices. The Falkland (Malvinas) specimens are also notably similar in their stout, straight, broad-based, spinose leaves to the leafy twigs assigned to *Cyparissidium* sp. A. from the Vryheid Formation (Artinskian) of the Karoo Basin by Anderson & Anderson (1985).

Incertae sedis

Dispersed seed, Fig. 9G

Material. NRM S047884-02, possibly an additional specimen on S047948.

Localities. North Arm (Site 1).

Description. A single seed (S047884-02: Fig. 9G) has a damaged transversely elliptical central body 4.5 mm long and 5.5 mm wide, flanked by marginal wings that are 2 mm in maximum width, extending slightly beyond the central body to have lengths of 5.5 mm, and which are contracted at the chalazal and micropylar ends. The seed is otherwise featureless.

Remarks. Winged seeds are widespread in Permian assemblages across Gondwanan and are typically assigned to *Samaropsis* Goepfert, *Cordaicarpus* Geinitz or various other genera (Maithy 1965; Millan 1981; McLoughlin 1992; Singh 2002; Bernades-de-Oliveira *et al.* 2007; Souza & Iannuzzi 2009) but relatively few can be assigned with consistency to particular plant clades. The specimen illustrated here (S047884-02: Fig. 9G) might fall within the broad circumscription of *Samaropsis* but has too few diagnostic characters to enable assignment to any one gymnosperm group represented in the leaf assemblages from the Falkland (Malvinas) Islands. A second, roughly circular 4.5-mm-diameter, object on sample S047948 from south of the settlement on Speedwell Island possibly represents a seed imprint but is too poorly preserved to resolve specific morphological features.

Forked roots, Fig. 9H–K

Material. NRM S047931, S047942, S047947, S047948.

Localities. Speedwell Island (north and south of settlement).

Description. Equi-dichotomous (Fig. 9I, K) to pseudo-monopodial-style (Fig. 9J) branched roots ranging from 0.3 to 5.0 mm wide (Fig. 9H, K). All forms with fine, discontinuous, longitudinal striae. No nodes, other modifications or appendages apparent.

Remarks. In the absence of internal chambers typical of *Vertebraria*, we suggest that the majority of such forked roots derive from non-glossopterid plants but they can not be ascribed to a particular clade. They typically occur in bleached palaeosols, either parallel to or transecting bedding.

Order and family uncertain

Genus *Australoxylon* Marguerier ex Blazer, 1975.

Type. *Australoxylon teixeirae* Marguerier ex Blazer, *U.S. Geol. Surv. Bull.*, 1396, p. 5. 1975.

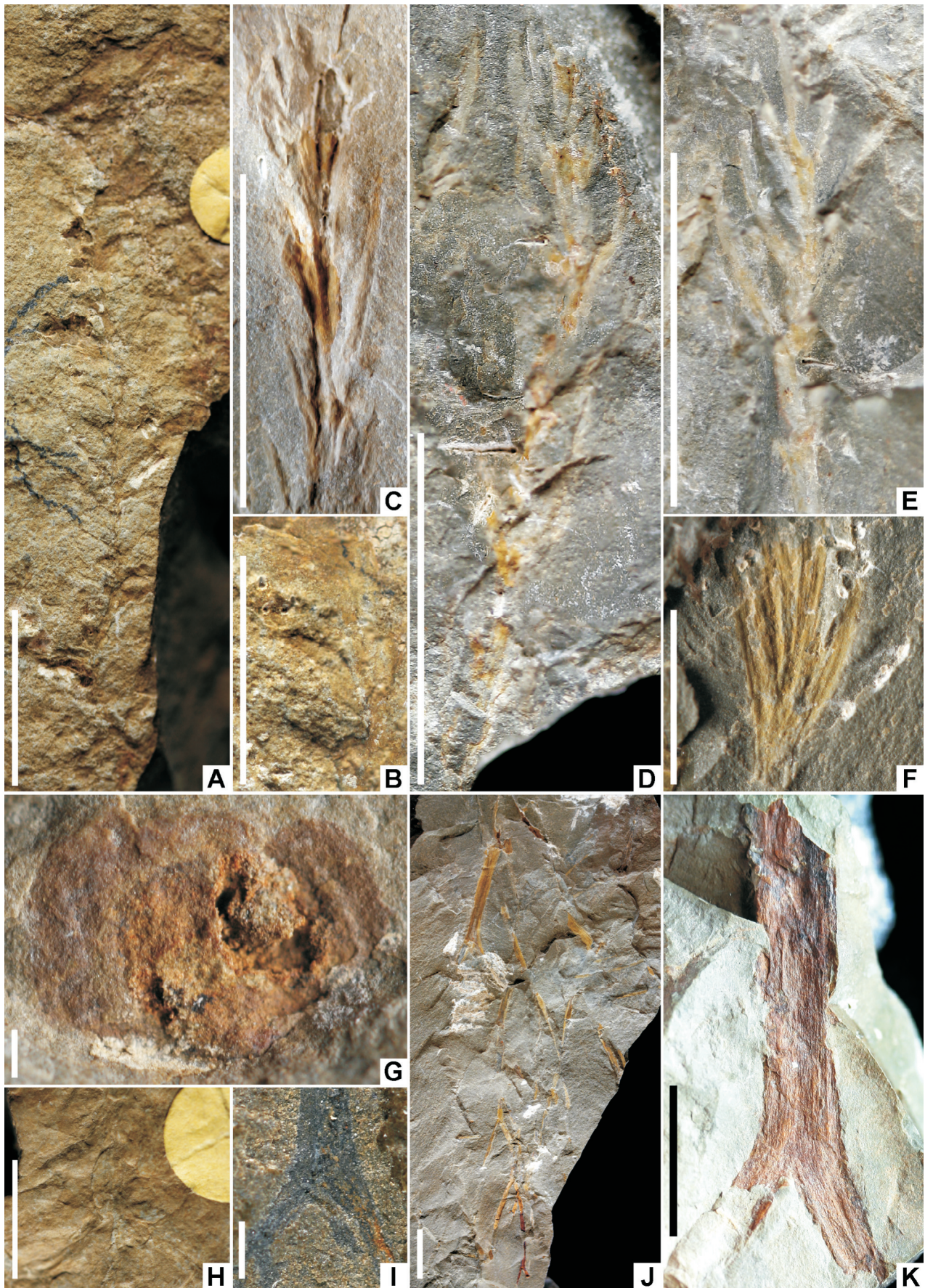


Figure 9. Conifer, seed and root remains from Permian strata of the Falkland (Malvinas) Islands. **A–F**, *Brasiliocladus* sp. cf. *B. acicularis* Yoshida; **G**, winged seed; **H–K**, branched roots. **A, B**, slender axis bearing ill-defined short spinose leaves; S047787. **C**, branch apex bearing acutely disposed, spirally arranged, spinose leaves; S047754-02. **D, E**, branch tips with slightly curved spinose leaves; S047921. **F**, cluster of spinose univeined leaves; S047924. **G**, winged seed with degraded central body; S047884-02. **H**, probable root system penetrating bedding plane with radially disposed rootlets, S047788. **I**, small forked roots; S047947. **J**, pseudomonopodial rooting system; S047931. **K**, large forked roots; S047942. Scale bars for **A, C–E, J, K** = 10 mm; **B, F, H** = 5 mm; **G, I** = 1 mm.

Nomenclatural note 1. *Australoxylon* was not validly published by Marguerier (1973a) because more than one species was described without designation of a type (ICBN, art. 38.5; Turland *et al.* 2018). This problem was not remedied in a subsequent publication by that author (Marguerier 1973b). The valid publication of *Australoxylon* was made effective (ICBN, art. 38.1, Turland *et al.* 2018) by Blazer (1975), whereby he selected *A. teixeirae* Marguerier as the type species. However, this species name was not validly published (ICBN, art. 38.5) by Marguerier (1973a), as the genus was not validly published in that paper.

Nomenclatural note 2. In 2001, after having reviewed the type slides, Bamford & Philippe (2001) determined that *Australoxylon* is probably a taxonomic synonym of *Novoguineoxylon* Boureau & Jongmans, 1955, as had been suggested by Marguerier herself (1973a, p. 49; see, however, her reservations about this synonymy in a subsequent article: Marguerier 1973b, p. 102). The *Novoguineoxylon* type was said to be ‘probably Jurassic’ in age (Boureau & Jongmans 1955). Few details were provided about its source, *viz.*: ‘Jass River bank close to its confluence with Ainim River’. Several units crop out in this area located in the central ‘Birds Head’ region of West Papua, Indonesia. Of these, the Jass Formation is dated as Late Cretaceous, and the Ainim Formation is considered Permo-Triassic in age (Playford & Rigby 2008). Boureau & Jongmans (1955) did not state whether the wood was found *in situ*. Relationships between *Australoxylon* and [*Carpentierixylon*], a genus Marguerier intended to publish (Marguerier 1985) are even less clear.

Australoxylon lafoniense (Halle) B. Giraud, 1991, Figs 10–12
Selected synonymy

1911 *Dadoxylon lafoniense* Halle, pp. 64–68, pl. 4, figs 1–7.

1923 *Dadoxylon bakeri* Seward & Walton, pp. 325–328, pl. 22, figs 19–22, text-figs 4, 5.

1972 *Polysolenoxylon lafoniense* (Halle) Maheshwari, p. 32, pl. 12, fig. 7, pl. 13, figs 1–7.

1976 *Barakaroxydon lafoniense* (Halle) Guerra, pp. 260–262, fig. 2b.

1991 *Australoxylon lafoniense* (Halle) B. Giraud, p. 17.

Nomenclatural note 3. When describing this taxon, Halle (1911) used two wood specimens, specifying, however, that only the second one, collected from the Tranquilidad locality, had well-preserved secondary xylem. Therefore, we choose this specimen, S004042, as the lectotype for this name. The other syntype, S081825, has proven indeed to have poorly preserved secondary xylem, representing only the inner part of a juvenile wood.

Nomenclatural note 4. Maheshwari (1972, p. 32) recombined *Dadoxylon lafoniense* Halle as *Polysolenoxylon lafoniense* (Halle) Maheshwari. Despite his reference to the protologue being erroneous (he mentions pl. 9 instead of pl. 4), the combination can be considered valid (ICBN, art. 41.6). However, Maheshwari (1972) quoted ‘figs 1–7’, which means that he did not choose one of the syntypes as lectotype, hence this does not fulfill appropriate lectotypification. Lectotypification of *Dadoxylon lafoniense* by S004042, which is devoid of well-preserved pith features, thus makes *Polysolenoxylon lafoniense* (Halle) Maheshwari

a name without a relevant type. It is suggested that a replacement name (*nomen novum*, ICBN, art. 6.11) should be proposed, if necessary. As the diagnosis of *Polysolenoxylon* Kräusel & Dolianiti includes pith features, this replacement name would probably be better lectotypified by S081825.

Nomenclatural note 5. This fossil wood taxon has usually been listed by previous authors as *Australoxylon lafoniense* (Halle) Marguerier, [1973a]. However, despite assigning this taxon to *Australoxylon*, Marguerier did not create this combination (Marguerier 1973a,b). Prasad & Chandra (1981) published a comparison table for *Australoxylon* species, but did not include *Australoxylon lafoniense*. The new combination was first published by Giraud (1991, p. 17), hence, the correct designation of this name is *Australoxylon lafoniense* (Halle) B. Giraud, 1991.

Nomenclatural note 6. *Dadoxylon lafoniense* Halle is also the basionym for *Barakaroxydon lafoniense* (Halle) Guerra, 1978. The new combination is usually attributed to Schrage (1973; see, for example, Boersma & Brockmeyer 1987, or Crisafulli & Lutz 1997) but, being presented in an unpublished M.Sc. thesis, this does not qualify as valid publication. The assignment to *Barakaroxydon* Surange & Maithy, 1961 is based on features of the pith and other primary tissues. A name can only have one type. Lectotypification of *Dadoxylon lafoniense* by S004042, which is devoid of pith features, thus makes *Barakaroxydon lafoniense* (Halle) Guerra a name without a relevant type. It is suggested that a replacement name (*nomen novum*, ICBN, art. 6.11) should be proposed, if necessary. As the diagnosis of *Barakaroxydon* Surange & Maithy includes pith features, this replacement name would probably be better lectotypified by S081825 (however, see nomenclatural note 4 above).

Description of the lectotype (S004042). Tracheidoxyl, with no associated primary tissue; ring curvature suggesting a stem several centimetres in diameter; both true growth-rings and false-rings present (Fig. 10A–C); true rings prominent, of type E, up to 6.6 mm wide; transition from the early- to latewood gradual but short; latewood not well-developed (Fig. 10B–E), usually less than ten cells thick; false rings asymmetrical and usually incomplete (Fig. 10B, D); no intercellular spaces; tracheids usually opposite to their neighbours.

Rays homogenous and homocellular (Fig. 10J, K), all uniseriate and typically low, 1–(3)–5 cells high, with no intercellular spaces between ray cells.

Axial tracheids quadrangular in cross-section where the wood texture is well preserved (Fig. 10B–D); tracheid walls relatively thin, even in latewood (Fig. 10B, C); tracheid diameter relatively constant along radial rows. Intertracheary areolated pits on the radial walls of tracheids (Fig. 10G, H) circular, elliptical or obround, contiguous or separated, variably uni- to biseriate, in the earlywood alternate or opposite when biseriate; radial intertracheary pitting more abietinean in narrower tracheids; Sanio’s rims, pits on the tangential walls of tracheids, tertiary thickenings, tyloses, and septae are not evident. No axial parenchyma or axial and/or radial resin-canals observed.

Ray parenchyma cells elliptical in cross-section (Fig. 10K), with transverse walls at right angles to the radial orienta-

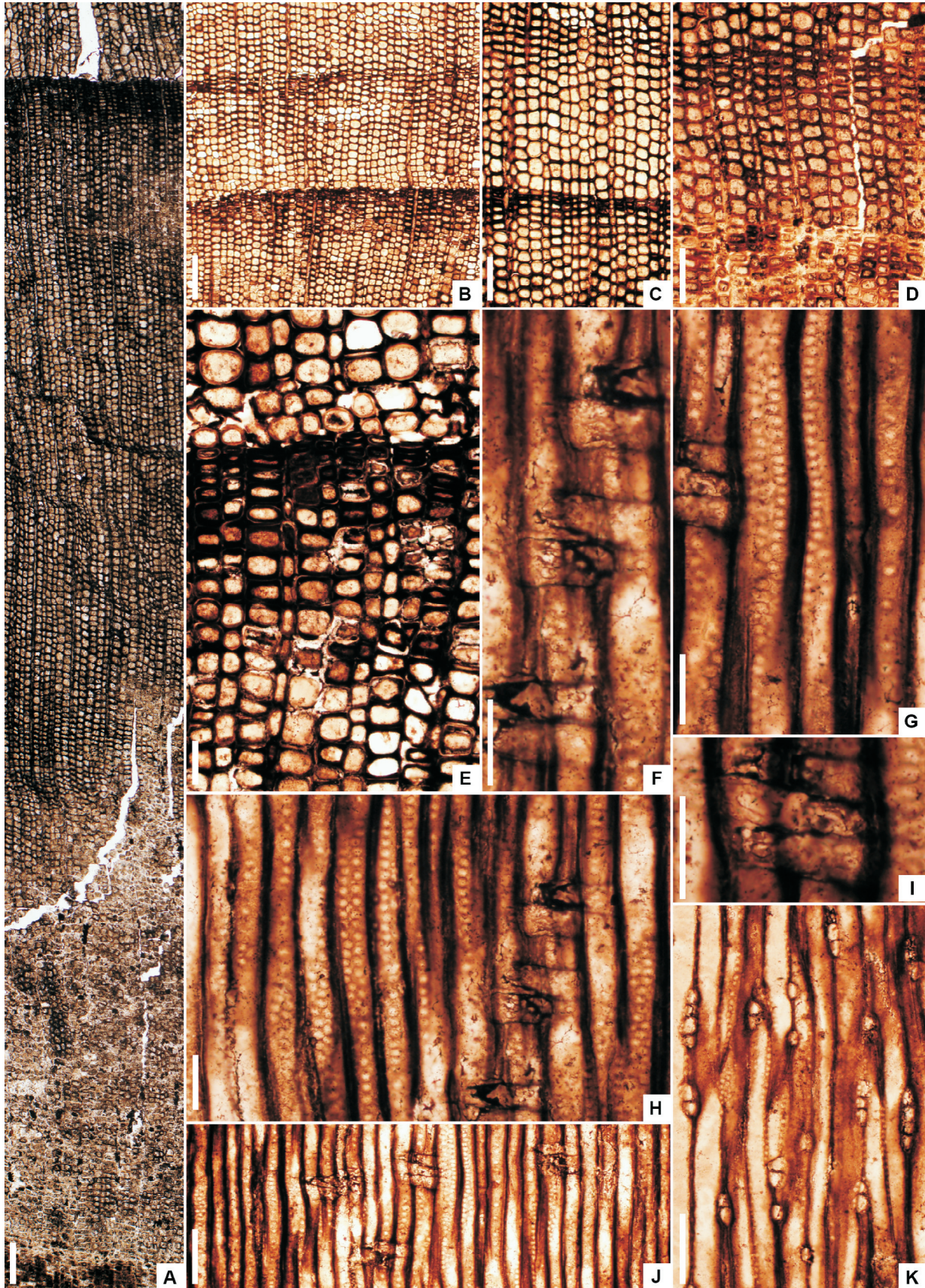


Figure 10. *Australoxylon lafoniense* (Halle) B. Giraud lectotype (selected here); S004042. A–E, transverse section; F–I, radial longitudinal section; K, tangential longitudinal section. A, thick, ill-preserved earlywood, several tens of cells wide. B, enlargement of a growth-ring boundary (below) and a symmetrical false-ring (above). C, enlargement of a well-preserved area showing polygonal cross-sections of relatively thin-walled tracheids. D, less well preserved area showing tracheid walls altered by microbial attack. E, enlargement of a growth-ring boundary, with severe microbial attack, note that the middle lamella is completely dissolved in several places. F, general view of the radial features, with pitted cross-fields. G, H, radial intertracheary pitting typical of *Australoxylon*. I, cross-fields with a few contiguous oculipores. J, variability of intertracheary pitting along a radius. K, low homocellular and homogenous rays, radial intertracheary pitting seen in section or secondarily twisted within a tangential plan. Scale bars = 200 μm for A, B; 100 μm for C, D, J, K; 50 μm for E–I.

tion; walls thin and unpitted, except in cross-fields; cross-field pits cupressoid with a broad pore (Fig. 10F, I), usually 4–6 per earlywood cross-field, with araucarioid disposition.

Description of other specimens. S004024, a specimen with the same provenance as the lectotype (from Tranquilidad locality: Fig. 11A–H, N), is better preserved and represents a more mature wood. It contains annual and false rings of uniform tracheids, together with some zones of crushed cells (Fig. 11A–C). In this specimen, ring widths reach 4.1 mm. Radial intertracheary bordered pitting is commonly biseriate (Fig. 11D, E, K) but locally up to triseriate, even approaching quadriseriate or disorganized in some tracheids near end walls or zones of twisting (Fig. 11G), which is typical for *Australoxylon*. Where partially degraded, oblique fibrils are evident in the tracheid walls (Fig. 11N). Cross-fields are as described for the lectotype (11E, F). In this specimen, the tangential section (Fig. 11H) reveals a bimodal distribution of ray heights as, besides low (3–6 cells high) rays, a few much higher examples (10–14 cells, and rarely up to 24 cells high) are present. Although some characters differ from the lectotype, no feature of the wood suggests that this mature example of secondary xylem is not conspecific with S004042; ray height increase with diameter being a classical xylological feature (Bannan 1937). Consequently, sample S004024 is assigned here to *Australoxylon lafoniense*.

As noted above, S081825 has a secondary xylem that is poorly preserved (12A–D). Nevertheless, those secondary xylem anatomical features available are consistent with the characters of *A. lafoniense*. This specimen is unique in the collection in preserving primary wood features, and Halle (1911, pl. 4, figs 1–4) illustrated several characters of the pith and primary xylem. Specimen S081825 represents a portion of juvenile wood with secondary xylem growth rings about 2 mm wide composed of narrow, relatively uniform tracheids (Fig. 12A). Latewood is typically <8 cells thick (Fig. 12B). Radial intertracheary pitting is ill-preserved (Fig. 12D); however, its cross-fields are typical for *Australoxylon*, with 3–4 broadly pored cupressoid contiguous and alternate oculipores. Rays are typically low and generally uniseriate (Fig. 12C). Pith cells are circular to polygonal in transverse section (Fig. 12H, I). Inner pith cells have radial diameters of 100–150 μm and longitudinal diameters of 40–80 μm . Cells become progressively smaller and more regimented towards the margins of the pith with diameters of 40–150 μm radially, and 30–60 μm longitudinally (Fig. 12J). The outer part of the pith contains semi-regularly arranged circular to elliptical tubes (interpreted here as resin canals) with maximum diameters of 500 μm that are rimmed by a 20–40- μm -thick epithelium (Fig. 12E–G). Endarch primary xylem wedges occur regularly around the periphery of the pith, some alternating between the positions of resin canals (Fig. 12E–F). The primary xylem consists of tracheids that are circular to square in cross-section and typically 10–20 μm in cross-sectional diameter (Fig. 12E–I).

Halle (1911) considered specimen S004040 (Fig. 11I, L, M) to be distinct from the other woods he described, although his identification of the wood was equivocal,

viz. *Dadoxylon* cf. *angustum* Felix. Marguerier (1973a) considered this specimen to be part of the same informal group (Group I) as *A. lafoniense* within *Australoxylon*. The specimen derives from a different locality (Bodie Creek House area) to the lectotype (Tranquilidad area), as evidenced here *fide* labels, although both may be sourced from the same stratigraphic unit (Praltos Member, Bay of Harbours Formation). S004040 is a portion of mature secondary xylem, a tracheidoxyl with no clear ring curvature. According to Halle (1911) it differs from *Dadoxylon lafoniense* in: 1, having thinner cell walls (Fig. 11I; although this character is very variable in both specimens, being controlled mainly by the intensity of microbial degradation, which results in swelling of the walls during the initial stage of attack); 2, having no growth rings (although careful observation reveals that growth rings are present but commonly crushed (Fig. 11I, L); 3, having much narrower rays (although this is probably a preservational feature, and our observations reveal many rays in S004040 to be of normal width (Fig. 11M); and 4, having particularly high rays of up to 25 cells. Rays in the lectotype of *A. lafoniense* (S004042) are indeed relatively low on average, but in S004024, with the same provenance, the rays reach 24 cells high. In S004040, as in the *Australoxylon* type wood, a bimodal distribution of ray height is apparent. Specimen S004040, being a more mature wood, is also the only specimen in which we identified some partly biseriate rays (Fig. 11M). Growth-ring widths reach 3.4 mm in S004040.

Other permineralized specimens in the collection (S004005, S004034, S004038, S004047, S004048) all represent portions of secondary wood that have variable quality of preservation. S004005 contains both strongly crushed and heavily degraded zones, but locally preserves rays up to 12 cells high (somewhat higher than the lectotype), and with 4–5, broad-pored, cupressoid pits in the cross-fields. Specimen S004034 has equivalent anatomical features to the lectotype but the cell walls are generally pale and somewhat degraded in thin section. This specimen is characterized by numerous discontinuous false rings less than four cells thick. Specimen S004038 has zones of strongly crushed wood, but the secondary xylem is otherwise well preserved and includes rays up to 15 cells high. Specimen S004047 has a high degree of compressed and distorted tissue. The few anatomical features measurable in this specimen are consistent with those of the lectotype. Similar to some of the samples mentioned above, specimen S004048 has uniseriate rays up to 15 cells high, but the cell walls are somewhat degraded and lack details of cross-field pitting. However, this specimen is notable in that it contains longitudinal cavities filled with arthropod coprolites (described below).

Remarks. Based on these anatomical data we consider that the principal well-preserved wood specimens (S004024, S004040 and S004042) are sufficiently similar to be assigned to a single species, *Australoxylon lafoniense* (Halle) B. Giraud. A moderate degree of anatomical variation is evident between and within specimens that may represent either phenological variance or taphonomic influence; for example, some axial tracheids are more



Figure 11. *Australoxylon lafoniense* (Halle) B. Giraud: anatomical features of additional specimens from the Falkland Islands. A–C (S004024-01) and I, L (S004040-01), transverse sections; D–G, J, K, N, (S004024-02), radial longitudinal sections; H (S004024-03) and M (S004040-03), tangential longitudinal section. A, a series of growth rings with intercalated false rings and crush zones. B, enlargement of growth ring boundaries and ill-defined false rings. C, enlargement of polygonal tracheid cross-sections. D, J, K, typical biseriate radial bordered pitting. E, biseriate radial pitting and low rays. F, cross-fields with a few contiguous oculipores. G, atypical triseriate to irregular radial pitting. H, M, rays of low to moderate height. I, thin-walled tracheids and ill-defined growth ring boundary. L, enlargement of wood showing compressional crushing. N, radial pitting on tracheids showing wall deterioration and separation of oblique fibrils. Scale bars = 500 μm for A, L; 200 μm for B; 100 μm for C, E, H, I, M; 50 μm for F, G, J; 20 μm for D, K, N.

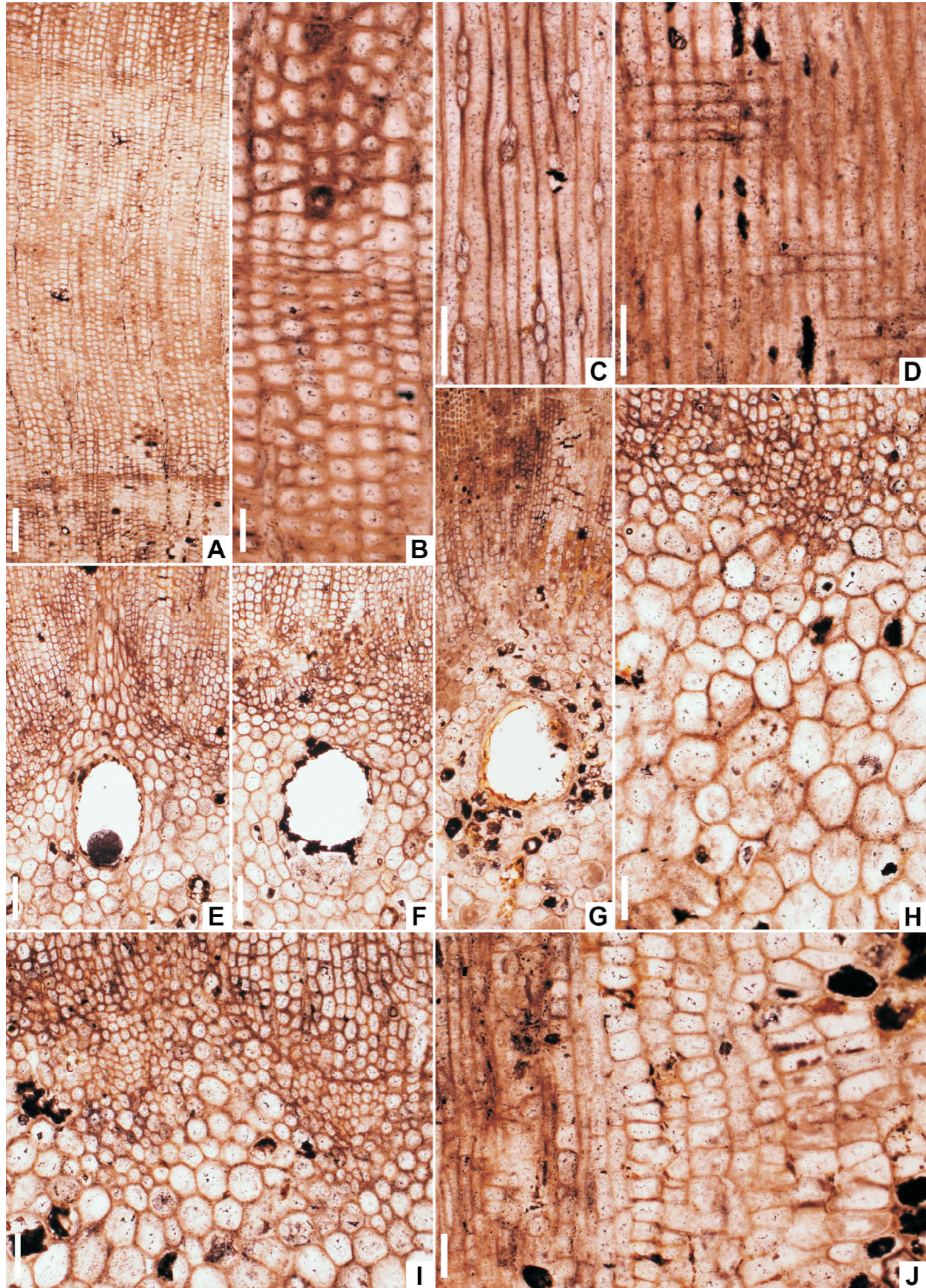


Figure 12. A young axis (S081825) with poorly preserved secondary wood that is anatomically consistent with *Australoxylon lafoniense* (Halle) B. Giraud, but also contains primary tissues. **A–B** and **E–I** transverse section (S081825-01); **C**, tangential longitudinal section (S081825-02); **D, J**, radial longitudinal section (S081825-03). **A**, wood with thick earlywood and little differentiated latewood. **B**, detail of a growth-ring, with thin latewood, limited to a few cell layers. **C**, low uniseriate (locally biseriate) homogenous and homocellular rays. **D**, secondary xylem with both intertracheary and cross-field pitting poorly preserved. **E, F** and **G**, endarch primary xylem wedges and resin canals with a thin epithelium in the pith. **H**, large polygonal medullary parenchyma and small-diameter primary xylem tracheids. **I**, two endarch primary xylem wedges. **J**, elongate primary xylem cells (left) and regimented, squat, medullary parenchyma (right). Scale bars = 200 μm for **A**, **E–G**; 100 μm for **C**, **H–J**; 50 μm for **B**.

rounded, rather than quadrangular, where subjected to microbial attack (Fig. 10E). It is beyond the scope of this paper to discuss the complex taxonomy of the genus. However, we note that given the xylological variability within a single specimen, it is not clear why more than 20 *Australoxylon* species have been described globally (Merloti & Kurzawe 2006).

Seward & Walton (1923) also described *Dadoxylon bakeri* from the Falkland (Malvinas) Islands from a supposedly new locality. However, they erroneously assigned Darwin Harbour as the original locality for S081825, whereas it comes from Arrow Harbour on the southern coast of the inner part of Choiseul Sound, as does the material studied by Seward and Walton. According to their table (Seward & Walton 1923, p. 328), *D. bakeri* differs from *D. lafoniense* mainly by its radial intertracheary pitting, 1–4 seriate in the former in contrast to 1–2 seriate in the latter. Our revision revealed both triseriate and quadriseriate pitting in S004024. We consider *Dadoxylon bakeri* Seward & Walton, 1923 to be a taxonomic synonym of *Dadoxylon lafoniense* Halle. Shortly afterwards, Walton (1925) synonymized *D. bakeri* with *D. arberi* Seward and *D. cf. angustum* Felix in Halle. Curiously, *Dadoxylon bakeri* was not treated by Merloti & Kurzawe (2006) in their revision of *Australoxylon*, although it was explicitly assigned to *Australoxylon* by Marguerier (1973a).

Maheshwari (1972) recombined *Dadoxylon bakeri* as *Damudoxylon bakeri* (Seward & Walton) Maheshwari. Thus, although we recognize only one species of wood yet documented from Permian strata of the Falkland (Malvinas) Islands on the basis of secondary xylem data, three genera might be recognized on the basis of inferred linkages between woods with secondary and primary tissues: *Barakaroxylon*, *Damudoxylon* and *Polysolenoxylon* (Maheshwari 1972; Schrage 1973). Of these, *Barakaroxylon* and *Polysolenoxylon* have canals in the pith like those of the only specimen in the Falkland (Malvinas) assemblage retaining primary tissues preserved (S081825). Clearly, many genera and species established for upper Paleozoic gymnosperm woods have a range of shared characters, and their taxonomy is in need of a global revision. For the present, we retain all the Falkland (Malvinas) Permian woods in a single species, *Australoxylon lafoniense* (Halle) B. Giraud.

Kingdom Fungi

Fungal hyphae (Basidiomycota?), Fig. 13A–K

Description. Fungi and fungal damage are preserved in several forms within *Australoxylon lafoniense* wood. Fungal damage is manifest as one- to several-millimetre-broad elliptical zones of disrupted and degraded secondary xylem evident particularly in transverse sections of specimens S004034 and S004024 (Fig. 13A).

Fungal hyphae are represented in several wood specimens by smooth, 1–3 μm diameter, irregularly branched filaments. Hyphae are commonly oriented longitudinally within tracheid lumens (Fig. 13E, G) but also run obliquely (Fig. 13B) or transversely, passing between cells via cross-field or radial intertracheal pits (Fig. 13F, H, I). In

many cases, strongly branched or irregularly meandroid hyphae adhere to the walls of tracheids and are particularly associated with areas containing numerous bordered pits (Fig. 13C–E). In a few cases, hyphae appear to initiate and radiate from opaque objects that might represent occluded bordered pits (Fig. 13B, K). In some cases, fungal or bacterial degradation has caused detachment of cell walls along the middle lamella providing a space that is exploited by hyphae (Fig. 10E, 13J). Although septa appear to be sparse, clamp connections (or similar thickenings) are apparent along some hyphae (Fig. 13E, F, J).

Remarks. The spindle-shaped (elliptical in transverse section) zones of secondary xylem degradation are reminiscent of the early stages of white pocket rot. Both white rot and hyphae with clamp connections are generated by members of Basidiomycota. Although such decay features and hyphae have been widely reported in Permian woods across Gondwana (e.g. Stubblefield & Taylor 1986; McLoughlin 1992; Slater *et al.* 2015; Harper *et al.* 2016, 2017; McLoughlin *et al.* 2019; Murthy *et al.* 2021), they can rarely be identified more precisely than to phylum level unless attached reproductive structures are available. Halle (1911) did not record hyphae in his collection of woods, and these remains are the first fossil fungi documented from the Falkland (Malvinas) Islands.

Bacteria and bacterial degradation features. Figs 10A, E, F, 11N, 12D, I, J, 13D, E

Description. Several woods contain minute ($<5\mu\text{m}$ wide) irregular, pock-marked or sinuous furrow-like degradation features on tracheid walls (Figs 10F, 13D, E). Some woods show an ‘exploded texture’ of tracheids with delaminated walls or cells separated from each other by degradation of the middle lamella (Fig. 10A, E). Rarely, differential degradation of tracheids emphasizes the presence of diagonal fibrils in their walls (Fig. 11N). A few woods possess opaque infillings within secondary xylem tracheids, ray cells or pith cells (Figs 10A, 12D, I, J).

Remarks. The contiguous furrows incised into the S2 layer of cell walls probably derive from tunnelling bacteria, which are common in the cell walls of modern dead woods in moist, oxygenated settings (Björödal *et al.* 2000; Jurgens & Blanchette 2006; Singh *et al.* 2016). Similar, though more regular features have been described recently from Cretaceous woods of South Africa (Philippe *et al.* 2022). Both brown rot fungi and bacteria can cause cell-wall separation, delamination, and fibril degradation like those cases illustrated herein (Blanchette 1995). Opaque occlusions of cell lumens may represent simply diagenetic mineral infillings, or possibly ergastic substances where clustered in the pith cells, where focused around resin canals (Fig. 12E, F), or where concentrated around zones of tissue decay (Zavada & Mentis 1992). If these are the remains of ergastic substances, then it implies that they were laid down as a response to biological or physical tissue damage while the tree was still living.

Phylum Arthropoda

Class Insecta

Superorder Odonatoptera Martynov, 1932

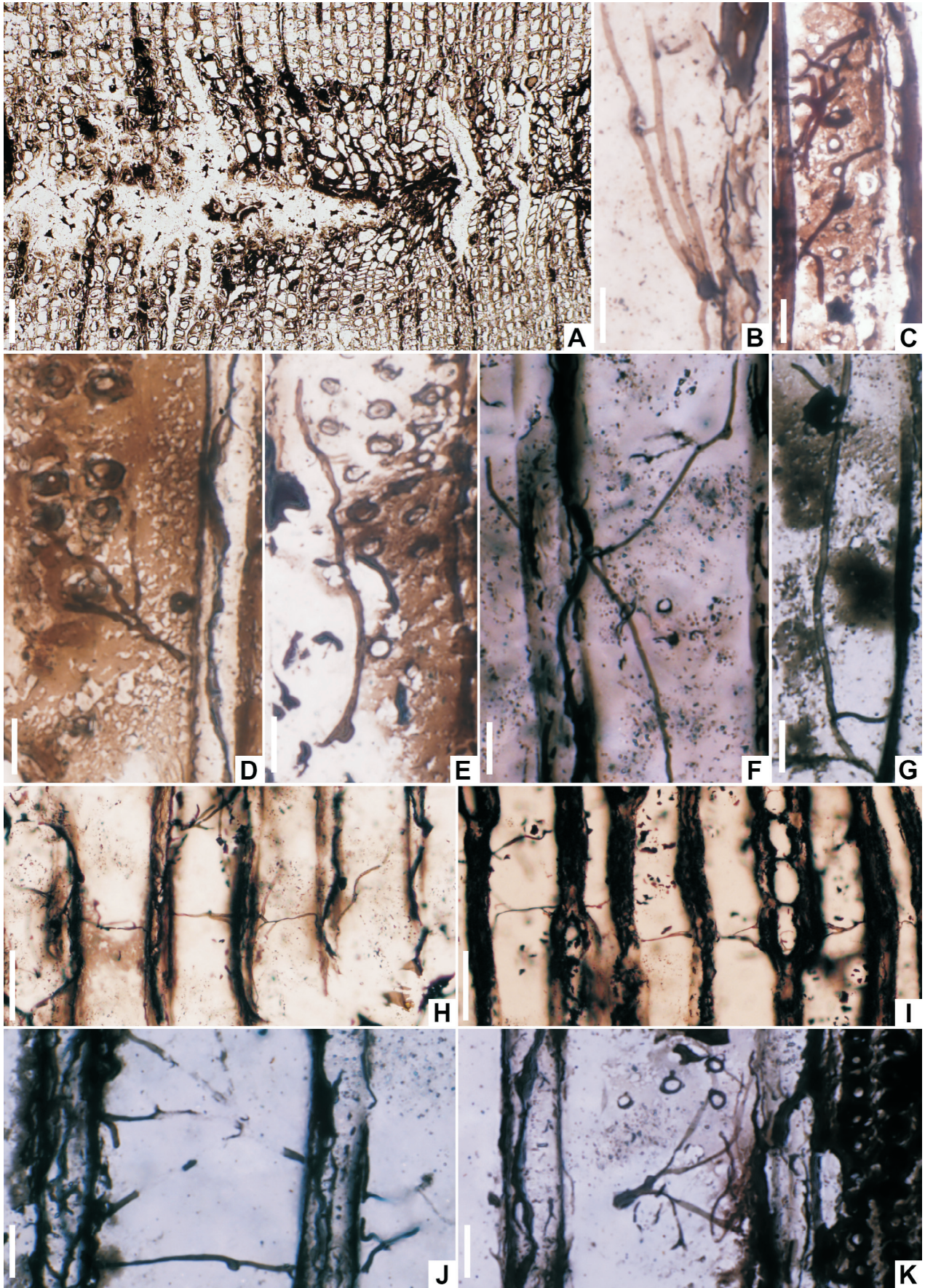


Figure 13. Fungi and fungal/bacterial damage in *Australoxylon lafonense* secondary wood. **A**, pocket of disrupted and degraded secondary xylem. **B, K**, hyphae branching and radiating obliquely through a tracheid lumen from a darkened (?)occluded pit. **C, D**, hyphae ramifying between pits on a tracheid wall. **E, F**, intra-tracheal hyphae with clamp connections or similar thickenings. **G**, branched hyphae passing between zones of granular degraded tracheid wall. **H, I**, thin hyphae passing transversely through cells via tracheary pores. **J**, branched hyphae with clamp connection/thickening exploiting lumen and space left by degradation of middle lamellae. **A**, S004024-01; **B–H, J, K**, S004024-02; **I**, S004024-03. Scale bars = 200 μm for **A**; 50 μm for **H, I**; 20 μm for **B–G, J, K**.

Superfamily Permagrionoidea Tillyard, 1928
Family Permagrionidae Tillyard, 1928

Genus *Permagrion* Tillyard, 1928

Permagrion falklandicum Tillyard, 1928, Fig. 14D–F

Remarks. Halle (1911) illustrated a single insect wing (described in his paper by Gerhard Holm) from the Bodie Creek Head area (possibly either Saladero Member of the Brenton Loch Formation or Praltos Member of the Bay of Harbours Formation). This remains the only Permian insect fossil recovered from the Falkland (Malvinas) Islands. Holm (in Halle 1911) assigned the wing simply to Palaeodictyoptera. Tillyard (1928) reinvestigated the specimen based on photographic enlargements and assigned it to a new genus and species: *Permagrion falklandicum* within Zygoptera (damselflies). More recently, Nel (2012) noted that there were many mistakes in Tillyard's (1928) account, and he provided a reversed halftone photograph, line drawing and revised description of the specimen. We provide a colour image of the impression fossil and enlargement of the venation details to provide additional clarity (Fig. 14D–F). Nel (2012) placed *P. falklandicum* in Permagrionoidea – considered to represent a basal group of damselfly-like Odonatoptera of protozygopteran grade. Protozygopterans have a palaeotemperate distribution in the Permian and are known from the Guadalupian of South Africa (Nel *et al.* 2022). Although the feeding habits of *P. falklandicum* are unknown, the morphologically similar extant damselflies are predatory.

Plant–arthropod interactions

Coprolites in wood, Fig. 14A–C

One specimen of permineralized wood cut in tangential longitudinal section (S004048-02) reveals wedge-shaped longitudinal cavities (up to 250 μm wide and >2 mm long) in the secondary wood that are tightly filled with coprolites (Fig. 14A). The coprolites are ellipsoid with rounded termini and, within any one cavity, they vary from 15 $\times$ 25 to 60 $\times$ 100 μm (Fig. 14B). The coprolites range from opaque to strongly translucent and are filled with fine platy to spiculate matter (Fig. 14C), apparently representing degraded cell wall fragments. Two smaller empty longitudinally elliptical perforations c. 100 μm in maximum dimensions are also present in this wood sample (Fig. 14A arrowed).

Similar coprolites have been recorded in Permian gymnosperm woods from Antarctica and South America (Weaver *et al.* 1997; Kellogg & Taylor 2004; Césari *et al.* 2012). Indeed, equivalent ellipsoid pellets in chambers within gymnosperm and fern woods are common in many upper Paleozoic and Mesozoic deposits and are typically interpreted to represent the coprolites of oribatid mites (Cichan & Taylor 1982; Labandeira *et al.* 1997; Ash 2000; Feng *et al.* 2010, 2022; D'Rozario *et al.* 2011; Slater *et al.* 2012; Strullu *et al.* 2012; McLoughlin & Strullu-Derrien 2016; McLoughlin & Bomfleur 2016). The material illustrated here (Fig. 14A–C) represents the first fossil record of oribatid mite borings from the Falkland (Malvinas)

Islands. The empty perforations (Fig. 14A) are similar to elliptical galleries inferred to have been generated by arthropods in Cretaceous woods of South Africa (Philippe *et al.* 2022). It is unclear whether they represent simply empty excavations by small oribatid mites or were generated by some other wood borer.

Leaf damage, Figs 5E, 6C, 15A–R

Recognition of biogenic damage on the Falkland (Malvinas) fossil foliage and stems is made difficult by their lack of organic remains, extensive staining by iron and manganese oxides, numerous adhering patches of claystone, deformation by roots and burrows, and common physical fragmentation or splitting of the leaves. Nevertheless, high-magnification observation of the impression fossils reveals a moderately diverse suite of damage types referable to several functional feeding groups. We have not attempted to quantify the abundance and distribution of the damage features, owing to the relatively small population of leaves and their mostly fragmentary nature. We illustrate a range of representative damage features to illustrate the diversity of biotic interactions evident in the Permian vegetation of the Falkland (Malvinas) Islands (Fig. 15A–R).

Lamina margin-feeding damage is represented by several examples of simple C-shaped scallops on the margin of *Glossopteris* leaves (Figs 6C, 15A) or deep, U-shaped excisions extending to the midrib (Fig. 15B, C) that are referable to DT12 and DT15, respectively, of Labandeira *et al.* (2007) – features that are common on *Glossopteris* leaves across Gondwana (McLoughlin 1994b; Prevec *et al.* 2009; Srivastava & Agnihotri 2011; Cariglino 2018; Cariglino *et al.* 2021). One *Glossopteris* leaf also shows a small V-shaped notch at the tip of the lamina (Fig. 5E) that might represent apical feeding (DT13). Unequivocal examples of hole-feeding damage are relatively sparse, but include fairly simple, 1–5 mm diameter, circular to elliptical excisions adjacent to the midrib (DT102; Fig. 15B) and larger, polylobate areas of tissue removal in mid-lamina regions (DT103; Fig. 15O).

Piercing-and-sucking (mucivory) is the most equivocal category of biotic interaction recognized in the assemblage owing to the small size and relatively few characters of the damage features. Nevertheless, we attribute various small (generally <0.5-mm-diameter) circular to elliptical scars located primarily on secondary veins of *Glossopteris*, glossopterid scale leaves, *Paracalamites* axes, and *Noeggerathiopsis* leaves to piercing-and-sucking damage (Fig. 15D–G), particularly in cases where these punctate features exhibit linear placement (Fig. 15D). Such damage is generally attributable to DT46–48 of Labandeira *et al.* (2007). *Phyllothea deliquescens* leaves bear solitary, roughly circular, scars associated with lamina swellings that may represent galls (Fig. 15K, L).

One damage feature is difficult to categorize. It consists of a chain of circular to elliptical scars of decreasing diameter (c. 1 mm to 0.2 mm distally) that flank the midrib of a *Glossopteris* leaf (Fig. 15P). The chain-like arrangement is reminiscent of piercing-and-sucking damage (e.g. DT138), with the progressive decrease in size correspond-

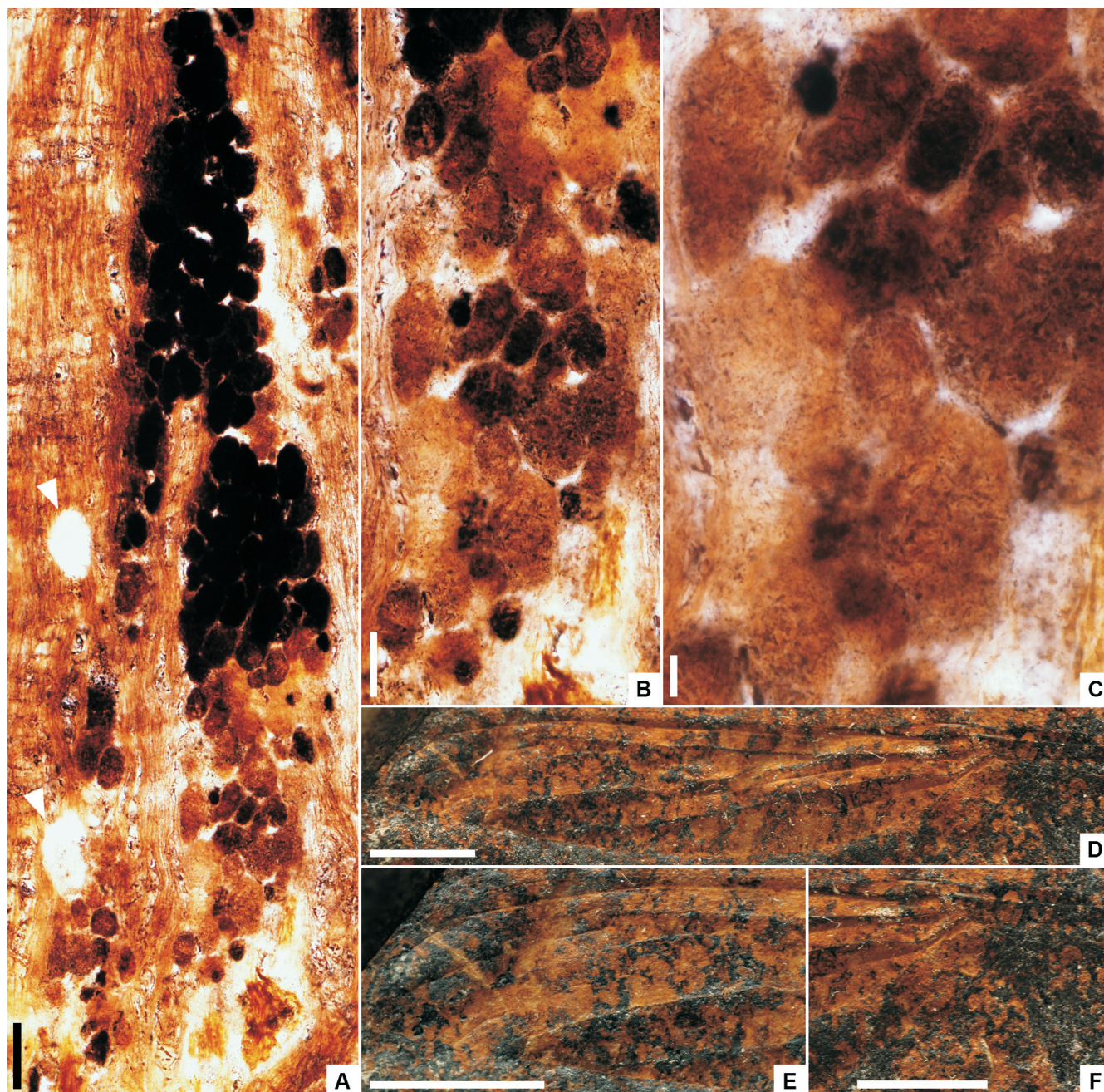


Figure 14. Arthropod damage and insect body fossil from Permian strata of the Falkland (Malvinas) Islands. **A–C**, oribatid mite excavations and coprolites in a radial longitudinal section of *Australoxylon lafoniense* secondary wood; arrows in **A** indicate additional empty excavations generally smaller than those occupied by oribatid mite coprolites; S004048-02. **D–F**, imprint of the near-complete wing of *Permagrion falklandicum* Tillyard, 1928 (holotype NRM Ar 2168). Scale bars in **A** = 100 μ m; **B** = 50 μ m; **C** = 20 μ m; **D–F** = 5 mm.

ing to the thinning of the lamina away from the midrib. However, the positioning of the scars both across and between multiple adjacent secondary veins, and the progressive change in shape is more suggestive of insect oviposition scars. In this case, the progression in size of scar could be interpreted as a series of failed oviposition sites, as the insect probed for the thicker tissue towards the midrib, with the largest, ultimate scar representing the successful oviposition site. This is supported by the change in shape of the scars from smaller, rounded scars to the oval to lenticular ultimate scar that is more typical of oviposition damage seen in glossopterids (e.g. DT100–102). Regardless, this category of progressive scarring has not been published previously from Gondwanan Permian floras (McLoughlin *et al.* 2021a).

Oviposition scars are among the most common and diverse features preserved on the fossil plants of the Falkland (Malvinas) Islands. They include simple, small, spindle-shaped scars arranged parallel to the secondary veins in the outer lamina (Fig. 15N, O), and more elliptical, regularly spaced scars attributable to DT101 on the inner lamina of *Glossopteris* leaves (Fig. 15B, Q). Circular (Fig. 15C) to spindle-shaped scars (similar to DT85) on the midribs of *Glossopteris* leaves might be attributable to either oviposition damage or galls. Oviposition damage is also common as both elliptical (Fig. 15H, J) and circular (Fig. 15I) scars on *Paracalamites* axes. One *Phyllothea deliquescens* leaf bears double rows of clustered, transversely oblong, oviposition scars (Fig. 15M).

Surface feeding damage is equivocal but might be

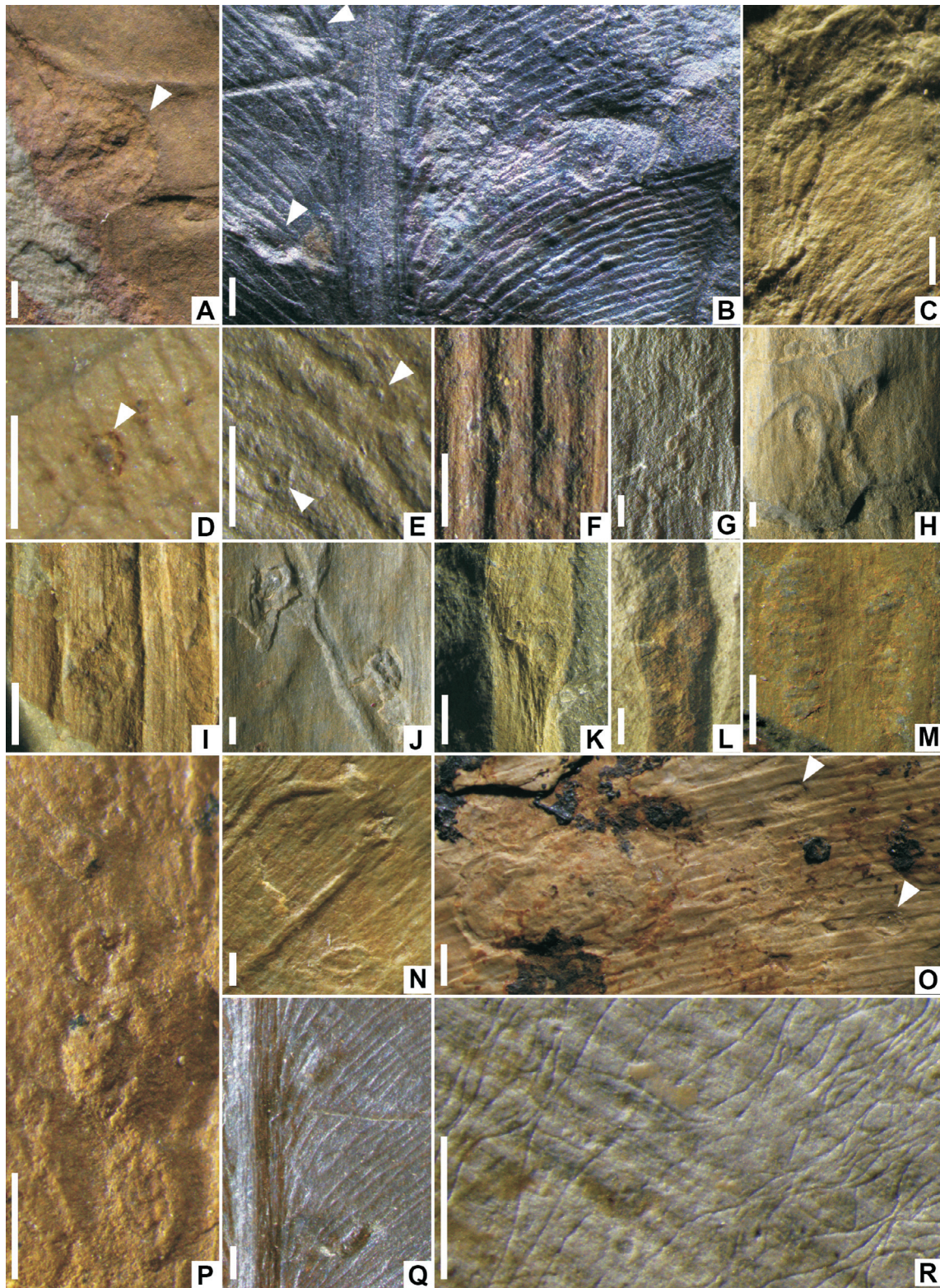


Figure 15. Arthropod and fungal interactions with leaves and axes. **A**, U-shaped margin feeding damage with roughened reaction rim (arrowed); S047799. **B**, two elliptical oviposition scars to left of midrib (arrowed), one area of surface feeding adjacent to midrib on right, one deep U-shaped margin feeding damage on far right; S04778b. **C**, oviposition scar on lower midrib and deep margin feeding at upper right; S047832. **D**, piercing-and-sucking damage (arrowed) arranged in a row on adjacent veins of a glossopterid scale leaf; S047786. **E**, small, circular piercing-and-sucking damage scars (arrowed) over secondary veins; S047953. **F**, small, elliptical oviposition or piercing-and-sucking scars between ribs of *Paracalamites* sp.; S047939. **G**, small, circular piercing-and-sucking damage scars on *Noeggerathiopsis* sp.; S047934-01. **H**, pair of elliptical oviposition scars on *Paracalamites* sp. axis; S047752a-02. **I**, circular oviposition scar between ribs on *Paracalamites* sp. axis; S047752b. **J**, pair of elliptical oviposition scars on *Paracalamites* sp. axis; S047806. **K**, **L**, solitary galls on *Phyllothea deliquescens* leaves; S047890 and S047898, respectively. **M**, two rows of transversely orientated, tightly spaced oviposition scars; S047890. **N**, elliptical oviposition scars on *Glossopteris* lamina and linear features representing burrows underlying leaf; S047877. **O**, large polylobate hole-feeding damage and several elliptical oviposition scars (arrowed) on *Glossopteris*; S047835-02. **P**, chain of elliptical to circular features with central pit on and between secondary veins adjacent to midrib, possibly representing the site of probing and oviposition; S047884-01. **Q**, two elliptical oviposition scars parallel to secondary veins on *Glossopteris*; S047778a-02. **R**, fine network of ramifying filament impressions on a *Glossopteris* morphotype MF07 leaf surface here interpreted to possibly represent fungal hyphae (note that the secondary venation runs from lower right to upper left); S047777-01. Scale bars = 1 mm.

represented by several roughened areas on the lateral parts of *Glossopteris* leaves. We detected no indications of skeletonization or leaf mining, although linear features superficially similar to mining traces (Fig. 15J, N) are common and result from differential compression of the leaves over rootlets and burrows in the underlying sediments.

One *Glossopteris* leaf bears a complex array of filamentous indentations (Fig. 15R) arranged generally at a tangent to the secondary venation, and commonly concentrated around areas of piercing-and-sucking damage. These extremely thin (<20- μ m-wide) filaments are not identifiable with confidence. They possibly represent the indentations left by fungal hyphae that covered the leaf during the initial stages of post-mortem decay. The slender filaments (equivalent to about one cell diameter thick) appear to be too fine to represent root traces of vascular plants. Moreover, irregularly orientated fungal hyphae of similar size are known on many examples of post-Paleozoic leaf compressions (Bajpai & Maheshwari 1988; Wang *et al.* 2017; Maslova *et al.* 2020; McLoughlin *et al.* 2021b). Alternatively, if these leaves were deposited in an aquatic environment, then the indentations might relate to filamentous algae overprinting the lamina. Additional interpretations are that these filamentous structures might represent traces of minute burrowing invertebrates, imprints of arachnid webs, or desiccation creases on the leaf after dehiscence. However, these interpretations are less convincing based on the arrangement of the threads and their branching pattern, especially the presence of some perpendicular cross-connections between filaments.

Although some damage types may be unique to the Falkland (Malvinas) plant assemblage, the general representation of arthropod functional feeding groups is consistent with that recorded for Permian assemblages from other regions of Gondwana, with the dominance of external foliage feeding, galling, piercing and sucking, oviposition scarring and wood boring (Prevec *et al.* 2009, 2010; Srivastava & Agnihotri 2011; Edirisooriya *et al.* 2018; Cariglino *et al.* 2021; McLoughlin *et al.* 2021). Clearly a broad range of feeding and egg-laying strategies produced by many insect groups were represented in the Permian terrestrial ecosystems of the Falkland (Malvinas) Islands. On that basis, future sampling of these plant beds should provide an opportunity to find additional insect body fossils beyond the single fossil wing currently known from the succession.

DISCUSSION

Age and correlation of strata

The Permian succession on the Falkland (Malvinas) Islands has not yielded palynological data, nor have bentonites within this interval been sampled for datable zircons to provide absolute age controls on the strata (Stone & Horan 2016). Available freshwater bivalve assemblages and trace fossils from the Permian succession are not strongly age diagnostic (Aldiss & Edwards 1999; Trewin *et al.* 2002; Simões *et al.* 2012). Thus, dating of the

entire Permian succession on the Falklands (Malvinas) has been constrained primarily by equivocal lithostratigraphic correlations with South African and Argentinean successions. Plant macrofossils offer an additional tool for dating the Permian succession on the islands, although there are significant hurdles to overcome with respect to their biostratigraphic application.

None of the sphenophytes (e.g. *Paracalamites*, *Phyllotheca*) or the cordaitalean leaves *Noeggerathiopsis* provide robust age-constraints, as these all have long Carboniferous–Permian stratigraphic ranges. The conifer *Brasilio-cladus* has been described from the middle and upper sections of the lower Permian (Artinskian–Kungurian) Rio Bonito Formation in Brazil. In the Falklands (Malvinas), it occurs in the uppermost unit of the succession (Egg Harbour Member, Bay of Harbours Formation). However, records of this genus in Gondwanan successions are sparse and its full stratigraphic range remains uncertain.

Biostratigraphic studies utilizing *Glossopteris*-dominated floras currently suffer from a poor understanding of the effects of taphonomy, habitat, climate, and local environmental factors on floral composition and individual leaf form, a paucity of high-resolution radiometric dates, and a lack of consensus in the methodologies applied to the description and identification of *Glossopteris*. In broad terms, most of the glossopterid leaf morphotypes recognized in our study (from the Saladero Member of the Brenton Loch Formation and Praltos and Egg Harbour members, Bay of Harbours Formation) have greatest similarities to forms recorded from Guadalupian–Lopingian strata of the Karoo Basin (Volkrust and Normandien formations). Some morphotypes also have similarities to forms recorded from the Bonete Formation (Cisuralian) and the La Golondrina Formation (Guadalupian–Lopingian) in Argentina – the broad span of ages of these units providing little resolution for correlation of strata in the Falklands (Malvinas). The original identifications of *Glossopteris* leaves from the Falkland (Malvinas) Islands by Halle (1911) and Seward & Walton (1923) employed broad-based concepts of species that did not provide a strong basis for constraining the age of the floras. The use of new and more robust taxonomic approaches, such as the employment of quantitative characters herein, and multivariate analyses, will necessitate thorough revision of all foliage taxa across Gondwana. This is a daunting task but will likely provide a more reliable and consistent taxonomic approach to identifying fossil leaves and will clarify the geographic and stratigraphic ranges of *Glossopteris* species. Until then, the biostratigraphic utility of Permian floras across Gondwana will remain compromised and the outcomes of any comparisons equivocal.

Comparisons with South African lithostratigraphic units and their floras probably provide the best opportunity for geological and biostratigraphic correlations with the Falkland (Malvinas) Islands. Aside from the close palaeoproximity of the islands to the Permian margin of South Africa, the Main Karoo Basin and neighbouring contemporaneous basins, such as the Lebombo Basin, have well-studied deposits that have yielded prolific Permian floras (Anderson & Anderson 1985; Bordy & Prevec 2008,

2015; Prevec *et al.* 2009, 2010, 2022; Botha *et al.* 2020; Balarino *et al.* 2024). Moreover, the southern parts of the Karoo Basin have yielded an ever-growing number of absolute ages to support the robust vertebrate biostratigraphy that has been the focus of much palaeontological research over the past 50 years (Kitching 1995; Viglietti *et al.* 2016; Smith *et al.* 2020). Additionally, South Africa is one of few regions in Gondwana where an almost continuous succession of terrestrial Permian deposits has been preserved, yielding rich fossil evidence of both plants and animals.

Comparisons with the Argentinean fossil record present significantly greater challenges. The lack of absolute age constraints, and factors such as extensive regional faulting, have hindered efforts to correlate and constrain the ages of Paleozoic units in Argentina. Consequently, biostratigraphic studies utilizing both plant micro- and macrofossils have played an important role in the past and continue to be a research focus. Although these studies continue to be invaluable in terms of relative dating, comparisons and correlations with floras in other parts of Gondwana are lagging. Additionally, the absence of definitively upper Permian deposits in Argentina limits the potential utility of these successions in a broader biostratigraphic context. For example, similarities between some Falklands (Malvinas) leaf morphotypes and a few long-ranging glossopterid taxa known from Argentina might contribute to overestimations of the age of geological units.

The absence of glossopterid ovulate reproductive organs from the Falkland (Malvinas) fossil assemblage is disappointing, since these remains not only provide insights into the palaeobiology of this plant group (McLoughlin & Prevec 2021) but are more readily identifiable and provide much better constraints on the age of Gondwanan Permian terrestrial strata than leaf-based taxa (McLoughlin 1993b, 2011; Bordy & Prevec 2008, Cariglino 2013, 2015; McLoughlin & Prevec 2019). Despite their absence from Halle's collection, the prospect of finding glossopterid fructifications in the future seems promising given the apparent abundance of fossil leaf mats at many localities across the islands.

Owing to the complex taxonomic problems with accurately and consistently identifying Permian Gondwanan wood genera, permineralized gymnosperm secondary woods have not been widely used for correlating and dating strata across the supercontinent. Nevertheless, woods potentially equivalent to *Australoxylon lafoniense* have been reported from various uppermost lower to upper Permian strata elsewhere in Gondwana. For example, Walton (1925) considered that the Falkland (Malvinas) wood he described as *Dadoxylon bakeri* Walton (in Seward & Walton 1923), and considered here to be a synonym of *Australoxylon lafoniense*, does not differ from what was previously named *D. arberi* by Seward, and he assigned to this taxon material from the 'Upper part of the lower Beaufort beds in Klipgat, Murraysbay District, Cape Province'. *Australoxylon lafoniense* has been assigned to *Polysolenoxylon* by some workers (Maheshwari 1972). Rösler (1978) proposed an informal 'Polysolenoxylon zone'

(within the upper Cisuralian Irati Formation of Brazil) as part of his 'Taoflora D' biostratigraphic stage in the Paraná Basin, Brazil. Correlations based on secondary xylem fragments are risky and we argue that a thorough taxonomic reappraisal of Gondwanan Permian woods will be necessary before they can be used as reliable stratigraphic tools.

Environmental implications

Wood ring widths reach up to 6.6 mm in specimen S004042, which is relatively broad compared to growth features in modern high-latitude conifers, suggesting that neither temperature nor water availability were strongly limiting factors for the growth of the Falkland (Malvinas) Permian forests. Similar values, in the 5–10 mm range, were observed for *Australoxylon teixeirae* by Marguerier (1973a) from southern Africa. The comparatively small amount of latewood within the growth-rings of *A. lafoniense*, and its weak differentiation from the earlywood, should probably not be interpreted as characteristic of a low degree of seasonality, but rather as an endogenous feature, typical for *Australoxylon*. Marguerier (1973a) observed similar growth-ring features in *A. teixeirae*. In this latter species, she also observed false rings similar to those evident in *A. lafoniense*. We are cautious about interpreting the significance of such false rings, which have been often considered characteristic of flood, drought, earthquake, herbivory, or other intraseasonal environmental disruptions.

Despite being relatively common in Lopingian floras across Gondwana (Archangelsky & de la Sota 1960; Rohn & Rösler 1986; McLoughlin 1992; Galtier & Taylor 1994; Goswami *et al.* 2006; Prevec *et al.* 2009; Slater *et al.* 2015), macrofossils of ferns are notably absent from the Falkland (Malvinas) Island assemblages. This seems unlikely to be the function of a palaeoclimate inconducive to fern growth given the similar palaeolatitudinal setting of the Falkland (Malvinas) Islands to adjacent basins in southern Africa and South America in which ferns are fairly common. Rather, it may relate to local depositional settings and taphonomic processes. The Falkland (Malvinas) assemblages, in addition to being deficient in ferns, contain moderately common stems and foliar remains of conifers, which are generally regarded as more typical of upland vegetation in Gondwanan Permian assemblages (McLoughlin 1993a; Wheeler & Götz 2016; Gastaldo *et al.* 2020). This combination of conifer abundance and fern absence might reflect a basin-margin setting for the deposits of the Bay of Harbours Formation, from which most of Halle's collections derive. The fossil floras otherwise contain a representation of plant groups that is fairly typical of palaeotemperate humid settings of the Guadalupian–Lopingian in southern Gondwana.

Fungal, bacterial and arthropod damage appear to be relatively common in the Falkland (Malvinas) Islands Permian woods. They attest to complex (multi-organism) saprotrophic relationships with the dead wood of glossopterids and/or other gymnosperms in the Gondwanan coastal forests of the Falklands (Malvinas). Similar fossils and traces in woods elsewhere in Gondwana suggest that

these saprotrophic relationships were widespread across the vast palaeotemperate glossopterid biome.

Potential for future research

Halle's Permian plant collections were obtained over a relatively short period during fieldwork that also encompassed extensive mapping and exploration of Devonian strata, intrusive rocks and Quaternary unconsolidated deposits and geomorphology. Subsequent studies have regularly noted the presence of Permian plant remains, particularly through the upper part of the Lafonia Group, but no systematic sampling has been carried out. Further, no thorough palynological study of the Lafonia Group has been undertaken thus far. Given the apparent widespread distribution and exposure of plant-bearing deposits and their lithological similarities to the succession in the Karoo Basin, we suggest that a future field study undertaking systematic sampling of the Permian succession for plant macrofossils and sporomorphs would likely yield rich fossil assemblages that could provide more useful data for biostratigraphic correlation between the Lafonia Group and the South African and South American Permian successions.

Somewhat counter-intuitively, smaller collections of *Glossopteris* leaves can lead to the identification of an inflated number of morphospecies. It is only through systematic bulk-collecting of these floras, and accounting for the intraspecific variability and phenotypic variation across geographically separated populations, that a realistic assessment of their diversity can be achieved. Additionally, larger collections are likely to yield fertile glossopterid material, which tends to have greater potential for biostratigraphic applications, at least in part because of the greater number of available diagnostic features.

Palynostratigraphic studies and CA-IDTIMS dating of zircons from thin tuffs, noted by Aldiss & Edwards (1999) to be distributed sporadically through the Lafonia Group, should also provide tighter age controls of the plant assemblages, which would in turn further constrain the ages of correlative biozones in South Africa and South America. These results would also likely provide better age constraints on strata in offshore structural depressions (Stone 2016; Lovечchio *et al.* 2019), which would have implications for hydrocarbon exploration and resolving the complex tectonic history of the Falkland (Malvinas) region.

S.M. was funded by grants from the Swedish Research Council (VR grant numbers 2018-04527 and 2022-03920). R.P. was funded by Genus (DST-NRF Centre of Excellence in Palaeosciences; Grant). B.C. was funded by CONICET Postdoctoral External Scholarship Program for Young Researchers, Resolution D.N° 4279/2016. We thank two anonymous reviewers for their constructive comments on the manuscript. We dedicate this paper to Prof. Bruce Rubidge on his retirement and in honour of his extensive work on South African and Gondwanan Permian-Triassic palaeontology and biostratigraphy.

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