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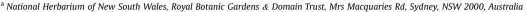
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The Albian fern flora of Alexander Island, Antarctica

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ABSTRACT

The Albian Alexander Island macrofossil flora from the Antarctic Peninsula preserves a diverse community of liverworts (Marchantiophyta), ferns (Polypodiopsida), Lycopodiales, Equisetales, Cycadales, Ginkgoales, seed-ferns (Bennettitales and Pentoxylales), Coniferales, and the first representatives of angiospermous leaves in Antarctica. Despite the presence of angiosperms in this assemblage, ferns are the most diverse element of the flora and are also ecologically dominant, while angiosperms contribute a smaller component to floristic diversity and have low abundance. Here we describe 11 fern taxa from this assemblage. The fossils are assigned to Cladophlebis, Sphenopteris and two newly created genera. The new genera and species are described under Adiantitophyllum serratum gen. et. sp. nov. and Nunatakia alexanderensis gen. et. sp. nov., and the new species are recognized as Cladophlebis dissecta sp. nov., Cladophlebis drinnanii sp. nov., Cladophlebis macloughlinii sp. nov. and Sphenopteris sinuosa sp. nov. In total, there are 24 fern species known from Alexander Island. In comparison to older floras (Jurassic) there is a greater diversity of ferns, while latest Cretaceous floras preserve significantly fewer fern species and more angiosperms. Possible factors that might account for such high fern diversity are high rainfall or generally humid conditions, regular disturbances by flooding and occasionally fire, and the preservation of a diverse range of fern communities that represent several palaeoenvironments.

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1. Introduction

Jurassic and Cretaceous macrofloras in the Antarctic are confined to the Transantarctic Mountains and West Antarctica. The Transantarctic Mountains preserve a Devonian to Jurassic foreland basin sequence, and the last phase of sedimentation is associated with extensive volcanism as a result of Gondwana fragmentation. The Jurassic sequences in the Transantarctic Mountains are host to silicified dipterid ferns from the Lower Jurassic at Shafer Peak and Mount Carson (Bomfleur and Kerp, 2010; Bomfleur et al., 2011) and the Middle Jurassic at Storm Peak (Yao et al., 1991). Other fern groups in the Jurassic on the Transantarctic Mountains include the Matoniaceae (Matonidium) and Dicksoniaceae (Coniopteris) (Bomfleur et al., 2011). Additional gymnospermous plant fossils occur at various localities (e.g., Plumstead, 1962, 1963; Townrow, 1967a,b) including standing trees (Jefferson et al., 1983). In contrast, West Antarctica formed part of an active margin setting with sedimentation in forearc, intraarc, and backarc basins. Jurassic floras include those found in the Hope Bay and associated floras of the Botany Bay Group (Halle, 1913b; Gee, 1989; Rees, 1990; Rees and Cleal, 2004), which have been recently dated as Middle Jurassic (Hunter et al., 2005). Other Jurassic floras include those of the South Orkney Islands (Cantrill, 2000b), further south in the Latady Basin (Cantrill and Hunter, 2005), and the Alexander Island forearc basin (Taylor et al., 1979). Alexander Island lies on the west side of the Antarctic Peninsula where it preserves a thick forearc-basin sequence (Butterworth et al., 1988; Doubleday et al., 1993; Macdonald et al., 1999). Here plant fossils are found in Lower-Middle Jurassic, Upper Jurassic, and Cretaceous horizons (Taylor et al., 1979; Nichols and Cantrill, 2002).

Cretaceous deposits are lacking in the Transantarctic Mountains, but are widespread in the Antarctic Peninsula region. Apart from Alexander Island, macrofloras are known from the South Shetland Islands (Aptian to Maastrichtian, e.g., Cantrill, 1997, 1998, 2000a; Césari et al., 1999; Césari, 2006; Vera, 2007, 2009, 2012, 2013) and the Larsen Basin on the east side of the Antarctic Peninsula (e.g., Hathway et al., 1998; Eklund, 2003; Eklund et al., 2004; Hayes et al., 2006; Kvacek, 2014). Ferns have been described in detail from several of these floras including those of the South Shetland Islands (e.g., Philippe et al., 1995; Torres et al., 1997; Cantrill, 1997, 1998,

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2000a; Césari et al., 1999; Nagalingum, 2002, 2007; Césari, 2006; Vera, 2007, 2009, 2012, 2013) and Alexander Island (Cantrill, 1995, 1996; Cantrill and Nagalingum, 2005; Nagalingum and Cantrill, 2006). Within the Fossil Bluff Group of Alexander Island the best-preserved plant material derives from the Lower Cretaceous Triton Point Formation—a unit of fluvial deposited sandstones and mudstones (Nichols and Cantrill, 2002). The fossil forest horizons of the Triton Point Formation are late Albian in age, based on the age of bracketing marine molluscan faunas (Kelly and Moncreiff, 1992; Moncreiff and Kelly, 1993).

The earliest investigations of the Alexander Island flora were conducted by Jefferson (1981, 1982a,b, 1983; Jefferson et al., 1983). Jefferson described 22 fern palaeotaxa (i.e., non-Linnaean 'species' groups), together with bryophytes, cycads, seed-ferns (Pentoxylales and Bennettitales), ginkgoes, and conifers. Since Jefferson's work several groups in the flora have been re-examined and re-described based on further collections. Liverworts are represented by three genera and ten species, and are the second most diverse group after ferns (Cantrill, 1997). Pentoxylaleans are represented by leaves, ovulate cones, and stems (3 species; Howe and Cantrill, 2001). Conifers are known from five wood taxa and nine species of foliage remains; this group is relatively abundant within the flora (Falcon-Lang and Cantrill, 2000; Cantrill and Falcon-Lang, 2001; Falcon-Lang et al., 2001). The angiosperm leaves in the Alexander Island flora are the oldest flowering plant macrofossils on the Antarctic Peninsula (Cantrill and Nichols, 1996). In total, there are seven species of angiosperm leaves, but they contribute a relatively small percentage to the floristic diversity (Cantrill and Nichols, 1996: Falcon-Lang et al., 2001). Additional groups, which are yet to be formally described, are relatively low in species diversity, and represent lycopods (1 sp.), equisetaleans (1 sp.), bennettitaleans (2-3 spp.), cycads (2 spp.), and ginkgoaleans (1 sp.) (Falcon-Lang et al., 2001).

By far the greatest contributor to the relative diversity of the Alexander Island flora is ferns (Falcon-Lang et al., 2001). Preliminary diversity calculations estimated that ferns contribute 39% to the Alexander Island fossil flora diversity (Falcon-Lang et al., 2001). Several of the ferns from Alexander Island have been described, and are allied to Osmundaceae, Dipteridaceae, Matoniaceae, Gleicheniaceae, and Marsileaceae (Cantrill, 1995; Cantrill and Nagalingum, 2005; Nagalingum and Cantrill, 2006; Nagalingum, 2007). Additional Alexander Island ferns, but of unknown affinity, have been ascribed to Aculea, Alamatus, Coniopteris, Microphyllopteris, and Sphenopteris (Cantrill, 1996; Cantrill and Nagalingum, 2005). In total, thirteen fern species have been formally described from this assemblage. Here we present a taxonomic study of a further eleven fern species from Alexander Island, Antarctica. Together with other published descriptions (Cantrill, 1995, 1996; Cantrill and Nagalingum, 2005; Nagalingum and Cantrill, 2006; Nagalingum, 2007) this paper completes the description of the fossil fern flora of Alexander Island.

2. Materials and methods

Fossils from Alexander Island were collected by D. J. Cantrill and field workers from the British Antarctic Survey (BAS), Cambridge, U.K. The fossils were obtained from outcrops at Coal Nunatak, Citadel Basin, Titan Nunataks, Pagoda Ridge and Phobos Ridge; all occur in the Triton Point Formation of the Fossil Bluff Group (Fig. 1). Material from 63 localities were examined and all the material is housed in the BAS Palaeontological collection under prefix KG. Material illustrated here is held in the BAS type and figured collection (Figs. 2–16). Locality number series from KG. 1672 to 1706 represent collections made during

early survey work, KG. 2814 to 2821 were collected by T. H. Jefferson while KG. 4600 to 4745 were made by D. J. Cantrill. Locality details are held in the BAS geological collection database records.

The fern fossils were not macerated for sporangia and spores because they are preserved as impressions. Specimens are described according to standard fern morphological terms (e.g., Tryon and Tryon, 1982; Kramer, 1990a). The determination of fronds, primary pinnae, secondary pinnae and pinnules is highly problematic in the investigation of fossil ferns as complete material is often lacking. Therefore, the smallest discernable unit was regarded as a pinnule and higher orders as secondary pinnae etc. 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.

3. Systematic palaeontology

CLASS POLYPODIOPSIDA sensu Smith et al., 2006 INCERTAE SEDIS

3.1. Cladophlebis Brongniart emend. Seward 1894

Type Species: Cladophlebis albertsii (Dunker) Brongniart

Remarks. Foliage of Cladophlebis is very common in Mesozoic floras from all regions of the world. Brongniart (1849) instituted this genus for Mesozoic fern fronds, but did not provide a diagnosis. Seward (1894) later discussed the status of Cladophlebis, and presented a diagnosis, as follows: 'Fronds pinnately divided, pinnae spreading; lobes or pinnules attached by the entire base or slightly contracted towards the place of attachment, rarely somewhat auriculate, acuminate or obtuse, occasionally dentate, especially at the apex, not rarely sub-falcately curved upwards; midrib strong at base and towards the summit dissolving into branches, secondary veins given off at a more or less acute angle, dichotomous a little above the base, and repeatedly dichotomous'. However, this diagnosis incorporates very general foliar morphology and venation characters, and consequently, can encompass a wide range of forms. Frenguelli (1947), in contrast, provided a very detailed list of 12 characters such as venation, pinnule shape and arrangement; however, he did not formally emend the diagnosis. Because of the detailed diagnosis, Frenguelli's (1947) list excludes species that would otherwise be incorporated into the genus, but does not provide a more natural group of taxa because Cladophlebis is an artificial genus based on foliar morphology and venation. As a consequence, most of Frenguelli's (1947) criteria require several exceptions in order to incorporate many taxa of a general cladophleboid appearance.

Most usage of the genus name *Cladophlebis* (e.g., Crabtree, 1988; Gee, 1989; Taylor et al., 2009) encompasses the description given by Seward (1894). Hence, Seward's (1894) definition is adopted herein, but two exceptions are noted. Firstly, the midvein does not 'dissolve into branches' at the apex, but usually terminates at the apex, which is typical of most described *Cladophlebis*. Also, the secondary veins are not always 'dichotomous ... and repeatedly dichotomous', but can be undivided.

Cladophlebis pinnules have been recovered on the same axis as the osmundaceous, fertile *Todites* or are preserved in association with it (Harris, 1961; Gee, 1989; Banerji, 1992) and as a consequence sterile *Cladophlebis* are typically assigned to Osmundaceae. However, as circumscription of the genus is broad and based entirely on

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