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Cretaceous high-latitude terrestrial ecosystems: an example from Alexander Island, Antarctica

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Abstract. A thin wedge of non-marine sedimentary strata occurs within the largely marine Fossil Bluff Group on Alexander Island, Antarctica. The late Albian Triton Point Member of the Neptune Glacier Formation records deposition by braided and meandering river systems that preserve *in situ* stands of vegetation. Floristic analysis coupled with sedimentological investigations allows the recognition of a variety of plant communities. Hepatophytes were primary colonizers of fresh sediment, but also occurred in back swamp settings, and as a ground layer in fern thickets. Ferns such as *Aculea* and *Alamatus* formed extensive thickets on sandy substrates; scattered amongst the fern thickets were small shrubby podocarps and stands of araucarian conifers. Back swamp vegetation was characterized by a diversity of podocarp conifers and ferns. Angiosperms were also present and occupied a variety of niches from small streamside herbs to probable trees in back swamp settings. The late Albian Alexander Island flora gives a unique insight into the vegetation dynamics of polar regions during periods of greenhouse warmth.

Keywords. Antarctica. Alexander Island. Cretaceous. Albian. Flora. Palaeoecology.

Introduction

Global warmth during the Cretaceous enabled complex plant communities to flourish in high palaeolatitudes (*e.g.* Spicer *et al.*, 1992; Douglas and Williams, 1982). These communities experienced a unique combination of climatic conditions not seen on the earth today; polar warmth coupled with a strongly seasonal light regime. Although plant communities are known from high latitudes in the Northern (*e.g.* Parrish and Spicer, 1988) and Southern (*e.g.* southeastern Australia; Douglas, 1969, 1973) hemispheres, relatively few studies have addressed the palaeoecology and vegetational structure of these communities (Douglas and Williams, 1982; Spicer *et al.*, 1992). Cretaceous strata are relatively rare in the Antarctic but extensive deposits do occur in the Antarctic Peninsula region (figure 1). Alexander Island, located at a palaeolatitude of c. 70ºS during the Albian, contains an extensive record of vegetation growing in polar latitudes. This record is preserved within a fluvial sequence as leaf litter layers on the top of palaeosoil horizons. Analysis of the floristic composition, in conjunction with sedimentological and palaeoecological investigations, gives a unique insight of polar vegetation during a period of greenhouse warmth.

Palaeoenvironment

The Antarctic Peninsula has been traditionally interpreted as a Mesozoic Andean-type arc-trench system (Storey and Garrett, 1985) with subduction of palaeo-Pacific crust beneath the western margin and the formation of back-arc and retro-arc deposits to the east (MacDonald and Butterworth, 1990). Alexander Island comprises an accretionary complex (Le May Group) that is overlain by a thick fore-arc basin sequence (Fossil Bluff Group). The fore-arc sequence is largely marine, but towards the top of the sequence a thin wedge of prograded non-marine strata occurs (Triton Point Member; Neptune Glacier Formation, Moncrieff and Kelly, 1993; Kelly and Moncrieff, 1992). The Triton Point Member is only 200 m thick at Triton Point but thickens southwards to over 1 km thick around the southern nunataks of Coal, Titan and Citadel Bastion (figure 1.D).

Within the Triton Point Member two broad lithofacies are recognised (Cantrill and Nichols, 1996). The lower part of the sequence is dominated by trough crossbedded sandstone sheets up to 10 m thick and 100 to 300 m wide. These are interpreted as being deposited by sandy to pebbly braided rivers within a broad channel belt. Slightly finer-grained facies are interbedded with these sheets and comprise medium or fine sandstones up to 1.5 m thick. These beds are commonly ripple-cross or planar laminated, more rarely normally graded, and are interpreted as overbank flooding events. Intermittent volcanic ac-

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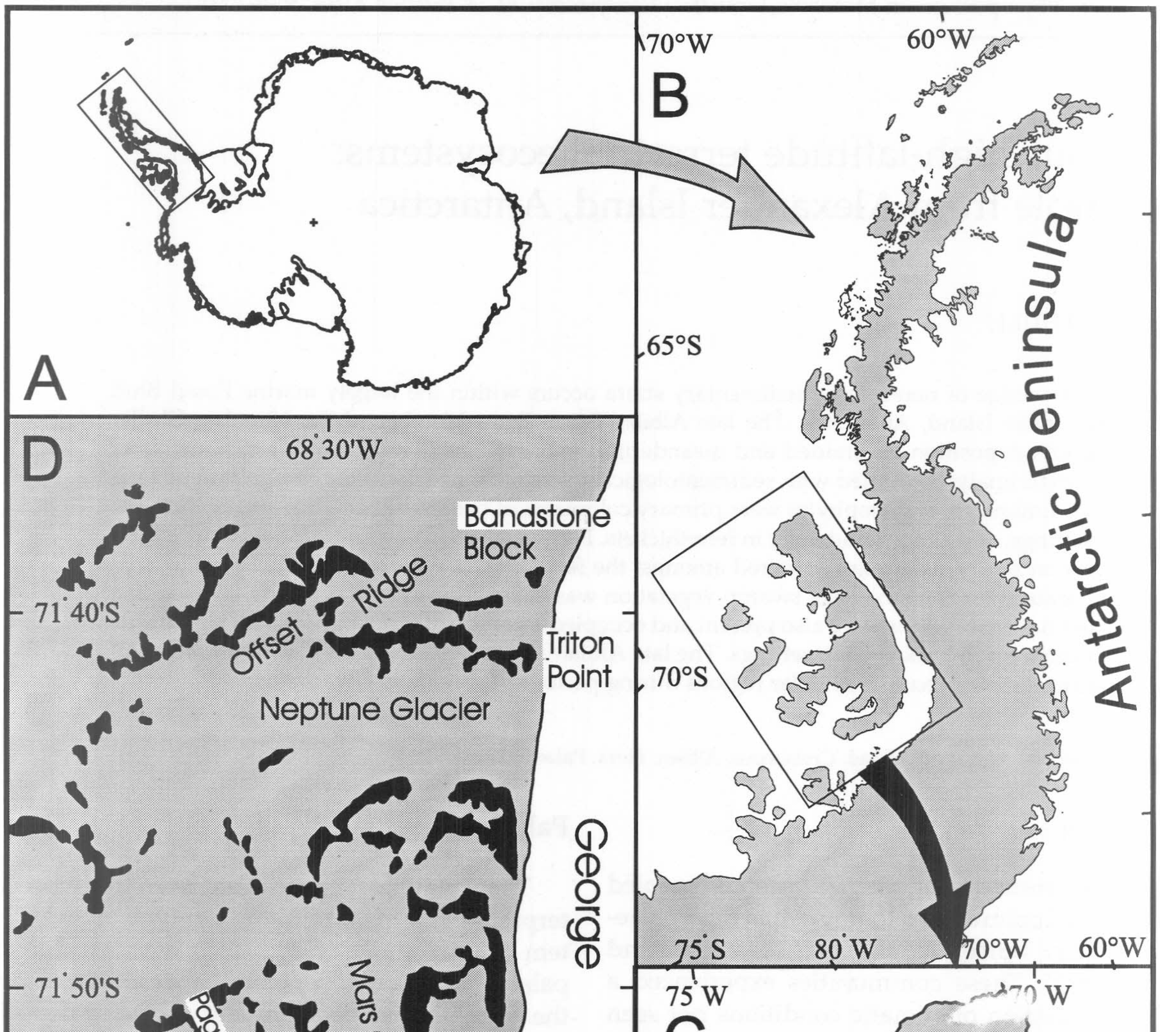

Figure 1. Locality map. **A,** Antarctica showing position of inset B. **B,** Antarctic Peninsula showing the position of Alexander Island. **C,** Alexander Island. **D,** outcrop map for southern Alexander Island showing key localities mentioned in text.

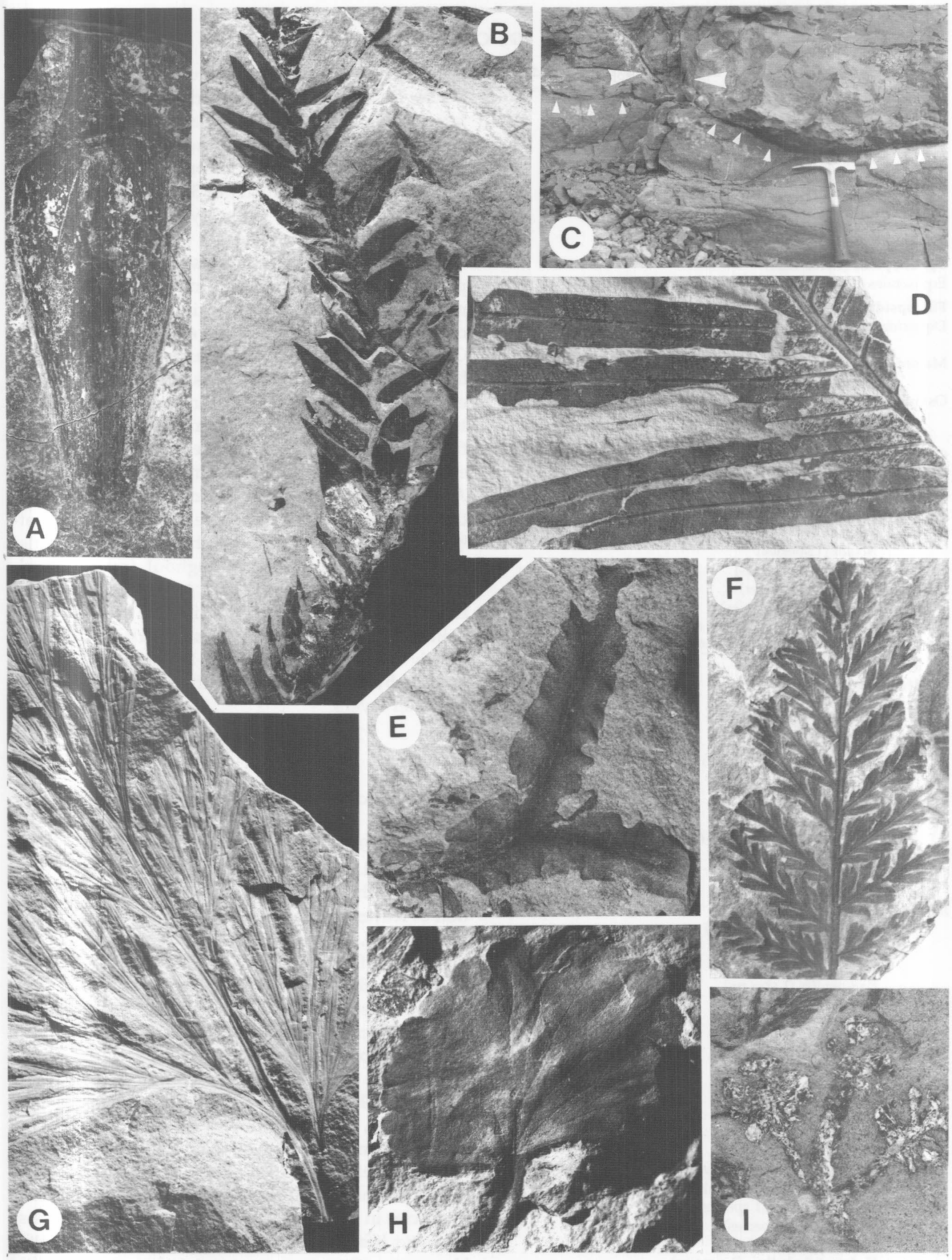

Figure 2. Floristic components of the Alexander Island vegetation. **A,** ***Araucarites*** sp. KG. 4741.64 (x2). **B,** ***Pagiophyllum*** foliage associated with araucarian scales. KG. 2815.165 (x1). **C,** *in situ* fern trunk (large arrows) on palaeosoil (small arrows) at KG 4737, note the topographic relief and vertical rootlets near the hammer. **D,** cf. ***Matonia*** sp. KG 2816.88 (x1). **E,** ***Metzgerites undulatus*** Cantrill, KG. 1704.4a (x2.5). F, cf. ***Sphenopteris sueroi*** Archangelsky, KG. 2815.168a (x1.5). **G,** ***Alamatus bifarius*** Douglas, KG. 4745.22 (x1). **H,** ***Hydrocotylophyllum alexanderi*** Cantrill, KG. 2815.171a (x2.5). **I,** cf. ***Athrotaxites*** sp., KG. 2816.97 (x1).

Table 1. Floristic composition of the Albian Alexander Island flora.

- **Hepatopsida** (liverworts)
  - Marchantiales
    - *Marchantites* (5 species)
    - *Hepaticites* (3 species)
    - *Thallites* (2 species)
  - Metzgeriales (1 species)
- **Lycopsida** (lycopods)
  - Selaginellales (1 species)
- **Sphenopsida** (horse-tails)
  - Equisetales (1 species)
- **Filicopsida** (ferns)*
  - Dipteridaceae
    - *Hausmania* (1 species)
  - Matoniaceae
    - *Matonia* (1 species)
  - Osmundaceae
    - *Cladophlebis* (6 species)
    - *Phyllopteroides* (2 species)
  - Gleicheniaceae
    - *Gleichenites* (1 species)
  - ?Lophosoriaceae
    - *Microphyllopteris* (2 species)
  - *Incertae sedis*
    - *Aculea* (1 species)
    - *Adiantites* (1 species)
    - *Alamatus* (1 species)
    - *Sphenopteris* (4 species)

(*In total, fern component comprises approximately 14 genera and 26 species, many awaiting formal description).

- **Coniferopsida**
- **Coniferales** (conifers)
  - Araucariaceae
    - *Araucaria* (2 species)
    - *Araucarites* (2 species)
    - *Araucarioxylon* (1 species)
    - *Araucariopitys* (1 species)
  - Podocarpaceae
    - *Podocarpites* (1 species)
    - *Podocarpoxylon* (2 species)
  - Taxodiaceae
    - *Athrotaxites* (1 species)
    - *Taxodioxylon* (1 species)
  - *Incertae sedis*
    - *Brachyphyllum* (1 species)
    - *Elatocladus* (2 species)
    - *Pagiophyllum* (1 species)
    - *Podozamites* (1 species)
- **Other minor gymnosperms**
  - Bennettitales (extinct)
    - *Ptilophyllum* (2 species)
  - Cycadales (cycads) (1 species)
  - Ginkgoales (ginkgos)
    - *Ginkgoites* (1 species)
  - Pentoxylales (extinct)
    - *Taeniopteris* (3 species)
- **Angiospermopsida** (flowering plants)
    - *Araliaephyllum* (1 species)
    - *Dicotylophyllum* (1 species)
    - *Ficophyllum* (1 species)
    - *Gnafalea* (2 species)
    - *Hydrocotylophyllum* (1 species)
    - *Timothyia* (1 species)

tivity is also indicated by thick (up to 6 m), air-fall ash deposits. A general decrease in the thickness of the sandstone sheets up section indicates decreasing gradient and channel depth through time. The upper part of Coal Nunatak is denoted by a change in lithofacies to finer-grained, more arc derived material, and in particular air fall and reworked tuffaceous deposits. Sandstone sheets become more lensoid in geometry, ranging from 1.5 to 3.0 m thick and a few tens of metres wide. These typically sharp-based, normally-graded, sandstones show crossbedding, ripple-cross and planar laminations, and are interpreted as fluvial channel fill units. Individual channels were shallower, flow velocities were slower, and channels narrower than lower in the sequence. Overbank deposits are poorly exposed and probably biased towards the coarser beds. These are represented by medium-grained sandstone beds, with decimetre-scale ripple and planar laminations. This suggests that overbank flood events were of relatively high energy, depositing sheets of sand on the floodplain. Air-fall ash deposits are more common than lower in the sequence, and also truncate forest levels indicating catastrophic disruption to the vegetation. Rootlet horizons are widespread throughout and are developed on nearly all lithofacies types. The development of the soils only rarely disrupts primary sedimentary structures and are thus considered to be relatively immature. The tops of the soil horizons are marked by thin leaf deposits that are interpreted as leaf litter layers.

Floristics

The Alexander Island flora is one of the richest Cretaceous floras in the Southern Hemisphere (Truswell, 1991), yet most taxa have yet to be formally described. Indeed there are relatively few investigations of the flora. Jefferson studied the preservation of leaves (Jefferson, 1982a) and wood (Jefferson, 1982b, 1987), and generally outlined the floristic composition (Jefferson, 1981, 1983) of the vegetation. More recently systematic investigations of the flora have revealed a previously unsuspected diversity of hepatophytes (10 species; Cantrill, 1997; figure 2.E) and angiosperms (7 species; Cantrill and Nichols, 1996; figure 2.H). Lycopods are rare with just one species (table 1). However, this is not unusual in macrofloras, where lycophytes are often underrepresented when compared to their frequency in palynofloras (Dettmann, 1986). Ferns make up c. 35% of the taxonomic diversity, and many can be compared to species in southern Australia (e.g. *Aculea* Douglas, *Alamatus bifarius* Douglas; figure 2.G; Cantrill, 1996). However, other taxa compare most closely with species in South America (*e.g. Microphyllopteris* Arber, *Sphenopteris sueroi* Archangelsky; figure 2.F). The family Osmundaceae is represented by *Phyllopteroides* Medwell and *Cladophlebis* Brongniart, the Matoniaceae by *Matonia* R. Br. (figure 2.D), and the Dipteridaceae by *Hausmannia* Dunker (Cantrill, 1995). In addition, the probable presence of the Cyatheaceae or Dicksoniaceae is indicated by petrified fern petioles, and the Lophosoriaceae by foliage referred to *Microphyllopteris*. Other families also thought to be present include the Schizaeaceae (Truswell, 1991)(table 1).

Seed plants are well represented and include Ginkgoales (*Ginkgoites* Seward), Cycadales (*Pseudoctenis* Seward), Pentoxylales (*Taeniopteris* Brongniart, *Carnoconites* Srivastava), Bennettitales (*Ptilophyllum* Morris, 2 species), Coniferales (12 species; figure 2.B), and angiosperms (7 species; Cantrill and Nichols, 1996) (table 1). Coniferous plants can be assigned to extant families such as Araucariaceae (figure 2.A), Podocarpaceae, and Taxodiaceae (figure 2.I) based on attached cones and associated cone scales (Cantrill and Falcon-Lang, 2001), and this is supported by wood anatomy (Falcon-Lang and Cantrill, 2000). One of the most recent discoveries is a diverse angiosperm component within these Late Albian deposits (table 1). The angiosperms range from small herbaceous forms (e.g. *Hydrocotylophyllum alexanderi* Cantrill, figure 2.H) to probable trees (e.g. *Araliaphyllum quiquelobatus* Cantrill).

Palaeoecology

Integrated sedimentological and palaeontological studies have been used to infer plant community structure (e.g. Cantrill and Nichols, 1996). Palaeosoils with *in situ* leaf litter at their tops are widespread, and bedding plane exposures of these deposits enable the spatial distribution of plant taxa to be assessed. Fresh surfaces deposited by flood events are initially colonised by liverworts as indicated by monospecific mats of liverworts on the top of bedding surfaces (Cantrill, 1997). The liverworts appear to be substrate specific with different taxa occurring on sandstones (*Marchantites rosulatus* Cantrill) or mudstones (*Thallites bicostatus* Cantrill). Liverworts also occur in established plant communities where they have been identified as forming a ground layer beneath fern thickets (e.g. *M. pinnatus* Cantrill, *M. taenioides* Cantrill; Cantrill, 1996). Other forms have not been constrained to any particular palaeoenvironmental setting and probably represent components of the forest communities (e.g. *Metzgerites undulatus* Cantrill, figure 2.E).

Pteridophytes are rarely found in growth position and more commonly occur as isolated portions of foliage incorporated in overbank units. Some *in situ* associations have been recognized and include bedding surfaces with flattened plants of *Aculea* and *Alamatus*. These represent fern dominated thickets (Cantrill, 1996). Within this community are small podocarpaceous shrubs and rare araucarian trees. Although *in situ* plant communities are common, leaf litter associations characterize a number of settings. Backswamp overbank deposits are characterized by at least two types of associations. The dominant leaf component is thought to represent the overstorey elements. At KG. 4737 (figure 1) *Taeniopteris* is the dominant overstorey component with minor angiosperms (e.g. *Araliaphyllum quiquelobatus*) and a sparse understorey of ferns (*Cladophlebis* sp., *Hausmannia*) as indicated by *in situ* plants (figure 2.C). More commonly backswamp overbank settings are composed of a *Podozamites* fern association (e.g. KG. 4747) or an *Elatocladus*-fern-liverwort association (e.g. KG. 4667).

Bennettitales are relatively rare in the sequence being confined to drifted assemblages in the braided river channel belts. This suggests they were derived from more upland regions or grew in disturbed sites within the braided channel. Another small leaved *Ptilophyllum* species occurs within mudstones in the upper part of the succession. *Ginkgoites* is generally confined to mudstone (overbank) environments in the lower part of the sequence, but becomes abundant in the upper strata, particularly in environments adjacent to meandering channels.

Forest horizons are represented by *in situ* tree stumps in both cliff sections and as bedding plane exposures (Jefferson, 1987). Standing trees up to 8 m tall have been observed in cliff section, but tree heights could have been substantially taller. Using the allometric approach of Niklas (1994) heights up to 29 m are indicated (Falcon-Lang and Cantrill, 2000). The habit of the trees does not appear to have been cone shaped; there being no evidence of whorled branch arrangements on the trunks, and those trees that are branched tend towards a pseudomonopodial habit. The preserved forest floors indicate a range of densities from stands with over 500 stems per hectare, to dispersed clumps of individuals as found in open woodlands today. The high density stands are thought to represent colonisation stands, perhaps after flood events, as they tend to have small trunk diameters; these trunk diameters are relatively uniform, compared with less dense stands. Tree ring sequences indicate that trees attained ages of greater than 180 years (Chapman, 1994). The coniferous trees also show a distinct spatial arrangement. The lower braided river system is dominated by podocarps with araucarians being absent (Falcon-Lang *et al.*, in press). The upper part of Coal Nunatak is characterized by both dense podocarp forest in backswamp settings and less dense araucarian stands on sandy substrates.

Discussion

The polar Cretaceous flora from Alexander Island is unusual in its high within floral diversity of liverworts when compared to lower latitude floras. High within floral diversity of liverworts appears to be a feature of high-latitude vegetation during periods of greenhouse warmth. High-latitude Cretaceous (Aptian to Albian) floras in southeastern Australia (c. 60-80° S) also have a high liverwort diversity (21% Aptian; 15% Albian). In contrast, lower latitude floras of Australia (e.g. Queensland; Walkom, 1918, 1919) apparently lack liverworts. A similar situation occurs between Antarctica and South America. In the Aptian of Antarctica (Cerro Negro Formation) liverworts make up c. 20% within floral diversity. In comparison the lower latitude floras of the Aptian Baqueró Formation have over 96 plant taxa (Riccardi, 1988), but only one liverwort species (Halle, 1911). It is possible that the unique conditions of polar warmth coupled with a strongly seasonal light regime favours these plants.

An examination of *in situ* leaf litter layers indicates that the vegetation is not uniform but comprises distinct plant associations. This is also supported by drifted leaf assemblages that have a species composition different from the *in situ* vegetation, indicating derivation from other plant communities. Plant associations are consistently found in similar sedimentary settings suggesting a strong degree of environmental control. It seems highly likely that processes such as flood frequency, substrate type, time since colonisation, and hydrology played an important role in determining the type of plant communities that developed at particular sites.

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