



# Early Cretaceous Gleicheniaceae and Matoniaceae (Gleicheniales) from Alexander Island, Antarctica

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## Abstract

The first Cretaceous representatives of Matoniaceae and Gleicheniaceae in the Antarctic are described from the Albian flora of Alexander Island. Two new species are recognized, one is assigned to *Matonia*, and another to the emended gleicheniaceous form-genus *Gleicheniaceaphyllum*. The taxonomy of fossil genera assigned to Gleicheniaceae is problematic, and as an alternative to the invalid genus *Gleichenites*, we propose that *Microphylopteris* be utilised as a form-genus for species that have either an unknown branching pattern or pseudo-dichotomous branching without resting buds; *Microphylopteris* is reserved for ferns that cannot be ascribed conclusively to Gleicheniaceae. Alternatively, *Gleicheniaceaphyllum* should be used for gleicheniaceous material that has a resting bud amongst two to four primary branches. *Gleicheniaceaphyllum acutum* sp. nov. is preserved as sterile and fertile fronds, pinnae and pinnules. The other new species, *Matonia jeffersonii* sp. nov., occurs as sterile and fertile pinnae and pinnules, and is aligned to Matoniaceae based on the presence of circular-oval sori with peltate indusia. The two taxa are inferred to have either a pedate or scrambling habit. These morphologies are relatively common at Alexander Island, compared to other high latitude fossil floras, and are interpreted as an adaptation to the high disturbance, polar conditions and unusual photoperiod experienced at Alexander Island during the Early Cretaceous. The theory that angiosperms caused the demise of ferns is discussed in relation to the Matoniaceae and Gleicheniaceae, and there does not appear to be association between angiosperm expansion and the decline of these two fern families.

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## 1. Introduction

The Alexander Island fossil assemblage (Late Albian; Moncrieff and Kelly, 1993) represents one of the most recent floras in which ferns and conifers were

floristically more diverse than angiosperms. On Alexander Island the greatest contributor to relative diversity is ferns and it was estimated that ferns contribute 39% to the overall floristic diversity of the fossil assemblage (Falcon-Lang et al., 2001). In total there are 25 fossil fern species that can be recognized in the Alexander Island flora (Nagalingum, 2003). However, only three are formally described: *Hausmannia papilio* Feruglio emend. Herbst, *Aculea acicularis* Cantrill, and *Alamatus bifarius* Douglas (Cantrill, 1995, 1996). Of these three species, only *H. papilio* is ascribed to a

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family, the Dipteridaceae, and it is preserved as fronds divided into two reniform to wedge-shaped laminae with reticulate venation (Cantrill, 1995). Its palaeoecology suggests that it grew along streams and was a pioneer species. *Aculea acicularis* and *A. bifarius* are of unknown affinity (Cantrill, 1996). These two species are similar by their narrow needle-like pinnules, and are preserved in situ indicating they formed fern thickets between scattered coniferous trees (Cantrill, 1996). In this paper we report two new fern species from the Alexander Island fossil flora that can be ascribed to Gleicheniaceae and Matoniaceae.

In Antarctica, evidence for Mesozoic Matoniaceae is limited with only one provisional record of the family from the Middle Triassic at Fremouw Peak (Millay and Taylor, 1990). The material, ascribed to *Soloropteris rupax* Millay and Taylor, is represented by petrified rhizomes that exhibit morphology most similar to extant *Matonia* (Millay and Taylor, 1990). Additional recently described material from this locality confirms the presence of the family through the description of anatomically preserved foliage with attached sporangia (Klavins et al., 2004). Another Antarctic record of Matoniaceae is a leaf described as cf. *Matonidium* (Rees, 1990). This fossil taxon is preserved in the Early to Middle Jurassic Hope Bay flora, and it is represented by one isolated pinna. However, affinity with Matoniaceae is doubtful, as it is sterile and lacks reproductive characters that allow it to be assigned to Matoniaceae.

Gleicheniaceae fossils from the Mesozoic of Antarctica are sparse; there are two examples known from the Triassic and none from either the Jurassic or Cretaceous. In Triassic rocks from Antarctica there are gleicheniaceous permineralised leaf fragments with sporangia and spores, described as *Gleichenipteris antarcticus* Phipps et al. (Phipps et al., 2000). The authors classified this taxon amongst Gleicheniaceae based on characters such as an oblique annulus, short sporangial stalks, spore counts (up to 50 per sporangium), and the absence of an indusium. The species may represent the fertile foliage of an associated permineralised rhizome, *Antarctipteris sclericaulis* Millay and Taylor, which was also putatively assigned to Gleicheniaceae (Millay and Taylor, 1990). Gleicheniaceae has not been recorded from the Jurassic of Antarctica. Early Cretaceous Antarctic macrofossils (e.g., *Gleichenites* in Torres et al., 1997; Cesari et al., 1999) appear gleicheniaceous by their small pinnules, however, they lack synapomorphies characteristic of the family, and therefore, cannot be assigned to Gleicheniaceae (Cantrill, 1998).

Gleicheniaceae and Matoniaceae, although recognized from permineralized material, are not known as near-complete fossil foliage in the Mesozoic of Antarctica. Here we describe the first Antarctic Mesozoic macrofossil examples of these families, recovered from the Albian, Early Cretaceous, Alexander Island assemblage. This paper is part of an ongoing project investigating the taxonomic composition of the fern flora of Alexander Island.

## 2. Geological setting

The Antarctic Peninsula represents the eroded roots of a long-lived continental island arc (Whitham, 1993) with Alexander Island forming part of the fore-arc region (McCarron and Larter, 1998). On the eastern side of Alexander Island, the Fossil Bluff Group was deposited in a narrow (<60 km wide), elongate fore-arc basin, fault-bounded to the west by the accretionary complex of the Le May Group and to the east by the magmatic arc itself (McCarron and Millar, 1997). Within this basin there are at least 7 km of Early Jurassic to mid-Cretaceous sedimentary rocks that are subdivided into seven formations (Butterworth et al., 1988; Doubleday et al., 1993; Moncrieff and Kelly, 1993). The Triton Point Formation consists of a wedge-like package of fluvial sedimentary rocks that thicken from 200 m at Triton Point in the north of the study area to c. 950 m at Citadel Bastion, Titan Nunataks and Coal Nunatak in the south (Cantrill and Nichols, 1996). The Triton Point Formation comprises a distinctive regressive unit that grades from marine into terrestrial deposits. These fluvial strata have been assigned a Late Albian age on the basis of bracketing molluscan faunas (105 Ma; Kelly and Moncrieff, 1992).

The sedimentology of the Triton Point Formation has been studied separately in the northern part (Triton Point to Pagoda Ridge) and the southern part (Citadel Bastion to Titan Nunataks) of the field area (Fig. 1d). In the northern province, the sedimentary succession is interpreted as the product of a braided alluvial plain environment (Moncrieff, 1989). In the southern province, two sedimentary member units are present (Nichols and Cantrill, 2002). The lower unit, the Citadel Bastion Member (>700 m thick) is interpreted as a braided alluvial plain deposit, whereas the upper unit, the Coal Nunatak Member (~130 m thick) is interpreted as a coastal plain meander belt deposit (Nichols and Cantrill, 2002). Petrographic analysis indicates that most sediments were derived from the magmatic arc with a small input from the accretionary complex, and

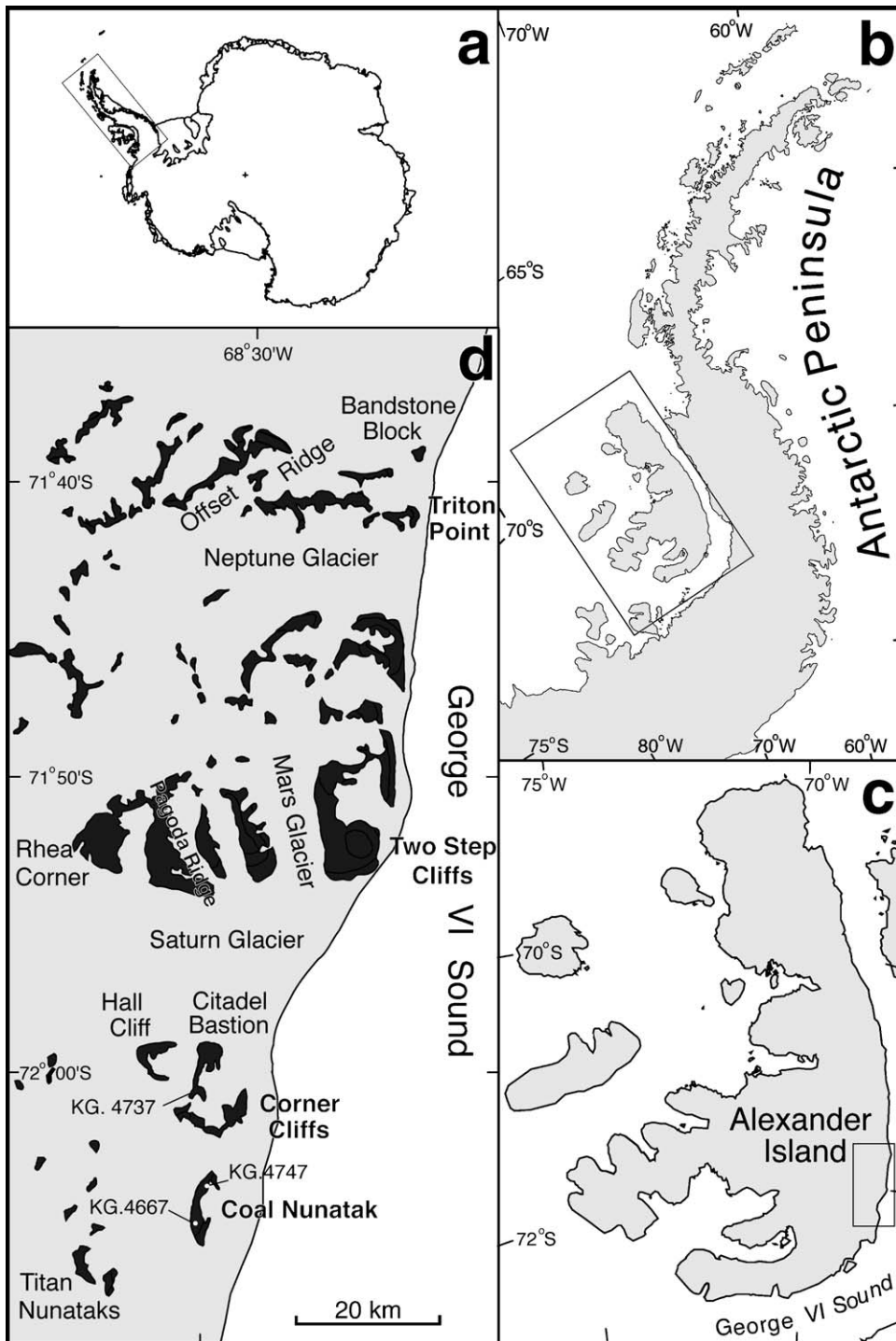


Fig. 1. Location map for Alexander Island, Antarctic Peninsula, Antarctica. (a) Antarctica showing position of inset b. (b) Antarctic Peninsula showing the position of Alexander Island inset c. (c) Alexander Island showing position of inset d. (d) Outcrop map for southern Alexander Island; major localities referred to in the text are indicated.

palaeocurrents, which are predominantly westerly, support this interpretation (Browne, 1996). Numerous palaeosols within the sequence preserve vegetation in

growth position, which allows, in conjunction with the sedimentology, interpretation of community structure (e.g., Cantrill, 1996) and ecology of individual species.

### 3. Materials and methods

Fossils from Alexander Island (Fig. 1) were collected by D.J. Cantrill and field workers from the British Antarctic Survey, Cambridge, U.K. The fossils were obtained from outcrops at Coal Nunatak, Citadel Basin, Titan Nunataks, Pagoda Ridge and Phobos Ridge. The fern fossils were not macerated for sporangia and spores because they are preserved as impressions. All of the Alexander Island specimens examined in this study are housed at the British Antarctic Survey and are given the prefix KG.

All specimens were examined under an Olympus SZH-10 stereo microscope, and photographed using Kodak Technical Pan film. Line drawings were made using a camera lucida attached to the Olympus microscope.

### 4. Systematic palaeontology

Order GLEICHENIALES  
Family MATONIACEAE

*Matonia* R. Brown 1829

*Type species: Matonia pectinata* R. Brown.

*Remarks:* The most common Mesozoic genera of Matoniaceae are *Phlebopteris*, *Matonidium* and *Matonia*; all are similar in pinna and frond morphology, but are distinguished by features of the sorus. *Phlebopteris* can be separated from *Matonia* and *Matonidium* by the absence of an indusium (Hirmer and Hoerhammer, 1936). Both *Matonidium* and *Matonia* are very similar, but the principle difference lies in the size of the indusium relative to the sorus. In *Matonia* the indusium completely covers the sorus, whereas in *Matonidium* it partially covers the sorus, and sporangia are partially exposed. The presence and size of the indusium are regarded as representative of a series of evolutionary changes beginning with an unprotected sorus in *Phlebopteris* to partial protection in *Matonidium*, and then full protection in *Matonia* (Hirmer and Hoerhammer, 1936; Harris, 1961; van Konijnenburg-van Cittert, 1993). However, this evolutionary scenario has been questioned by Klavins et al. (2004) due to the occurrence of the fossil *Tomaniopteris katonii* Klavins et al. (early Middle Triassic). This fossil is indusiate, and is significant because it predates the appearance of exindusiate *Phlebopteris* and partially indusiate *Matonidium*—therefore, the evolutionary hypothesis of soral evolution from exindusiate to indusiate is no longer supported by the fossil record (Klavins et al., 2004). Furthermore,

many workers have recognised that sori on a single frond in extant Matoniaceae can be indusiate and exindusiate (Seward, 1899; Harris, 1980; Kramer, 1990b; van Konijnenburg-van Cittert, 1993; Klavins et al., 2004). Examination of fertile fronds of extant *Matonia pectinata* R. Brown reveal that all three morphological states consistent with each of the fossil genera can all be found on one pinna (material examined at Missouri Botanical Garden and New York Botanical Garden Herbaria). These different morphologies represent different stages of maturation of the sorus. When mature, the sorus consists of a fully expanded indusium that completely covers the sporangia (as in *Matonia*), after this stage the indusium shrivels and only partially covers the sporangia (*Matonidium*). Subsequently, the indusium detaches leaving an exindusiate sorus consisting of a receptacle or ‘placenta’ and surrounding sporangia (*Phlebopteris*), and ultimately the indusium plus sporangia are shed leaving the receptacle or ‘placenta’ in the centre of a depression on the abaxial surface of the pinna.

The variability in the sori of modern taxa highlights two important implications when examining fossil Matoniaceae. Firstly, as noted by van Konijnenburg-van Cittert (1993) and Klavins et al. (2004), closer examination of currently recognised exindusiate fossils (i.e., *Phlebopteris*) may reveal that the exindusiate taxa are indusiate. Additionally, in cases where there are few specimens, caution must be taken in describing fossils as exindusiate (i.e., assignment to *Phlebopteris*) because the delicate nature of the indusium may have resulted in preservation of exindusiate fossils, although the parent plant may have been indusiate.

Numerous additional Mesozoic genera have been established for species with soral, indusial and venation features separate from *Matonia*, *Matonidium* and *Phlebopteris*. *Nathorstia* was originally established by Heer (1880), and was later redescribed by Krassilov (1965) and van Konijnenburg-van Cittert (1993). Some members of *Nathorstia* are similar to *Matonia* by the presence of an indusium, pinnate fronds, and round or oval sori. However, *Nathorstia* differs from *Matonia* by its secondary veins inserted at 90° to the midvein, and tertiary veins dichotomising equally at the margins. In contrast, *Matonia* has secondary veins that are less than or equal to 90°, and tertiary veins arising by anastomoses. Skog (1988) established *Delosorus* for three taxa restricted to the Early Cretaceous Potomac Group (Skog, 1988; Skog and Litwin, 1995). *Delosorus* is distinct with lobed pinnules and bipinnate fragments. *Piazopteris* was diagnosed from the Jurassic of Israel (Lorch, 1967). It has bipinnate foliage and a palmate frond, whereas other members of the family have pin-



nate foliage and pedate fronds. *Aninopteris* was established due to its constricted pinnule bases and long pinnules (over 70 mm)—other matoniaceous genera, in particular *Phlebopteris*, do not have constricted pinnule bases and pinnules are typically less than 70 mm in length (Givulescu and Popa, 1998). *Selenocarpus* is unique within Matoniaceae by its crescent-shaped sorus (van Konijnenburg-van Cittert, 1993), all other members of the family have oval to circular sori.

Berry (1911) established the genus *Knowltonella* for Cretaceous North American sterile foliage with pedate branching. He ascribed the pinnae to Matoniaceae believing the pedate branching to be a characteristic feature of the family, however, this frond morphology is also found in other fern families. Rushforth (1970) noted that *Knowltonella* may be aligned with Matoniaceae, but also remarked that fertile fragments were required to prove such an affinity. Despite this, *Knowltonella* was included in a later list of matoniaceous genera (Tidwell and Ash, 1994).

Another poorly understood genus is the monotypic *Matoniella* Hirmer and Hoerhammer, which was established for Cretaceous specimens from Germany. The specimens were originally described as *Matonia* based on the presence of an indusium. However, upon re-examination of the specimens, the material was separated from *Matonia* because the indusium could not be detected, and the genus *Matoniella* was established (Hirmer and Hoerhammer, 1936). At present the status of this genus is uncertain, and the specimens and genus require reinvestigation (van Konijnenburg-van Cittert, 1993).

Extant Matoniaceae is represented by two genera: *Matonia* and *Phanerosorus* (Kramer, 1990b). Extant *Matonia* grows via an underground rhizome and, at each node, iteratively produces a long stipe bearing an erect pedate frond. *Phanerosorus* has dichotomous rhizomes with pendant pseudo-dichotomous fronds.

*Matonia jeffersonii* sp. nov.

Figs. 2–5.

1981 cf. *Phlebopteris dunkeri* Schenk; Jefferson, p. 82–83, Plate 4.5, Figs. 8–13.

1983 cf. *Phlebopteris dunkeri* Schenk; Jefferson, Figs. 5, 9 and 10.

non 1990 cf. *Phlebopteris dunkeri* Schenk; Rees, p. 206, Plate 21, Fig B.

*Holotype*: KG. 2816.27b (Fig. 3b).

*Type locality and unit*: British Antarctic Survey locality KG. 2816 located on the eastern side of Titan Nunatak,

southeastern Alexander Island, Antarctica. Late Albian, Triton Point Formation, Fossil Bluff Group.

*Etymology*: In honour of T.H. Jefferson who first studied the Alexander Island flora.

*Material examined*: Twenty-four sterile fragments as follows: KG. 1704.4a, c, .5; KG. 2816.29, .31, .77, .88, .87a–k, .93; KG. 2821.10; KG. 4730.24, .26, .27; thirteen fertile fragments as follows: KG. 1704.25; KG. 2816.19, .27a, b, .28–.30, .87a, b, g; KG. 4659.10; KG. 4730.151.

*Diagnosis*: Pinnules sub-opposite to alternate, lanceolate, rarely slightly falcate; greater than 4 mm wide, typically 9 mm wide; base not constricted. Margins entire or irregularly incised. Pinnule midvein inserted at less than 90°; secondary veins opposite, rarely alternate, inserted at 50–90°, marginal angle greater than 50°. Anastomoses present. Sori circular or oval, interveinal, one sorus between two adjacent secondary veins.

*Description*: The incomplete sterile and fertile fragments are pinnate, but their overall shape is unknown. The largest pinna fragment is 86 mm long by 86 mm wide. The rachis is 2–3 mm wide and is flanked by 2 mm of lamina on both sides resulting in a total width of 6–7 mm (Figs. 2e and 3b). Pinnules are sub-opposite to alternate (Figs. 2e and 3b). Pinnule density is approximately five every 50 mm along one side of the rachis. Adjacent pinnules rarely overlap and are separated by up to 4.5 mm. The pinnule lamina is continuous with adjacent pinnules by the lamina along the rachis. At the pinnule base, a flange is formed by a gentle curvature of the basicopic region. The majority of pinnules are incomplete as they lack apices, but one fragment has an acute apex (Fig. 3a); the largest fragment is 108 mm long by 8 mm wide and is detached (Fig. 3c). Pinnules are 4–10.5 mm wide, but are typically 9 mm wide. The pinnules are lanceolate and in some cases slightly falcate, although the complete shape is unknown. The margins are entire, but may be incised at least one to two times (Figs. 2a,d and 3a).

The pinnule midvein departs the rachis at 45–67° (Figs. 2e, 3b and 4b). Secondary veins are opposite, or in one specimen they are alternate, with seven to eight secondary veins every 50 mm along one side of the pinnule midvein (i.e., one secondary vein every 1.4–1.6 mm). Secondary veins are prominent and arise at 51–90° to the midvein. Sterile pinnules produce secondary veins at less than 70° to the midvein, and fertile pinnules have secondary veins up to 90°. Secondary veins arch immediately adjacent to the midvein, pass straight to and intersect the pinnule margin at 53–81°; marginal angles are usually larger in fertile pinnules. Tertiary veins are 44–59° to the secondary vein. Anastomoses

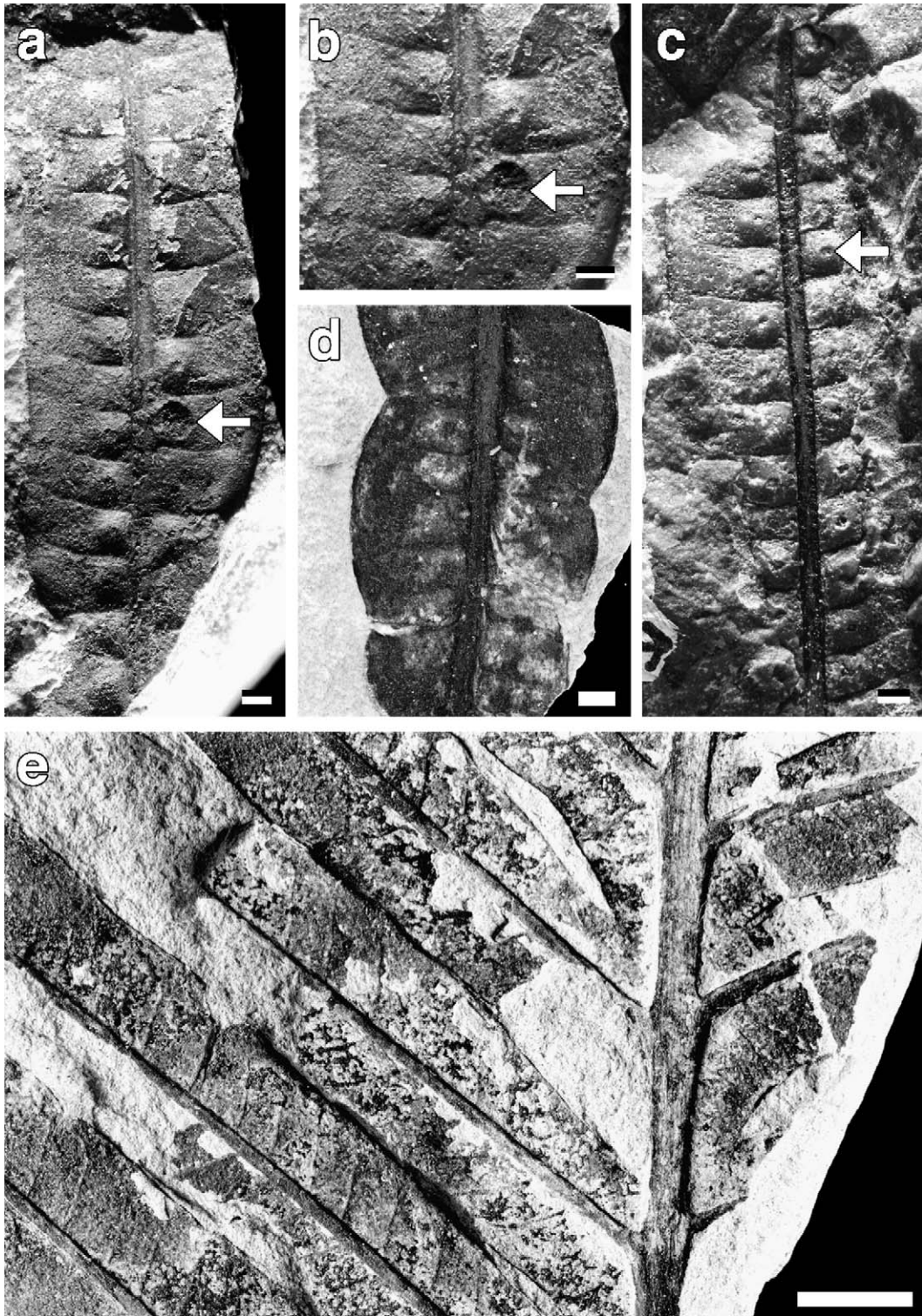


Fig. 2. Gross morphology of *Matonia jeffersonii*. (a) Incomplete, isolated fertile pinnule with interveinal sori, including a sunken indusiate sorus (arrowed), KG. 2816.29. (b) Enlarged view of (a) showing raised exindusiate sori and a sunken indusiate sorus (arrowed), KG. 2816.29. (c) Incomplete, isolated fertile pinnule with raised exindusiate sori; in the centre of the sori are receptacle/'placenta' bases (receptacle/'placenta' base arrowed), KG. 2816.30. (d) Incomplete, isolated fertile pinnule showing incised margin, KG. 4659.10. (e) Portion of sterile pinna with pinnules in a sub-opposite to alternate arrangement, KG. 2816.88. Scale bars: a-d=1 mm; e=5 mm.



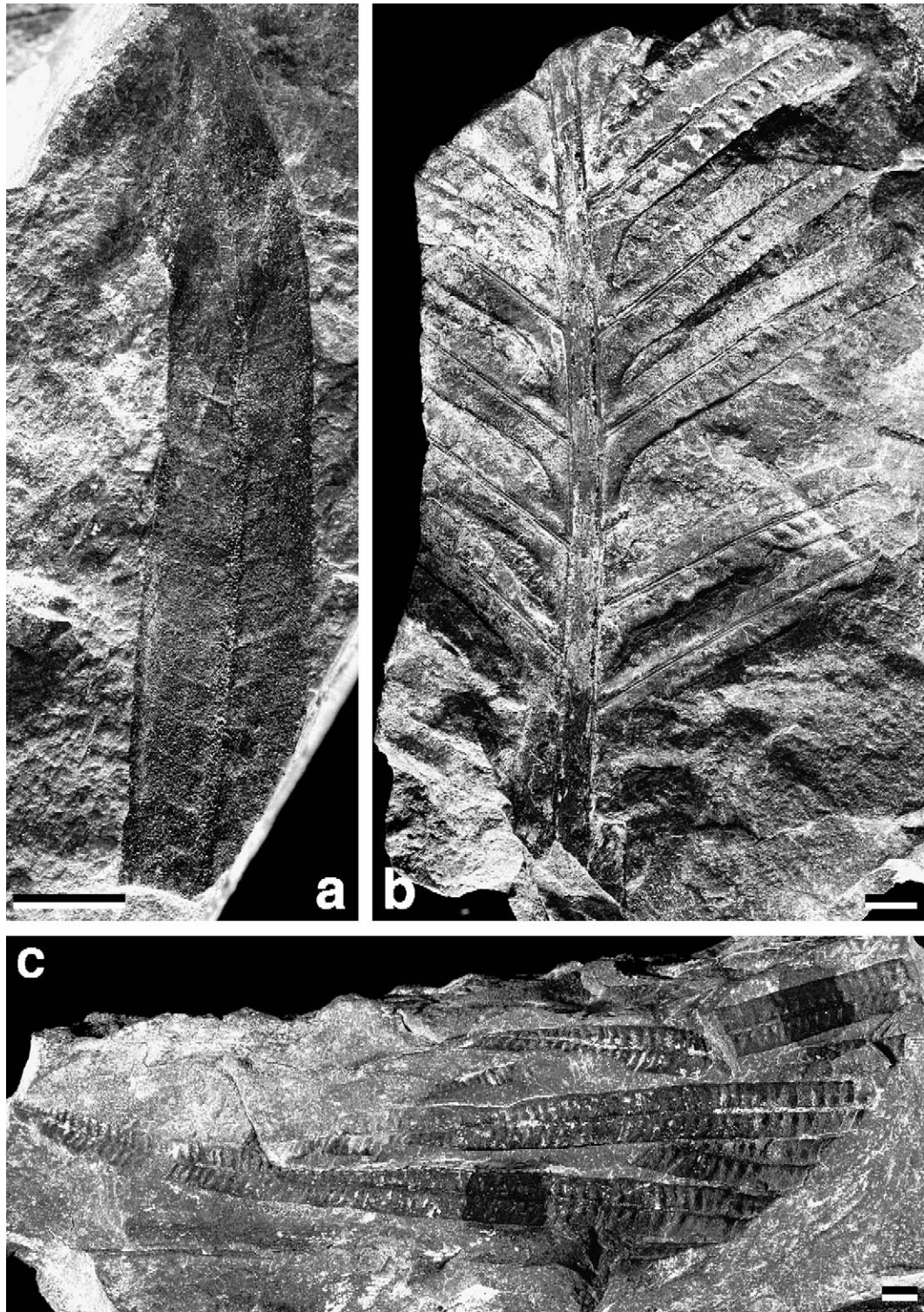


Fig. 3. Gross morphology of *Matonia jeffersonii*. (a) Tapering pinnule apex, KG. 2816.28. (b) Secondary pinna, KG. 2816.27b, holotype. (c) Fertile pinnule with straight margin, KG. 2816.27a. Scale bars: a–c=5 mm.

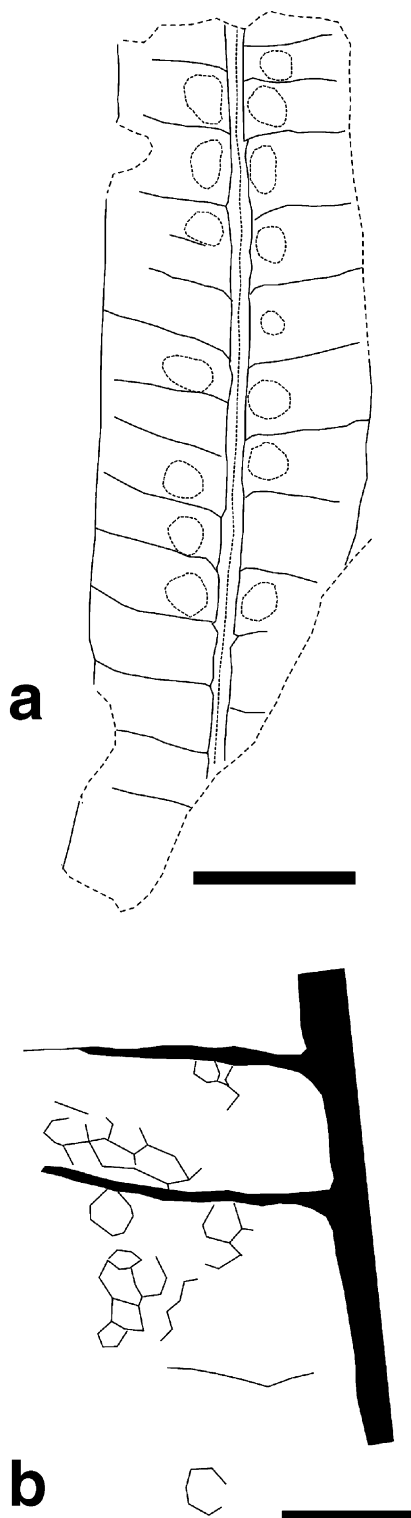


Fig. 4. Line drawings of *Matonia jeffersonii*. (a) Fertile pinnule, note interveinal sori and arching of secondary veins near midrib, KG. 2816.29. (b) Anastomosing tertiary veins between larger secondary veins, KG. 2816.87a. Scale bars: a=5 mm; b=1 mm.

present, irregularly pentagonal to hexagonal in shape, and the length to width ratio is 1:1 (Fig. 4b).

Sori are borne on pinna fragments that are either completely fertile, or have fertile distal pinnules and sterile proximal pinnules. There are up to 15 sori per pinnule occurring along both sides of the midvein, and there is one sorus between a pair of adjacent secondary veins (Figs. 2a–c and 4a). Sori are circular, 1 mm in diameter, or oval, 2 mm long by 1 mm wide. Sporangia could not be discerned because they were completely covered by a peltate indusium. When the indusium and sporangia have been shed the receptacle/‘placenta’ is visible in the centre of the sorus, and the receptacle is 0.25 mm in diameter. At the base of some receptacles are radiating structures that probably represent stalks of sporangia, indicating that the sporangia were arranged in a ring around the receptacle.

*Remarks:* The sori of *Matonia jeffersonii* are smooth oval or circular, comprising an indusium covering the sporangia. Intermediates with shrunken indusia revealing the sporangia below or detached indusium with sporangia remaining were not seen. *Matonia jeffersonii* sori vary according to the stage of maturity when they were preserved and which surface of the pinna is exposed. When the adaxial surface is revealed the midrib is raised above the rock surface and the sori form a cavity (Figs. 2e and 5b). Conversely when the abaxial surface is exposed the midrib forms a groove and the sori are raised (Figs. 2a–c and 5d). Specimens with a raised structure in the centre of a depression represent a detached sorus where the indusium and sporangia have been shed leaving only the receptacle/‘placenta’ in the centre (Fig. 5c). The counterparts to the specimens with a detached sorus appear to have a raised sorus and a depression in the centre corresponding to the receptacle/‘placenta’ (Figs. 2c arrowed, and 5d arrowed as RS and RP). When the indusium remains attached to the specimen (Fig. 5c) the sorus on the fossil appears to have a flattened surface (Figs. 2a,b arrowed, and 5d arrowed as SI).

The specimens, herein described as *Matonia jeffersonii*, were assigned to cf. B *Phlebopteris dunkerii* by Jefferson (1981, 1983) who recorded the presence of the indusium, but did not recognise it as a character that is absent in *Phlebopteris*. The specimens can be assigned to *Matonia* based on the circular to oval indusia that completely cover the sporangia, and anastomosing venation. van Konijnenburg-van Cittert (1993) noted that fossil Matoniaceae that have an expanded peltate indusium are placed in the genus *Matonia*—the sori of *M. jeffersonii* have this indusial morphology, and therefore, are assigned to *Matonia*.



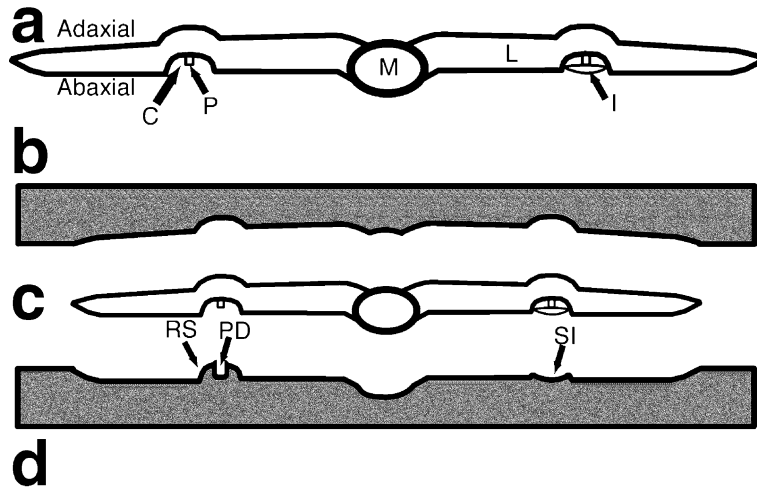


Fig. 5. Schematic interpretations of the sori of *Matonia jeffersonii*. (a) Transverse section of a fertile frond lamina (L) with midrib (M) and sori. One sorus is exindusiate with sporangia previously shed, leaving the receptacle/'placenta' (P) and a cavity (C). The other sorus is indusiate (indusium, I) with sporangia (not drawn) that are usually not visible below the indusium. (b) Fossil counterpart of adaxial surface showing raised midrib and sunken sori. (c) Fossil specimen. (d) Fossil counterpart of abaxial surface showing a lowered midrib, raised sorus (R) with a central depression (PD) corresponding to the receptacle/'placenta' and a sorus with indusium attached (SI).

Jefferson's specimens were synonymised with a fossils referred to cf. *Phlebopteris dunkerii* from Williams Point, Livingston Island (Rees, 1990). However, the Livingston Island specimen is distinct by its pinnules inserted at 75–90°, and discontinuous pinnules that are not connected along the rachis, whereas at Alexander Island the pinnules are inserted at 45–67°, connected along the rachis by a lamina, and are over ten times longer than pinnules of the Livingston Island fern (pinnule widths are closely comparable).

*Matonia* is unique within Matoniaceae as it is represented by both extinct and extant species. In the mature frond of the extant species *M. pectinata*, the longest pinnules are 40 mm (Seward, 1899). By comparison, the fossil taxon *Matonia jeffersonii* is considerably larger as its incomplete pinnules are up to 108 mm (Table 1). The fossil and extant species further differ by the larger sori of *M. pectinata* that are 9 mm in

diameter compared to 1–2 mm in *M. jeffersonii*. The fossil taxon *Anonipteris formosa* Givulescu and Popa (Givulescu and Popa, 1998) has pinnules of comparable length to *M. jeffersonii*: 70–100 mm long in *A. formosa*, and up to 108 mm in *M. jeffersonii*. However, *Anonipteris* is distinguished by its constricted and rounded pinnule bases, whereas the pinnule bases of *M. jeffersonii* are not constricted and are decurrent with a slight flange.

*Matonia braunii* (Goeppert) Harris is known from the Liassic of Germany and Greenland, and the Jurassic of Yorkshire, England (Harris, 1980). The sori of *M. braunii* terminate a vein whereas those of *M. jeffersonii* are interveinal. The venation of *M. braunii* can be distinguished by a marginal angle of 35° and two bifurcations of the secondary veins (Table 1). In contrast, *M. jeffersonii* marginal angles are 53–81° and secondary veins do not bifurcate.

Table 1  
Selected species assigned to *Matonia* and their morphology

	Pinna		Pinnule		Secondary venation	
	Length	Width	Length	Width	Pattern	Angle
<i>M. jeffersonii</i>	86	86	108*	4–10.5	Do not bifurcate; anastomoses	51–90°. (Marginal: 53–81°)
<i>M. pectinata</i>	440	61	40	3	Bifurcate close to midrib; anastomoses	Up to 90°
<i>M. braunii</i>	200‡	–	18–25	2.5–3.5	Dichotomise twice; anastomoses	—(Marginal: 35°)
<i>M. mesozoica</i>	–	3	4–9	3	Dichotomise 3–4 times; anastomoses	30–40°
<i>M. brownii</i>	150‡	–	3–30	–5–9	Bifurcate close to midrib; anastomoses	–
<i>M. brownii</i> var. <i>magnipinnulum</i>	300‡	–	5–60	2.5–6	Bifurcate, anastomose, free at margin	–

All measurements in mm. Data from Seward (1899), Rushforth (1970), Appert (1973), Kramer (1990b), Harris (1980), and this study. Symbols: \*: incomplete, ‡: estimated length, -: unknown.

*Matonia mesozoica* Appert, from the Late Jurassic to Early Cretaceous of Madagascar (Appert, 1973), is substantially smaller than *M. jeffersonii* with fertile pinnules up to 9 mm long and 3 mm wide, compared to 108 mm long and 4–10.5 mm wide in *M. jeffersonii* (Table 1). As expected for smaller pinnules there are fewer sori (6–10 sori per pinnule) in *M. mesozoica*, whereas there are up to 15 sori on pinnules of *M. jeffersonii*. Other characters that separate the two species are the more acute secondary veins (30–40°) and the secondary veins that dichotomise three to four times in *M. mesozoica*, compared to the more obtuse secondary vein angles (51–90°) and lack of secondary vein dichotomies in *M. jeffersonii*.

*Matonidium brownii* was first described from the Lower Cretaceous of North America (Rushforth, 1970). When re-examined it was transferred to *Matonia* based on the presence of a large, peltate indusium that entirely covers the sporangia (van Konijnenburg-van Cittert, 1993). *Matonia brownii* has pinnules up to 30 mm long and up to 9 mm wide (Table 1). A larger frond, referred to as *M. brownii* var. *magnipinnulum* Rushforth, has pinnules 5–60 mm long and 2.5–6 mm wide (Table 1). Both the variety and species have smaller pinnules (up to 60 mm long and 6 mm wide) than *M. jeffersonii* (up to 108 mm long and 10.5 mm wide). Wedge-shaped sporangia were extracted from *M. brownii* (Rushforth, 1970), but comparison of sporangial characters is not possible as sporangia have not been isolated from *M. jeffersonii*. Other features such as secondary vein density, the presence of anastomoses and soral sizes are similar between the two species.

#### Family GLEICHENIACEAE

*Gleicheniaceaphyllum* Crabtree emend. Nagalingum and Cantrill

*Type species: Gleicheniaceaphyllum falcatum* Crabtree.

*Emended diagnosis:* Frond, indeterminate, pseudo-dichotomous, tripinnate. At a single node are two to four primary pinnae plus an arrested laminar bud. Primary pinnae variable in size and shape. Secondary pinnae alternate to sub-opposite, elongate. Pinnules small (less than 5 mm in width and length), alternate, elliptic to deltoid to falcate to rhombic, apex obtuse to acute. Pinnule venation consisting of a midvein and 2–5 pairs of lateral veins that branch once or twice.

*Remarks:* Gleicheniaceae are known from approximately 11 fossil genera (Table 2). Of these, six are foliage genera that are defined principally by gross morpho-

Table 2

Fossil genera assigned to Gleicheniaceae

Compression/impression foliage genus	Resting bud
<i>Gleicheniaceaphyllum</i>	Present
<i>Gleicheniopsis</i>	Absent
' <i>Gleichenites</i> '	Present/absent
<i>Didymosorus</i>	?
<i>Gleichenoides</i>	?
<i>Szea</i>	No
Permineralised genus	Material
<i>Gleichenipteris</i>	Sporangia
<i>Boodlepteris</i>	Sporangia
<i>Antarctipteris</i>	Rhizome
<i>Chansitheca</i>	Sporangia
<i>Oligocarpa</i>	Sporangia

logical characters, and the remaining five represent permineralised fossils diagnosed by anatomical features. As Gleicheniaceae are identified primarily by a resting bud in the axil of the frond 'dichotomy', consequently, some of the permineralised material is tentatively aligned to the family (e.g., *Szea*), and the affinities of the other taxa (e.g., *Chansitheca*) have been questioned due to the lack of detail on the reproductive characters (Collinson, 1996). Of the six foliage genera, only two have been recorded showing a resting bud, however, one of these (*Gleichenites*) has considerable nomenclatural problems (Cantrill, 1998). *Gleichenites* Goeppert 1836 was originally based on five Palaeozoic species with dichotomously branched foliage, but no evidence of a resting bud. The branching pattern was thought to indicate affinities with Gleicheniaceae, but all Goeppert's original taxa are now recognized as belonging to Palaeozoic seed fern groups (Arber, 1917), rendering the name a nomenclatural synonym of one of the Paleozoic seed fern taxa. Arber (1917) recognised this problem and created *Microphyllopteris* to incorporate pinnate, bipinnate or dichotomising fronds bearing small pinnules that are similar to the extant *Gleichenia*. This proposal has gained wide acceptance within Australia, New Zealand and India (Cantrill, 1998). Berry (1924) also noted the invalidity of *Gleichenites*, and, as an alternative for fossil material, the extant genus *Gleichenia* was proposed and used. This proposal was later rejected because fossils either differ from extant *Gleichenia* or lack adequate characters to allow placement in *Gleichenia* (Seward, 1927). Seward (1927) continued to assign gleicheniaceae-like fossils to *Gleichenites*. Although taxonomically invalid, many researchers continue to use *Gleichenites* Seward (non-Goeppert) today (e.g., van der Burgh and van Konijnenburg-

van Cittert, 1984; Herbst, 1996). A proposal to rectify this situation included the creation of the form-genus *Gleicheniaceaphyllum* (Crabtree, 1988); this genus encompasses sterile pseudo-dichotomous fronds of Gleicheniaceae showing the characteristic resting bud and bearing small, variously shaped pinnules.

As an alternative to *Gleichenites*, we propose that *Microphylopteris* be utilised as a form-genus for species that have either an *unknown* branching pattern or dichotomous branching *without* resting buds. Species assigned to *Microphylopteris* may also have characters similar to *Gleichenia*, i.e., small pinnules, exindusiate sori and sporangia with a complete, transverse or obliquely transverse annulus. These characters are not exclusive to Gleicheniaceae (Cantrill, 1998), and consequently *Microphylopteris* is proposed for ferns that cannot be ascribed conclusively to the family. Alternatively, *Gleicheniaceaphyllum* is reserved as a form-genus for gleicheniacean material that has a resting bud between a two- to four-branched dichotomy.

*Gleicheniaceaphyllum* was previously restricted to fronds with a resting bud and two primary branches (amongst other characters), however, our emended diagnosis now incorporates fronds that have a resting bud and up to four primary branches all arising at a single node. Extant genera also possess species with different branching types, e.g., *Dicranopteris*. In the absence of the resting bud, *Gleicheniaceaphyllum acutum* would be assigned to *Microphylopteris*.

Extant Gleicheniaceae incorporates six genera and two subfamilies (Kramer, 1990a). The subfamily Gleichenioideae comprises *Dicranopteris*, *Gleichenia*, *Gleichenella*, *Sticherus* and *Diplopterygium*; and the subfamily Stromatopteridaceae consists of *Stromatopteris*. *Dicranopteris* is unique by the twice or more forked veins, 8–16 sporangia per sorus and trichome-bearing resting buds (Tryon and Tryon, 1982; Kramer, 1990a). The other genera have simple or once-forked veins, fewer sporangia per sorus, and naked or scale-covered buds. *Gleichenia* is distinguished by its pinnules that are ovate, comparatively shorter (1–3 mm), and distinctly revolute. *Sticherus* and *Diplopterygium* have longer pinnules (up to 45 mm) that are flat (i.e., non-revolute); the former has once pinnate primary branches and those of the latter are twice pinnate. *Stromatopteris* is sometimes separated into Stromatopteridaceae (Tryon and Tryon, 1982). Although *G. acutum* is allied to Gleicheniaceae, anatomical, soral, and resting bud (hairs versus scales) characters are needed to identify its relationship to extant taxa.

In *G. acutum* the presence of a resting bud amongst the bases of four axes, i.e., all at one node (Fig. 7b)

indicates its affinity to Gleicheniaceae. Although in some cases the resting bud may later develop into an axis (e.g., *Gleichenia elongata* Bak.), both fossil and extant members of this family are characterised by a resting bud, i.e., an arrested axis formed in the node amongst new branches. This morphology arises through a series of ‘double dichotomies’, where one of the branches from each dichotomy fails to develop (Chryslers, 1943). At the first dichotomy, one branch becomes a primary axis and the other branch immediately divides. Of the two branches arising from this latter division, one branch continues as the main axis, and the development of the other branch is suppressed and it becomes the resting bud. Holttum (1954, 1957) recognized six principal frond branching types within Gleicheniaceae (Fig. 6; Types A–F). In Type A the two branches are leafy and do not branch further (Fig. 6a; e.g., *Diplopterygium bancroftii* (Hook.) A. R. Sm., and *Dicranopteris nervosa* (Kaulf.) Maxon); in Type B, the two branches are leafless and branch once (Fig. 6b; e.g., in some *Gleichenia*); and in Type C, the branches are also leafless but branch numerous times (Fig. 6c; e.g., *Sticherus*, *Gleichenia underwoodiana* (Maxon) C. Chr., *Gleichenia longipes* (Fée) H. Christ in Schwacke). In Type D, there is the addition of an accessory branch associated with each main branch, resulting in four branches per node (Fig. 6d). Although the accessory branches appear branch-like, anatomically they represent highly developed pinnules (Chryslers, 1943). At each node in the Type D frond, the accessory branches are leafy and oriented backwards, and the main branches are leafless and undergo further division. This type occurs in *Dicranopteris linearis* J. Underw., and *Dicranopteris flexuosa* (Schrad.) Underw. Types E and F are distinguished by their asymmetrical patterns of growth. In Type E (found in *Dicranopteris pectinata* (Willd.) Underw.) after the primary branches are produced, one branch (of a branch pair) dichotomises and bears a leafy pair of axes, but the other branch becomes the main branch and undergoes further divisions—this pattern continues for all branch pairs produced on the frond (Fig. 6e). A variant of Type E is *Gleichenia pteridella* H. Christ., which lacks accessory branches. Type F is similar to types D and E as four axes are produced at one node, and the two accessory branches are leafy. However, in Type F, the development of main branches is unequal: one of the main branches continues growth and becomes the main rachis, but growth of the other main branch is suppressed (Fig. 6f). In total there are three developed ‘branches’ (two accessory and one main branch) at a node.

Comparison of these six types to *G. acutum* reveals closest similarity to types D and E—where each main-



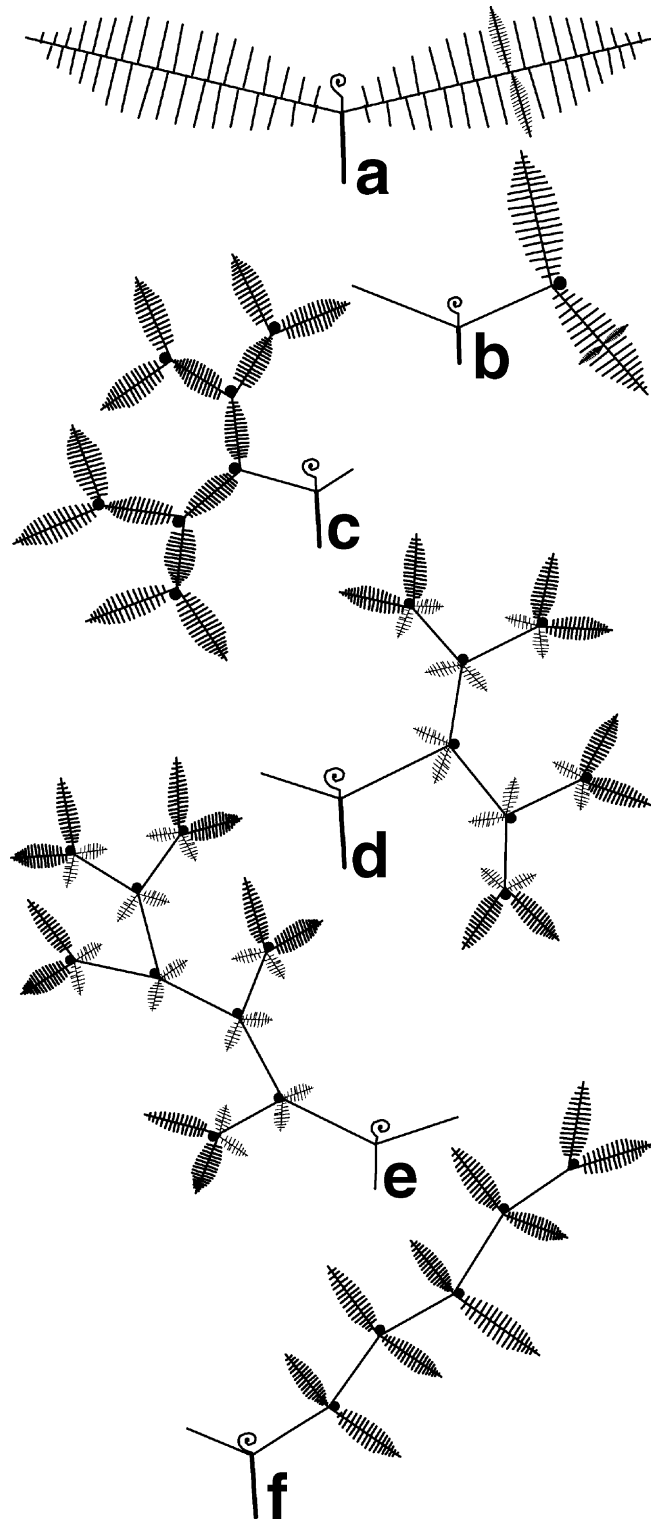


Fig. 6. Frond branching types in Gleicheniaceae. (a)–(f) Six of the principal branching types. The black dot indicates a permanently arrested bud, and the coil indicates a dormant bud that may or may not develop into an axis. After [Holtum \(1954\)](#).

branch pair has an accessory-branch pair—i.e., four branches per node. Due to the incomplete nature of the fossil it is difficult to determine which of these two types are found in *G. acutum*. In the fossil, two branches are leafy (Figs. 7c and 10a), and the two other branches are either too short or incomplete to determine if they were leafy or leafless and underwent further divisions. Furthermore, the lack of anatomical evidence prevents full interpretation of the morphology of this node. It is possible that the four branches arise from an unequal series of four dichotomies (cf. the double dichotomies as described by Chryslar (1943) in extant taxa); or the two leafy branches may represent accessory branches, i.e., are pinnule-like in vascular origin. The node alternatively may be interpreted as comprising two leafy branches, an unknown (leafy or leafless) branch, plus a branch arising out of the resting bud. However, in cases where a branch develops from the resting bud (e.g., *Dicranopteris cryptocarpa* (Hook.) Looser, and *Dicranopteris squamulosa* (Desv.) Looser), the resting bud is transformed into a branch, and the bud is no longer present. Comparison of this morphology to the fossil reveals that the alternative interpretation is highly unlikely because the fossil retains a resting bud, therefore, it does not seem possible that this fourth branch derived from the resting bud.

*Gleicheniaceaphyllum acutum* sp. nov.

Figs. 7–10.

1981 UNISORUS-DIMINUT; Jefferson, p. 60, Plate 4.1, Figs. 1–8 (all figured specimens and pars of listed specimens).

1981 BREVIPTERIS-RHOMBOID; Jefferson, p. 65, Plate 4.2, Figs. 1–5.

1982a cf. *Coniopteris* sp. Brongniart; Jefferson, Plate 1, Fig. a, d (illustration only).

1983 ?cf. *Gonatosorus nathorsti* Raciborski (*Coniopteris*-type fern); Jefferson, Fig. 5.11 (illustration only).

*Holotype*: KG. 2815.75a–76a (one specimen) (Figs. 7 and 10a, b).

*Type locality and unit*: British Antarctic Survey locality KG. 2815 from the southern part of Coal Nunatak, southeastern Alexander Island, Antarctica. Late Albian, Triton Point Formation, Fossil Bluff Group.

*Etymology*: Acutum, for the acute pinnule apices.

*Material examined*: Ninety sterile specimens as follows: KG. 1672.22; KG. 1701.19, .47; KG. 1703.15, .18, .27, .42, .61, .67–70, .74, .75, .116, .117, .122; KG. 1704.29; KG. 1719.5–7, .10, .17; KG. 2814.10, .22, .122, .128,

.139; KG. 2815.75a/76a (one specimen), .214, .217; KG. 2816.8, .9a, b, .14, .15, .18, .23, .25, .28, .54, .94, .206; KG. 2818.4; KG. 2820.12, .82, .91a–b, .92, .93, .100a, b, .102, .134; KG. 2821.15, .34, .35a, .36–38, .40, .41, .42a, .87; KG. 4716.7, .17; KG. 4717.1, .2, .4, .32; KG. 4724.3, .4, .6, .7, .21; KG. 4730.5, .13; KG. 4736.6–10, .16, .17, .19, .21, .22; KG. 4737.10; seventeen fertile specimens as follows: KG. 2815.194, .204–207, .210, .213, .216, .217; KG. 2816.4, .5, .20, .22; KG. 2817.10; KG. 2820.21b, .45, .101.

*Diagnosis*: Secondary pinnae are opposite to alternate; pinnules rhombic with an acute apex.

*Description*: Fronds at least 155 mm long, bearing four primary pinnae in one node with a resting bud at the centre of the node (Figs. 7b–d and 10a). Petiole at least 18 mm long by 2.5 mm wide. Primary pinnae incomplete, at least 137 mm long by 106 mm wide. Adjacent primary pinnae diverge at 10–105°.

There are two to seven secondary pinnae per 10 mm inserted at 45–110° (more acute angles in the distal region with smaller secondary pinnae), bases are 1–5 mm apart. Secondary pinnae opposite to alternate (Figs. 8 and 9a, c); both types of arrangement can be found on the same axis. Sterile and fertile secondary pinnae are 4.5–52 mm long by 1–4 mm wide, and are narrow oblong to linear. Pinnules are arranged alternately and diverge at 40–66° to the secondary rachis (Figs. 7, 8b and 9d). Pinnules are up to 2 mm long by 2 mm wide, rhombic, asymmetrical and widest at the base. There are six to eighteen pinnules per 10 mm, adjacent pinnules are not continuous, and are less than 1 mm apart or sometimes contiguous. The pinnule margin is obscure on the basisopic side but the acrosopic margin is straight or slightly constricted; apices are acute (Figs. 7a, 9c and 10b, d). One vein enters the pinnule and extends to the apex, bearing up to three secondary veins along one side of the midvein at 30–52°; secondary veins with one to two lateral veins (Fig. 10c).

Fertile and sterile pinnules are borne on the same axis, and the pinnules are not distinctly different in size. There is one sorus per pinnule (Fig. 9). Sori are less than 1 mm diameter, circular to elliptic with the greatest dimension parallel to the pinnule base. Sori are borne on or near the acrosopic margin and are raised or depressed relative to the lamina (Fig. 10d). The acrosopic margin may be recessed when a sorus is present, resulting in a crescent-shaped pinnule lamina. Sori have a central circular structure, 0.1 mm in diameter, probably representing the receptacle. Sporangial details are unknown.

*Remarks*: Jefferson (1982, 1983) published and illustrated *G. actum* as *Coniopteris*-type ferns. However, the terminal, reniform sori typical of *Coniopteris* differ

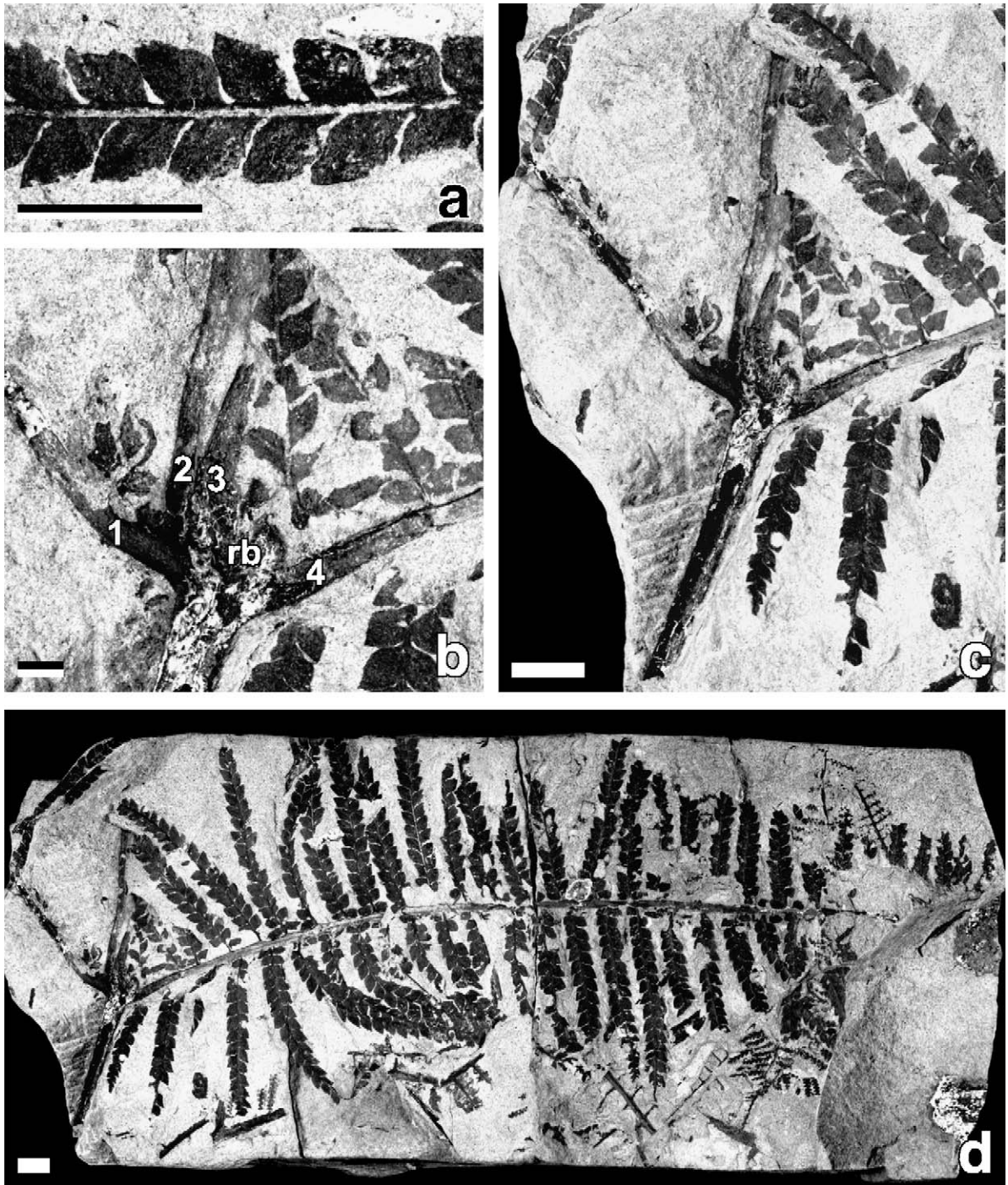


Fig. 7. Gross morphology of *Gleicheniaceaphyllum acutum*, holotype, KG. 2817.75a/76a (one specimen). (a) Portion of secondary pinna bearing rhombic pinnules with acute apices. (b) Resting bud (labeled rb) at the base of four secondary branches (labeled 1–4). (c) Resting bud at the base of four secondary branches and a petiole; note that the left- and rightmost secondary branches have primary pinnae attached. (d) Frond, complete specimen. Scale bars: a=5 mm; b=2 mm; c=5 mm; d=10 mm.

markedly from those of *G. acutum* that are circular to elliptic and occur on the pinnule lamina. The majority of *G. acutum* fragments have rhombic, asymmetric

pinnules with acute apices, however, two of the 107 specimens have unusual symmetrical pinnules with rounded apices, features more typical of a species of



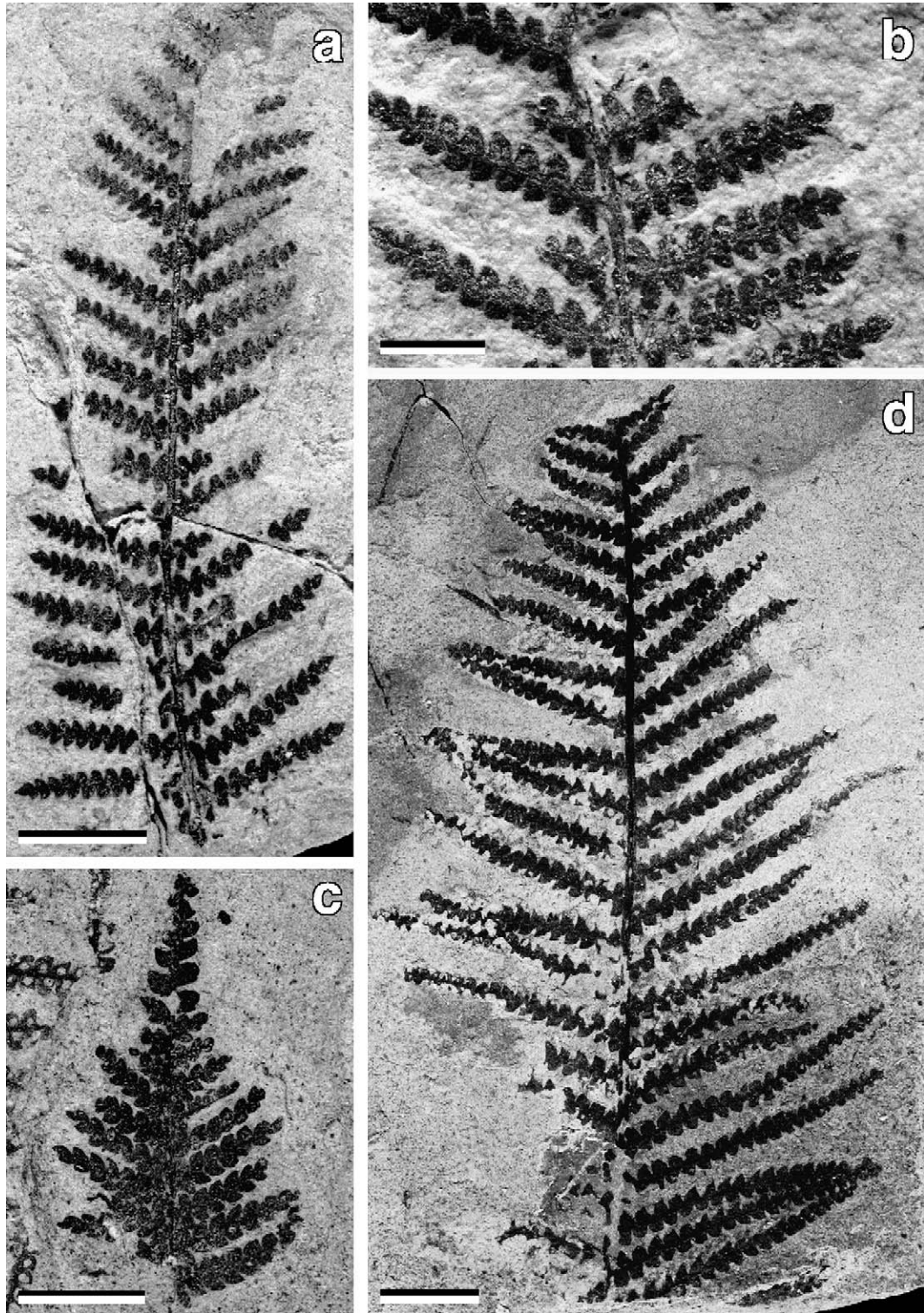


Fig. 8. Gross morphology of *Gleicheniaceaeophyllum acutum* primary pinnae. (a) Sterile primary pinna, KG. 2814.22. (b) Alternate pinnules with acute apices, KG. 2814.128. (c) Primary pinna apex, KG. 2816.20. (d) Sterile and fertile primary pinna, KG. 2816.206. Scale bars: a–d=5 mm.



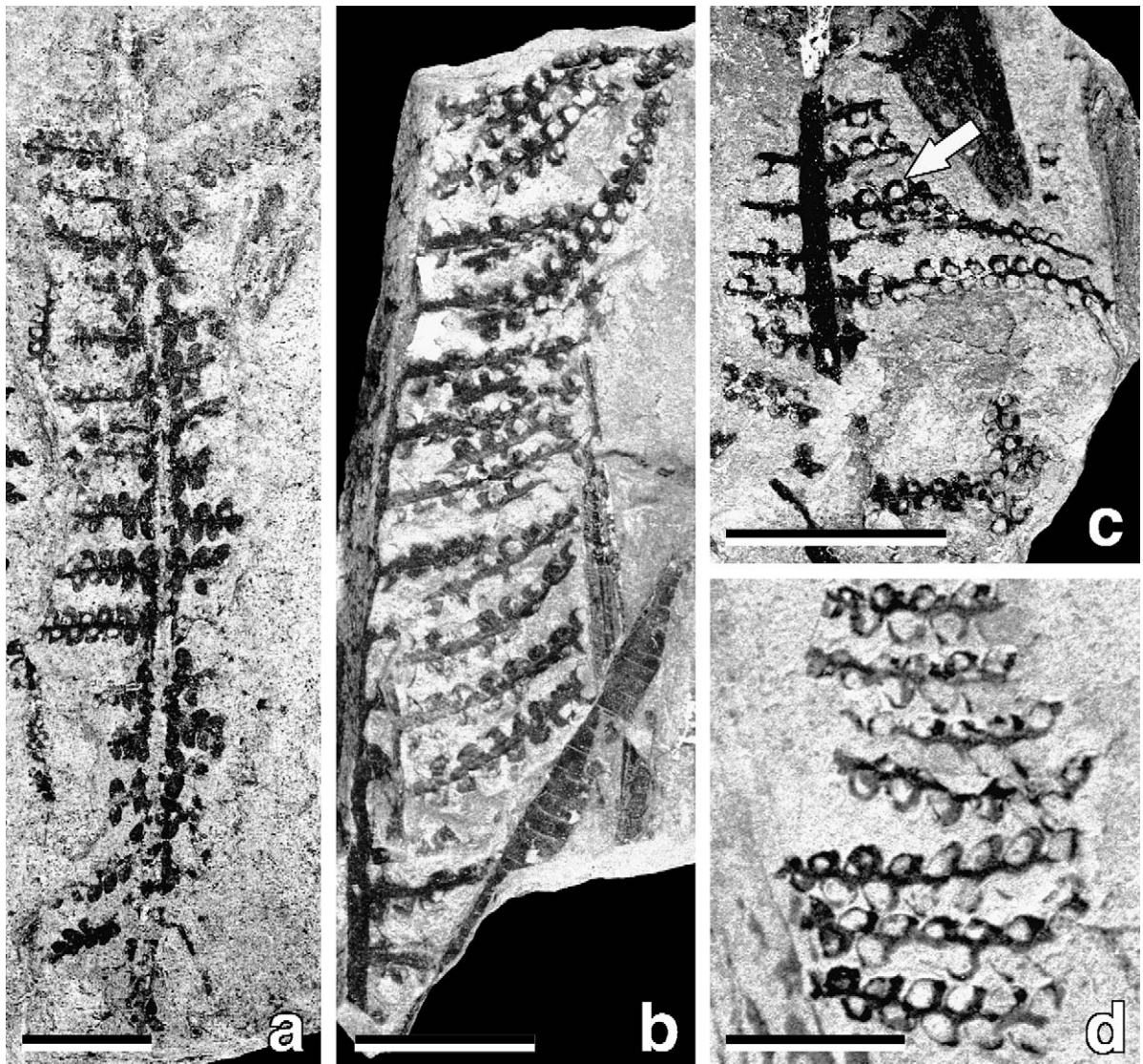


Fig. 9. Gross morphology of *Gleicheniaceaphyllum acutum* fertile primary (a–c) and secondary (d) pinnae. (a) KG. 2816.20. (b) KG. 2815.205. (c) Note pinnule with acute apex (arrowed), KG. 2815.204. (d) Note acute apices, KG. 2816.20. Scale bars: a–d=5 mm.

*Microphylopteris* also found at Alexander Island. The two specimens are possibly distorted or aberrant pinnae as other characters are consistent with *G. acutum*.

*Gleicheniaceaphyllum falcatum* Crabtree was recovered from Late Albian sediments in western USA (Crabtree, 1988), and was formerly the sole member of the genus *Gleicheniaceaphyllum*. This taxon differs from *G. acutum* principally by the presence of two primary branches, compared to four in *G. acutum*. Further differences lie in the obtuse to sub-acute pinnule apices and continuous pinnule laminae in the American species, compared to the acute apices and separate pinnules in the Antarctic taxon.

*Gleicheniaceaphyllum acutum* is similar to material typically described as *Microphylopteris*, but pinnules of *G. acutum* differ by their rhombic shape and acute apices. Many species of *Microphylopteris* (*Gleichenites*) have pinnules with blunt, obtuse apices and are typically ovate or oblong (e.g., see Arber, 1917; Seward, 1927; Herbst, 1962a,b; Bose and Sah, 1968).

In Antarctica, ferns with small *Microphylopteris*-like pinnules occur in several Cretaceous assemblages, but have not been recovered from older Jurassic and Triassic floras. *Gleichenites* sp. cf. *Gleichenites sanmartini* Halle was recorded from the Aptian President Head, Snow Island flora of the Cerro Negro Formation

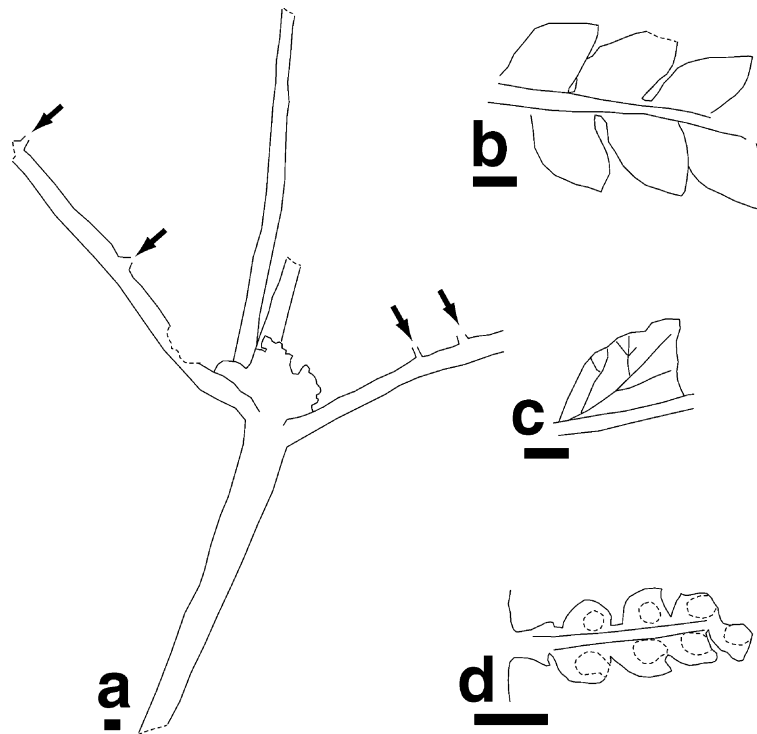


Fig. 10. Line drawings of *Gleicheniaceaphyllum acutum*. (a) A petiole with resting bud at the base of four primary branches; arrows indicate points of pinna attachment on two of the branches, KG. 2815.75a/76a. (b) Alternately inserted sterile pinnules with acute apices, KG. 2815.75a/76a. (c) Pinnule venation, KG. 2820.92. (d) Alternately inserted fertile pinnules, note acute apices on some pinnules, KG. 2815.204. Scale bars: a–d = 1 mm.

(Torres et al., 1997). The material comprises one fertile pinnate fragment, however pinnule shape, pinnule insertion angles, venation angles and pattern are not noted. It appears to be morphologically similar to and is probably synonymous with *Lophosoria cupulatus* Cantrill from the same locality and Byers Peninsula, Livingston Island (Cantrill, 1998, 2000). *Lophosoria cupulatus* also incorporates foliage described as *G. sanmartini* from Byers Peninsula, Livingston Island (Hernandez and Azcarate, 1971). *Lophosoria cupulatus* was assigned to the Lophosoriaceae principally due to the in situ occurrence of the lophosoriaceous spore *Cyatheacidites* and also by the numerous paraphyses and the presence of at least six sporangia in the sorus (Cantrill, 1998).

In addition to *Lophosoria*, the Byers Peninsula, Livingston Island flora has three species of *Gleichenites*: *Gleichenites sanmartini*, *Gleichenites argentinica* Berry emend. Herbst, and *Gleichenites* sp. (Cesari et al., 1999, 2001). *Gleichenites sanmartini* fragments are separate from *G. acutum* by its larger sori and the continuous pinnule laminae, whereas those of *G. acutum* consist of separate, discontinuous pinnules. *Gleichenites sanmartini* yielded in situ spores; the spores were distinct from *Cyatheacidites*, hence the

specimens were not transferred to *Lophosoria*. *Gleichenites argentinica* bears multiple sori per pinnule and its pinnules are longer (7 mm), whereas those of *G. acutum* (2 mm) bear one sorus per pinnule. The sterile fragment *Gleichenites* sp. matches *G. acutum* in pinnule morphology and secondary pinna arrangement; however, the lack of fertile material and the absence of the branching pattern precludes closer comparison to *G. acutum*.

## 5. Discussion

### 5.1. Palaeoecology and the polar environment

The ecology of the Alexander Island ferns can be inferred by examining their morphology and comparing the taxa to their extant relatives. The habit of *Matonia jeffersonii* was probably similar to extant and other fossil Matoniaceae in having pedate morphology. Extant *Matonia pectinata* bears pinnae that are 2 cm wide and fronds are up to 50 cm wide; using these values and the 8.6 cm width of *M. jeffersonii* pinna, the fossil frond could have attained sizes of 2 m in width. The *Gleicheniaceaphyllum acutum* growth habit, which can be inferred by the morphology of extant Gleiche-



niaceae, was probably scrambling, and fronds were likely large and spreading through indeterminate pseudo-dichotomies. Other pedate forms occurring at Alexander Island are *Hausmannia papilio* (Cantrill, 1995), and an undescribed species of pedate frond (Nagalingum, 2003). *Hausmannia papilio* has affinity to Dipteridaceae, and had pedate fronds estimated at 12 cm in width. The undescribed species of pedate frond is incomplete, and at least 8 cm wide and 5 cm long. Another undescribed fern, *Microphylopteris* (Nagalingum, 2003), exhibits vegetative morphology similar to extant Gleicheniaceae, and may have also had a scrambling, spreading habit.

In total, there are three species of ferns at Alexander Island that are interpreted as having a pedate habit and two taxa with a scrambling habit. These morphologies result in large fronds that occupy a large percentage of vegetation cover. The large fronds maximize light interception, allowing these ferns to colonize and dominate in exposed (i.e., lightly shaded), and recently disturbed (consequently sparsely vegetated) areas. Extant Matoniaceae, Dipteridaceae and Gleicheniaceae display this habitat preference, occupying sunny, lightly shaded sites, typically on exposed mountain slopes or rock cuttings, and, in the case of Gleicheniaceae, they also occur in open areas in moderate altitudes and lowland regions (Tryon and Tryon, 1982; Kramer, 1990a,b). These extant taxa also prefer nutrient-poor soils, and it is possible that the extinct taxa shared this ecological tolerance. On Alexander Island, paleosols with mycorrhizal root nodules suggest the occurrence of nutrient-poor soils (Falcon-Lang et al., 2001).

Facies studies at Alexander Island show the presence of open and disturbed environments (Falcon-Lang et al., 2001). Geological evidence also demonstrated the occurrence of large flooding events that covered the vegetation completely. Such disturbance events may have assisted the dominance of pedate and scrambling forms that could regenerate via underground rhizomes, and produce large (pedate and scrambling) fronds that could out-compete other taxa by intercepting the majority of available light.

Compared to other Early Cretaceous Southern Hemisphere polar floras (e.g., Australia: Drinnan and Chambers, 1986; McLoughlin et al., 2002; South America: Archangelsky, 2003), highly dissected ferns with a pedate or spreading habit are common at Alexander Island. The predominance of these forms may also be related to the polar conditions and unusual photoperiod experienced at Alexander Island, which lay at 75° S during the Cretaceous (Smith et al., 1994). The Early Cretaceous polar environment was

reconstructed as equable in the summer months with constant sunlight and warm conditions (Read and Francis, 1992). However, the winter season consisted of frost and extreme cold, and at least 2 months of unbroken darkness (Read and Francis, 1992). As current polar environments are not sufficiently warm to support similar ecologically diverse vegetation at Alexander Island, there are no modern plant analogues from which polar ecological strategies can be inferred. Similarly, empirical evidence demonstrating fern strategies for tolerating long periods of darkness has yet to be tested; however, conifers have been shown to tolerate warm, prolonged dark conditions (Read and Francis, 1992; Royer et al., 2003).

In winter conditions with cold and reduced day length, extant plants generally survive as either evergreens or regenerate as annuals. Using growth ring rates, conifers at Alexander Island were interpreted as evergreen and deciduous (Falcon-Lang and Cantrill, 2000). It is possible that ferns were evergreen, and the pinnae of *Matonia jeffersonii* appear thick and coriaceous, possibly as an adaptation to frost. However, it is unlikely that fronds of this fern, and others with relatively more delicate laminae, survived the freezing polar conditions. It is more likely that the ferns became dormant during winter darkness, and regenerated as annuals from underground rhizomes when the photoperiod altered. At this time there was competition to produce new fronds and maximize light interception for photosynthesis and growth—the most successful ferns being those that produced large and numerous fronds. This was probably best achieved through the pedate and scrambling habits, and hence *M. jeffersonii* and *G. acutum* would have been successful in the polar conditions at Alexander Island.

### 5.2. The 'demise' of ferns due to competitive displacement

Compared to the Mesozoic, extant Matoniaceae and Gleicheniaceae have restricted ranges and generally lower floristic importance. Matoniaceae is currently known only from the Malay Peninsula, and Gleicheniaceae occurs mostly in pan-tropical and temperate regions (Tryon and Tryon, 1982; Kramer, 1990a,b). Fossil evidence, however, demonstrates wider ranges of these families. Fossil Matoniaceae occurs throughout the Northern Hemisphere, particularly in Europe and North America, and is also recovered from Gondwanan floras of India and Madagascar (van Konijnenburg-van Cittert, 1993; Collinson, 1996). Fossil Gleicheniaceae is best known from the Northern Hemisphere (Green-

land, U.S.A., England) (Seward, 1927; Harris, 1931; Andrews and Pearsall, 1941; Gandolfo et al., 1997; Herendeen and Skog, 1998); most Southern Hemisphere so-called representatives (*Gleichenites* and *Microphylopteris*) lack gleicheniaceous synapomorphies such as pseudo-dichotomous branching with resting buds, and their affinity to the family is therefore doubtful (Cantrill, 1998). Possible factors contributing to the reduced range of Matoniaceae and Gleicheniaceae include a combination of unfavourable ecological conditions coupled with global climatic shifts and vegetational changes.

It has been suggested that competitive displacement, because of angiosperm diversification and expansion, was responsible for the decline in ferns during the Cretaceous (Crane, 1987). More recently, however, studies have shown that this does not apply to all fern groups (Nagalingum et al., 2002; Pryer et al., 2004; Schneider et al., 2004). The fossil record of fern spores in Australia and Antarctica demonstrates that although ferns declined during the Late Cretaceous, some individual fern families diversified and became more abundant (Nagalingum et al., 2002; Nagalingum, 2003). Similarly, divergence time estimates of extant taxa show that some groups, e.g., polypods, radiated during the Cretaceous (Pryer et al., 2004; Schneider et al., 2004).

The macrofossil record of Matoniaceae shows a high diversity and wide distribution during Triassic (Tidwell and Ash, 1994; Collinson, 1996). During the Jurassic the family decreased substantially in diversity and distribution, and this trend continued into the Cretaceous. There are no (or at most few) records known from Late and post-Cretaceous deposits (Collinson, 1996). Spore data from Australia and Antarctica shows that prior to and following the angiosperm radiation the abundance and diversity of Matoniaceae (and Dipteridaceae) were generally unchanged (Nagalingum et al., 2002; Nagalingum, 2003). Molecular data gives evidence for a limited Cretaceous radiation of Matoniaceae occurring as a divergence between the two modern genera, *Matonia* and *Phanerosorus* (Pryer et al., 2004; Schneider et al., 2004). Using all available evidence, it appears that the decline of Matoniaceae had occurred prior to angiosperm radiation—there were no further declines during the Cretaceous, rather the family underwent a limited radiation. As such *Matonia jeffersonii* appears subsequent to the decline of Matoniaceae, and is one of the last fossil records of the family.

Similarly, various sources of data suggest that Gleicheniaceae did not decline concomitant to angiosperm expansion. Collinson (1996) postulated that

true Gleicheniaceae appeared in the Cretaceous, and that Permian–Triassic so-called Gleicheniaceae were part of an extinct but related group. Recently published molecular divergence time estimates provide evidence for a Cretaceous origin of the extant crown group members (true Gleicheniaceae) (Pryer et al., 2004; Schneider et al., 2004). Spore data shows that Cretaceous Gleicheniaceae doubled in diversity and abundance (Nagalingum et al., 2002). Collectively, these data show that Gleicheniaceae radiated, rather than declined, during the Cretaceous. The gleicheniaceous taxon *Gleicheniaceaphyllum acutum* may represent a taxon that evolved during the Cretaceous radiation—more detailed soral and resting bud characters could link *G. acutum* more closely to modern genera.

## 6. Conclusions

The new species *Matonia jeffersonii* can be assigned to Matoniaceae based on the presence of circular to oval sori with a peltate indusium. The taxon is most similar to *Matonia* because the peltate indusium completely covers the sporangia. *Gleicheniaceaphyllum acutum* is distinct by the rhombic pinnules with acute apices. This species is assigned to Gleicheniaceae based on the presence of the synapomorphy of a resting bud surrounding by branches. The inferred pedate habit of *M. jeffersonii* and scrambling morphology of *G. acutum* were probably advantageous during the high disturbances, cold winters and unusual photoperiod occurring in this polar environment.

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