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Abstract: A compilation of data for Cretaceous and Cenozoic Antarctic fossil wood floras, predominantly from the James Ross Island Basin, provides a different perspective on floristic and vegetation change when compared with previous studies that have focused on leaf macrofossils or palynology. The wood record provides a filtered view of tree-forming elements within the vegetation, something that cannot be achieved from studies focusing on regional palynology or leaf floras. Four phases of vegetation development in the overstorey are recognized in the Cretaceous and Cenozoic of the Antarctic Peninsula based on the distribution and taxonomic composition of wood floras: Aptian–Albian coniferous forests; ?Cenomanian–Santonian mixed angiosperm forests; Campanian–Maastrichtian southern temperate forests; and Palaeocene–Eocene reduced diversity *Nothofagus* forests. Comparisons between the wood record and information derived from palynological and leaf floras have important implications for our understanding of the spatial composition of the vegetation. There is no doubt that climate change during the Cretaceous and Tertiary influenced the vegetational composition, but evolving palaeoenvironments in the Antarctic Peninsula region were probably of equal, if not greater, importance.

James Eights (1833) reported the first fossil wood from the Antarctic (South Shetland Islands, Antarctic Peninsula), a discovery that pointed to a once vegetated landmass in what is now an icy world. Today, as questions focus on trying to understand the Earth system more fully, it becomes more ever apparent that the high latitudes played an important role in evolution of biotas, development of Southern Hemisphere biogeography (Drinnan & Crane 1990; Cantrill & Poole 2002) and mediating global climates (Upchurch *et al.* 1998). Indeed, the high latitudes are most sensitive to climate fluctuation, yet there is no modern analogue today with which to compare the evidence from the past. An unparalleled record of life in the high southern latitudes is found on the Antarctic Peninsula, which has, in recent years, furthered our knowledge of the palaeoecology of this region through many systematic and climatological studies. It is therefore timely to bring together the works published over the past decade, and revise and update previous conceptions pertaining to the southern high latitudes such that this unique and dynamic ecosystem can be more fully understood.

Four major types of fossil plant material provide information for past vegetation, these include: leaf compressions and impressions; wood; palynomorphs; and dispersed cuticular material, all of which are present in the floras of the Antarctic Peninsula. The Antarctic record of terrestrial vegetation is derived predominantly from leaf and palynomorph records (e.g. Askin 1988, 1992). Abundant leaf floras have been described (e.g. Dusén 1908; Zastawniak 1981, 1990, 1993, 1994; Li & Shen 1990; Li 1994; Zhou & Li 1994; Zastawniak *et al.* 1995; Hayes 1999; Cantrill 2000; Dutra & Batten 2000; Hunt 2001), but these often lack cuticles making systematic identification more problematic. Flowers and fruits also occur, but these are rare (Gandolfo *et al.* 1998; Eklund 2003) and have not to date been extensively studied. By comparison, wood is abundant and thus makes an important contribution to a picture of biodiversity than would otherwise result predominantly from leaf and microfossil

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evidence. However, the paucity of solid taxonomic investigations has severely limited the ability to utilize this source of information. This paper synthesizes the recent data on the Cretaceous and Cenozoic of the Antarctic Peninsula region, based largely on wood records from the James Ross Island Basin (e.g. Gothan 1908; Torres *et al.* 1994a, b; Poole & Francis 1999, 2000; Poole *et al.* 2000*a–c*; Poole 2002). To help complete the picture, the fossil wood record from elsewhere in the Antarctic Peninsula (e.g. Torres & Lemoigne 1988, 1989; Chapman & Smellie 1992; Falcon-Lang & Cantrill 2000, 2001*a*; Poole & Cantrill 2001; Poole *et al.* 2001, 2003) has been used to fill the gaps in the James Ross Island Basin biodiversity record.

Geological setting

The Antarctic Peninsula is the remnant of a continental-margin magmatic arc of Mesozoic–Cenozoic age (Storey & Garrett 1985). Formed as a result of subduction of the palaeo-Pacific Plate beneath the western margin of the Antarctic Peninsula, it has good exposures of magmatic-arc, accretionary complex, and fore- and back-arc regions. These provide information on a diversity of environmental settings, many of which contain records of fossil wood. Forearc deposits exposed on the west side of the Antarctic Peninsula include the famous standing forests and associated leaf floras from Alexander Island (Jefferson 1982; Falcon-Lang & Cantrill 2001*a*). These are distal to the arc, and record braided and meandering fluvial environments on a narrow coastal plain (Cantrill & Nichols 1996; Nichols & Cantrill 2002) (Fig. 1). Further north, in the South Shetland Islands, Early Cretaceous (Aptian) intra-arc deposits record the burial of existing topography through the development of local calc-alkaline volcanic edifices (Hathway 1997) (Fig. 1). Fossil wood from palaeotopographic surfaces and entombed in ignimbrite flows record the interaction between vegetation and environmental processes (Falcon-Lang & Cantrill 2002). Similar volcanic-dominated

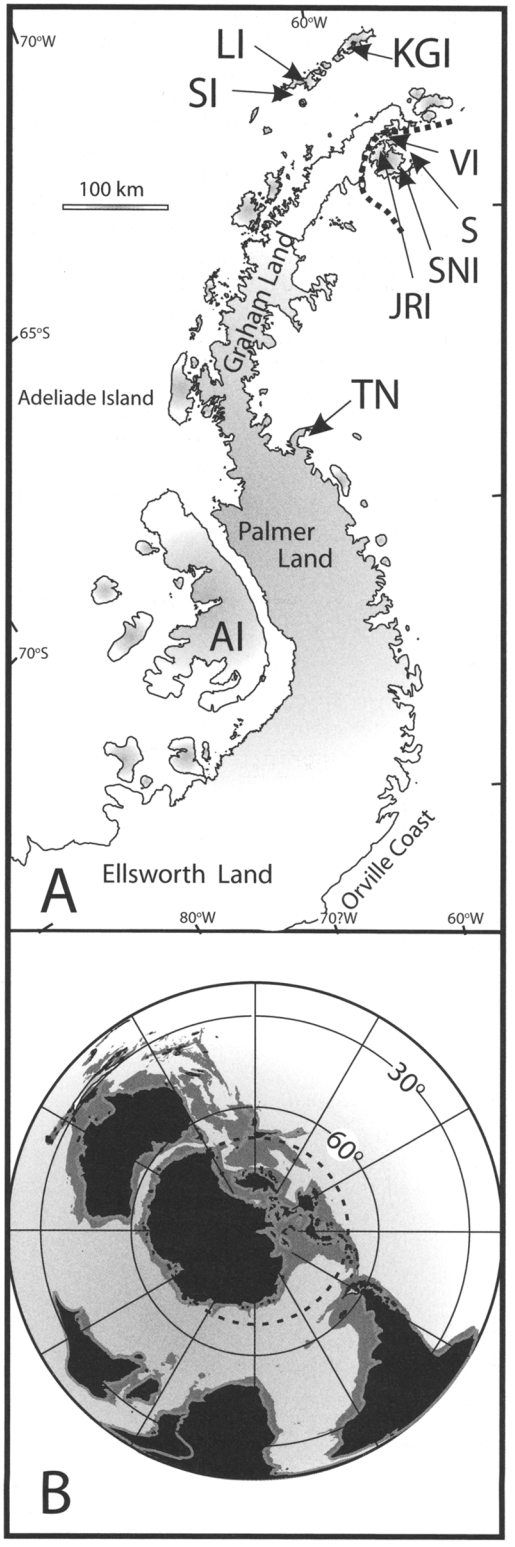


Fig. 1. (**A**) General locality map of the Antarctic Peninsula, with locations of places mentioned in the text. LI, Livingston Island; SI, Snow Island; KGI, King George Island; VI, Vega Island; S, Seymour Island; SNI, Snow Hill Island; JRI, James Ross Island; TN, Table Nunatak; AI, Alexander Island. (**B**) Reconstruction of Late Cretaceous (84 Ma) times showing the high-latitude setting of the palaeofloras, supplied by Dr R. A. Livermore. The dashed line indicates the polar circle.

environments extend from the Late Cretaceous to the ?Oligocene–Miocene in the South Shetland Islands and record the development of vegetation under these conditions. In contrast, the east side of the Antarctic Peninsula was rifted from the margin of Gondwana during the Jurassic. The Early Cretaceous (Aptian)–early Late Cretaceous (Turonian) of the James Ross Basin is characterized by deep submarine fan deposits. A major pulse in arc magmatism in the early Coniacian lead to the development of a complex fan-delta, slope and base-of-slope environment (Hidden Lake Formation: Whitham *et al.* 2006). Plant fossil material becomes increasingly common in the Hidden Lake Formation, and provides a record of vegetation from the eastern side of the Antarctic Peninsula.

This unparalleled record of diverse palaeoenvironments and associated biota from the Early Cretaceous to the Eocene was set in the high southern latitudes. During the Late Cretaceous and early Tertiary the Antarctic Peninsula extended from approximately 68 to 75°S, with Alexander Island lying at about 70°S and King George Island in the South Shetlands at 62°S (Fig. 1). At these palaeolatitudes plant growth was strongly influenced by the unique growing conditions not found on Earth today: a strongly seasonal polar light regime coupled with greenhouse conditions.

Floristic composition and turnover

Basal Cretaceous sedimentary rocks are lacking in the James Ross Island Basin, with the oldest Cretaceous strata being Aptian or slightly older. The oldest strata include the Lagrelius Point (Aptian: Riding *et al.* 1998), Kotick Point (early Albian: Keating *et al.* 1992; Riding & Crame 2002) and Pedersen Nunatak (Aptian: Hathway & Riding 2001) formations (Fig. 2). Unfortunately the record of plant macrofossils from

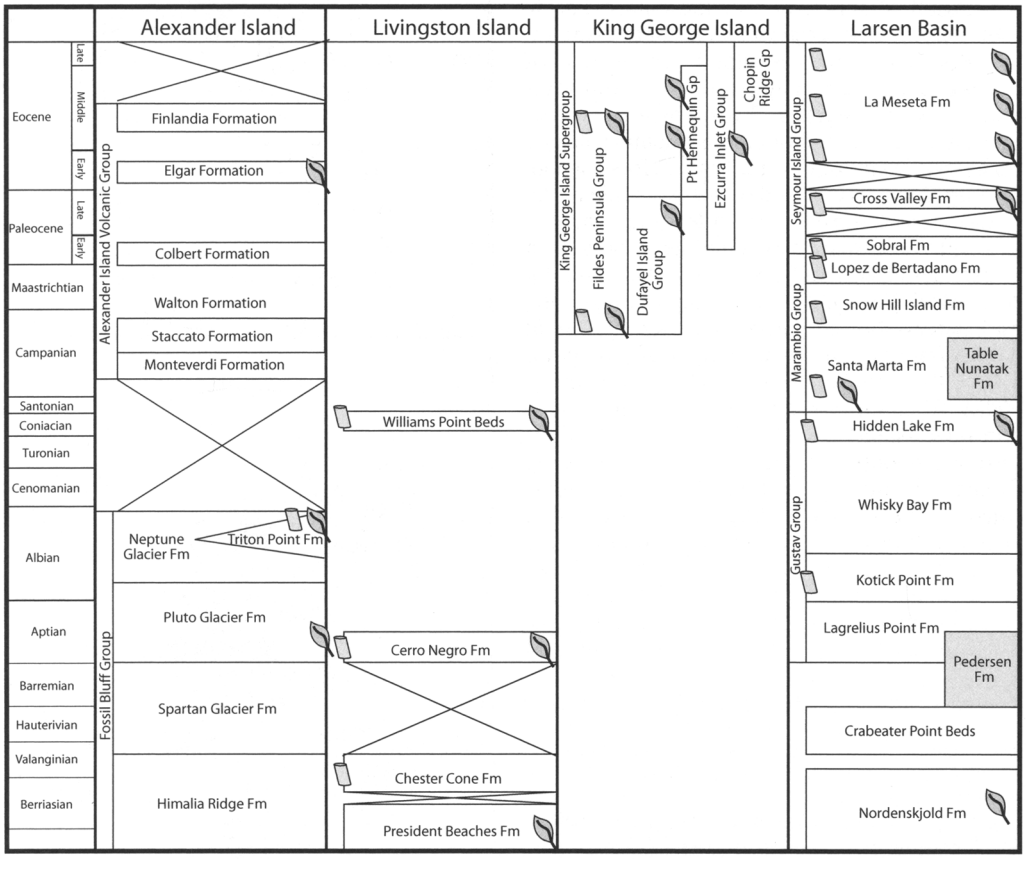


Fig. 2. Stratigraphic summary of key formations and groups for the Cretaceous and Palaeogene of the Antarctic Peninsula (East Antarctica not included). Units with fossil leaf material or wood material are marked. Note that the stratigraphic succession for King George Island is incomplete.

these units is poor. Lower Cretaceous (pre-Aptian) sedimentary rocks occur in the Fossil Bluff Group on Alexander Island (Himalia Ridge and Spartan Glacier formations: Butterworth *et al.* 1988), and on Byers Peninsula, Livingston Island (President Beaches and Chester Cone formations: Crame *et al.* 1993; Duane 1996) (Fig. 2). These strata accumulated in marine settings, generally lack wood, and contain only sparse foliage remains. Consequently, this discussion starts in the Aptian interval when fossil wood becomes more common and terrestrial settings are better documented.

Aptian and Albian interval

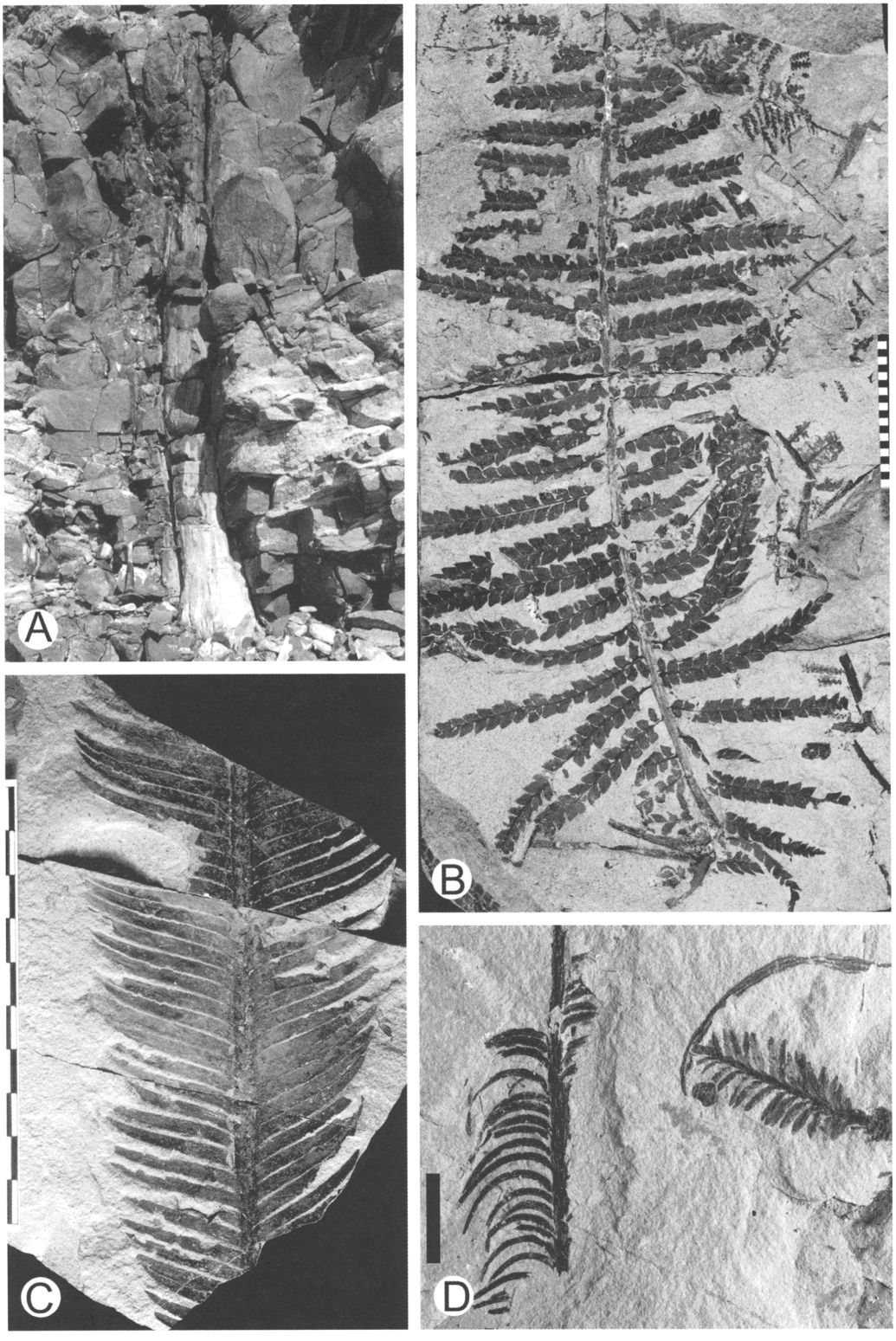
The basal Gustav Group, of the James Ross Island Basin, yields sparse fossil wood (Francis 1986; Ottone & Medina 1998; Francis & Poole 2002), and only wood from the early Albian Kotick Point Formation has been formally described (Ottone & Medina 1998). This material was assigned to *Agathoxylon* Hartig, a member of the Araucariaceae. It is unclear if this wood is contemporaneous with deposition, or reworked from older formations (Botany Bay Group). However, most of the wood preserved in the Gustav Group and overlying Marambio and Seymour Island groups is replaced by calcite, whereas Botany Bay Group wood is silicified. The limited number of samples from the Aptian and Albian within the James Ross Island Basin precludes making firm inferences about forest composition, but, fortunately, good Aptian wood floras in the South Shetland Islands (Cerro Negro Formation: Torres *et al.* 1982, 1997*a*; Falcon-Lang & Cantrill 2001*b*), and Albian wood floras from Alexander Island (Falcon-Lang & Cantrill 2001*a*) have been described. Both floras provide a picture of the forest component of the vegetation to both the north and south of the James Ross Island Basin. The general similarity in the composition of these floras enables us to assume that the vegetation within the James Ross Island Basin was comparable. Therefore, in order to set the scene for ensuing vegetational changes, we consider the floras of these two regions during an interval that within the James Ross Island Basin presently lacks data.

The Aptian Cerro Negro Formation in the South Shetland Islands crops out on Livingston Island (on Byers Peninsula) and Snow Island (at President Head) (Hathway 1997). This unit accumulated in a terrestrial intra-arc setting, and was dominated by volcanic processes. A diverse leaf flora occurs in a lacustrine sequence on President Head (Torres *et al.* 1997*a*, *b*: Cantrill 2000). The impression and compression floras from the lacustrine unit are rich in Bennettitales, conifers and other gymnospermous plants (e.g. *Pachypteris* Brongniart), with a minor fern and bryophyte component (Fig. 3C). The coniferous component is dominated by podocarps and taxodiaceous forms with rare araucarian remains (Fig. 3D). This leaf flora is similar in composition to those found within the non-marine units on Byers Peninsula (Hernández & Azcarárte 1971; Cesari *et al.* 1998, 1999), except that the latter are usually less diverse with just one or two taxa. In particular, Bennettitales (*Ptilophyllum* Morris) (Fig. 3C) are encountered more frequently and the floras are richer in araucarian elements in Byers Peninsula localities.

Palynofloras from the same units record only minor differences between the lacustrine unit assemblage (Cantrill 2000) and those in more fully terrestrial environments (Hathway *et al.* 1999). The palynoflora of the lacustrine environment is typically rich in pteridophyte spores, with diversity greater than that seen in the macrofossil record (Cantrill 2000). Localities are often dominated by single taxa, in particular *Cyathidites* Couper and less frequently *Cyatheacidites* Cookson ex Potonié (Lophosoriaceae). This is thought to reflect local abundance or colonization events, as the Lophosoriaceae is a colonizer of disturbed environments (Cantrill 1998). Lycophytes and bryophytes make up only a small component of the flora, whereas conifers tend to be more abundant. Conifer pollen is plentiful and dominated by podocarps, although yields are lower in the lacustrine units. This could be the result of taphonomic bias, as bisaccate grains tend to float and so do not readily become incorporated into lacustrine units.

Relative to the leaf floras, wood is more widespread and locally abundant within the Cerro Negro Formation, which complements and supplements the vegetational picture obtained from the palyno- and leaf floras. Palaeovalleys

Fig. 3. Aptian and Albian floras. (A) and (B) are late Albian Triton Point Formation flora, Alexander Island. (**A**) Standing tree with a pseudomonopodial habit. (**B**) *Tetragleichenites acuta* Nagalingum et Cantrill a gleicheniaceous fern. Scale bar shows 1 mm divisions, KG. 2817.75a/76a. (C) and (D) are Aptian flora from Snow Island, South Shetland Islands. (**C**) *Ptilophyllum Menendez* Cantrill. Scale bar shows 1 cm divisions, P. 2501.1. (**D**) *Elatocladus* sp., a podocarpaceous conifer. Scale bar shows 1 cm, P. 2501.21a.


A
B
C
D

contain incipient soils, and trunk wood is scattered across this surface (Hathway 1997; Falcon-Lang & Cantrill 2001*b*). The trees that forested this region were undoubtedly substantial, as evidenced by trunks up to 1.5 m in diameter. Ignimbrite flows on Byers Peninsula contain entrained charred logs up to 5 m in length representing the remains of forest stands that grew on the flanks of a volcanic edifice and which later became entombed during a subsequent eruption. Similar processes have been observed today in New Zealand (Clarkson *et al.* 1988). The leaf floras suggest that the Araucariaceae were important, but the wood record points to forest communities rich in podocarps (61%) with subsidiary araucarians (27%) alongside extinct groups such as *Sahnioxylon* Bose et Sah (12%) (Falcon-Lang & Cantrill 2001*b*; $n = 33$).

Angiosperms first appear as pollen records in early Albian strata on the eastern side of the Antarctic Peninsula (Dettmann & Thomson 1987), but do not appear in the leaf floras until the late Albian (Cantrill & Nichols 1996). The early pollen record is of a low-diversity angiosperm component (mostly *Clavatipollenites* Couper) indicative of a shrubby habit (Dettmann 1989). The late Albian leaf floras are also characterized by herbaceous (e.g. *Hydrocotyllophyllum* Teixeria) and shrubby (e.g. *Dicotylophyllum* Bandulska) forms, but a few leaf types probably represent more substantial plants, perhaps understorey trees (e.g. *Araliaephyllum* Ettingshausen, *Ficophyllum* Fontaine) (Cantrill & Nichols 1996).

The late Albian flora of Alexander Island, situated at a palaeolatitude of 75°S, represents one of the most complete and most southerly forests known to date (Fig. 3A). Within the leaf flora, gymnosperms dominate with arboreal elements such as Araucariaceae, subsidiary Podocarpaceae, minor Taxodiaceae, and an understorey composed of ginkopsids, taeniopterids, bennettitaleans, equisetites, ferns (Fig. 3B) and liverworts (Cantrill 2001*a*; Falcon-Lang *et al.* 2001; Howe & Cantrill 2001). This flora also records the first appearance of angiosperms in the leaf record (Cantrill & Nichols 1996). The famous standing forest horizons contain abundant wood and, although often poorly preserved, are rich in podocarps (85.3%), with fewer araucarians (13.2%) and taxodiaceous (1.5%) conifers (Falcon-Lang & Cantrill 2000; $n = 69$). The discrepancy concerning araucarian dominance may be due to the robust nature of araucarian foliage and reproductive structures (cone scales) having survived destructive taphonomic processes better than podocarps, and thus tending to be over-represented in the leaf record relative to the wood. Alternatively, the best-preserved forest horizons may be in sedimentary environments that lack araucarians and thus account for the deficit of araucarians in the wood flora. Typically, the araucarians are found in more proximal settings, in contrast to the podocarps and taxodiaceous conifers (Cantrill & Falcon-Lang 2001). The lack of angiosperm wood in Albian wood floras from Alexander Island (Falcon-Lang & Cantrill 2000) and the James Ross Island Basin (Ottone & Medina 1998) also supports a more shrubby, herbaceous habit of these first angiosperms.

Inferences pertaining to the physical structure of the vegetation that dominated the high southern latitudes at this time have been drawn from *in situ* 'forests' using stump diameter and density, and growth-ring sequences (e.g. Chaloner & Creber 1989; Falcon-Lang & Cantrill 2000). Alexander Island provides an ideal case study for such a fossil forest and has been studied for many decades (e.g. Jefferson 1981, 1982; Cantrill & Nichols 1996; Falcon-Lang *et al.* 2001; Howe & Cantrill 2001). This forest comprised stumps and standing trees of up to 8 m tall that have been observed in cliff sections (Cantrill 2001*a*). Using the allometric approach of Niklas (1994), it has been suggested that actual heights of 29 m were attained (Falcon-Lang & Cantrill 2000) by these trees which reached ages of more than 180 years (Chapman 1994). The habit of these trees do not appear to be cone-shaped (Brodribb & Hill 2004), as suggested in earlier publications (e.g. Chaloner & Creber 1989), as no evidence of whorled branch insertion have been found at this time (Cantrill 2001*a*). Where branching has been observed it appears to be towards a pseudomonopodial habit and this is more consistent with the habit of extant podocarps. Stand density ranges from a median of 568 stems per hectare (perhaps representing colonization stands: Falcon-Lang *et al.* 2001) to dispersed clumps of individuals similar to those in open woodland today (Cantrill 2001*a*). Such a maximum density would have ensured the minimization of mutual shading due to the low-angle radiation. The productivity of these forests has been thought to be as high as approximately 17.65 $m^3\ ha^{-1}\ a^{-1}$ (Creber & Francis 1999) based on Jefferson's (1981) data, but more recent studies based on revised data and additional fieldwork suggest that this is a drastic over-representation with high productivity probably being closer to 5.62–7.33 $m^3\ ha^{-1}\ a^{-1}$, similar to the warm temperate araucarian–podocarp stands in North Island, New Zealand today (Falcon-Lang *et al.* 2001).

The question of evergreen v. deciduous

habit for late Albian Antarctic conifers was investigated in detail by Falcon-Lang & Cantrill (2001*b*). Based on five independent techniques, they concluded that the canopy-forming vegetation that included conifers, ginkgos and taeniopterids was predominantly evergreen. Araucarians and podocarps, which dominated the vegetation, held on to their leaves for at least 5–13 years, whereas some of the rarer taxodiaceous conifers were evergreen but with much shorter leaf retention times. Other taxodiaceous conifers, ginkgos and taeniopterids were all deciduous along with the fern and angiosperm components of the understorey (Cantrill & Nichols 1996).

Without preserved *in situ* stumps, estimates of general density, productivity and height of the vegetation cannot be obtained. Therefore, extrapolation from the conclusions drawn by Falcon-Lang *et al.* (2001) suggest that the earlier mid-Cretaceous forests bordering the James Ross Island Basin had an estimated density and productivity similar to the Alexander Island forest. Nevertheless, with the increase in the abundance of the angiosperm component the density, productivity and forest heights would have changed due to different growth rates between angiosperms and conifers, and the influences they exerted on one another. Using growth-ring and palaeotemperature determinations, Specht *et al.* (1992) concluded that the productivity of the angiosperm-dominated vegetation of the Peninsula region during the Late Cretaceous would have remained high.

In summary, plant fossil evidence from wood, leaf and pollen floras indicates the Aptian and Albian overstorey was dominated by conifers, and the understorey dominated by ginkopsids, taeniopterids, bennettitaleans, equisetites, ferns and liverworts with a very minor angiospermous component. Such open-canopied, evergreen araucarian–podocapaceous conifer forests were characteristic of the mid-Cretaceous Pacific margins of the Gondwanan continent (Falcon-Lang & Cantrill 2000) extending from Alexander Island, probably across the James Ross Island Basin, to the South Shetland Islands and as far north as Patagonia and as far east as New Zealand.

Cenomanian–Santonian interval

The plant fossil record from the Cenomanian and Turonian are poorly known in the Antarctic Peninsula. The Whisky Bay Formation (late Albian–latest Turonian: Riding & Crame 2002) is the only unit where strata of this age occur in the James Ross Basin, where it is divided into three members in each of the two main areas of outcrop (Brandy Bay–Whisky Bay area and Gin Cove–Rum Cove area). However, the complex lateral variation makes it difficult to correlate between outcrops and between the threefold subdivision in different parts of the basin (Riding & Crame 2002). Furthermore, considerable problems still exist in identifying and defining Cenomanian strata within the Whisky Bay Formation (Riding & Crame 2002). Marine invertebrate assemblages of Cenomanian age co-occur with palynofloras that are best assigned to the late Albian (Riding & Crame 2002). No detailed collecting for fossil wood has yet taken place, but a few terrestrial microfloras (e.g. Dettmann & Thomson 1987; D 3057.3) point to low-angiosperm diversity (Dettmann 1989; Askin 1992). In the Cenomanian the angiosperm component of the vegetation probably still comprised largely shrubby, herbaceous forms, as evidenced by the deficit of angiosperm wood in deposits older than approximately 90 Ma (Fig. 4) (Cantrill & Poole 2002).

The overlying Coniacian Hidden Lake Formation is rich in angiosperm leaf material (Hayes 1996, 1999; Hayes *et al.* 2006) and contains angiospermous fossil wood, attesting to increasing dominance and radiation into canopy niches by this time. The exact timing of the radiation into the canopy is problematic because of the paucity of data from the Cenomanian and Turonian. Nevertheless, the fossil record documents an increase in angiosperm floral diversity throughout the mid–Late Cretaceous at the expense of ferns and lycophytes initially, and subsequently bryophytes/hepatophytes, bennettites and other gymnosperms (Cantrill & Poole 2002). Evidence suggests that initially these early angiosperms were colonizers occupying under- and middle-storey niches and only later expanding to become more arborescent and invading the overstorey. This invasion would have drastically changed the prevailing landscape and thus the ecosystem. For example, this change enabled ferns to colonize the new niches created by the angiosperms and thus began a fern rediversification (Cantrill & Poole 2002). Important palaeobotanical information on the vegetation during the Coniacian is derived from the Williams Point Beds on Livingston Island, dated as 88 Ma (R. Hunt pers. comm. 1999), lying at a palaeolatitude of approximately 62°S (Grunow *et al.* 1991). The wood, leaves and palynofloras are well preserved, unlike many sites around the Antarctic Peninsula where the palynomorphs are highly degraded or destroyed and the leaves are merely impressions and lack cuticle (Chapman & Smellie 1992). Both macrofossil and microfossil

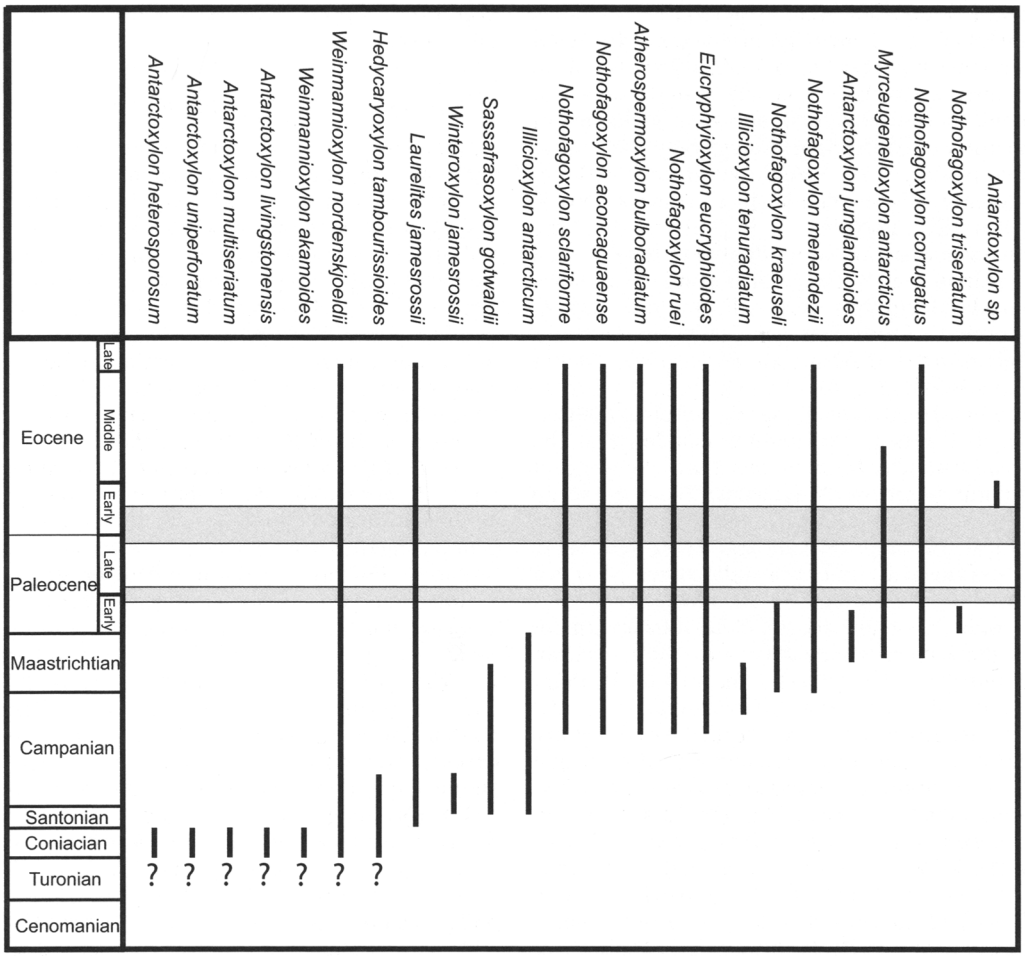


Fig. 4. Biostratigraphic range chart for angiosperm wood taxa (adapted from Cantrill & Poole 2005).

evidence from the Williams Point Beds suggest that the vegetation comprised conifer forest with a diverse angiosperm component. It still remains uncertain as to which group of plants dominated the canopy (Chapman & Smellie 1992; Poole & Cantrill 2001). Preliminary estimates of wood abundance from this locality suggest that between 67 and 81% of the samples are coniferous (Philippe *et al.* 1993; $n = 270$). Ferns, represented by leaves and petrified rachides, are abundant and diverse with large tree ferns and ?bennettites forming part of the arboreal component (Chapman & Smellie 1992; Poole & Cantrill 2001). Understorey fern taxa and Equisetites (Lacey & Lucas 1981) probably inhabited the moist forest floor and banks of streams. Thalloid liverworts (Lacey & Lucas 1981) and epiphytic ferns would have occupied moist shady banks, damp rocks, and trunks and branches of trees (Poole & Cantrill 2001). Unfortunately, this flora is still in need of a thorough revision as it was initially assigned a Triassic age (e.g. Orlando 1968), and the diverse leaf flora, representing many groups of non-woody plants, were assigned to Triassic organ taxa. A revision of the conifer and angiosperm wood component of the flora has already been undertaken by Poole & Cantrill (2001). They found that the size of the material indicates that the woody angiosperm taxa were from large trees. The coniferous element comprised of Araucariaceae and Podocarpaceae, whereas the angiosperms include two species assigned to the Monimiaceae and Cunoniaceae and four other taxa with affinities that lie with the 'Magnoliidae, Hamamelidae

and Rosidae' and were assigned to *Antarctoxylon* Poole et Cantrill, an organ genus for fossil woods of equivocal taxonomic affinity (Poole & Cantrill 2001). The early woody–arboreal angiosperm component shows no evidence of distinct growth rings, suggesting that these plants may have been evergreen. With an increase in the abundance of distinct growth rings after this time, it is probable that the angiosperms only later adapted to the seasonal Antarctic environment in becoming predominantly deciduous (Cantrill & Poole 2005). Another slightly younger Coniacian leaf flora occurs in the Hidden Lake Formation on James Ross Island (Fig. 5E–G). Although no cuticles are preserved, thus hindering systematic placement, Hayes (1996, 1999) concluded that the dominant leaf form in this flora shows great similarity to the Magnoliales with a strong component of sterculiaceous (Fig. 5E) and lauralean (Fig. 5F) forms, indicating that angiosperm diversity was well underway by this time.

Indeed, angiosperms had become dominant in the Antarctic macrofloras by the Coniacian (Cantrill & Poole 2002). The increased abundance of wood fragments suggests that the angiosperms were no longer herbaceous, shrubby understorey elements but had become a more important component of the canopy. The Santonian leaf floras still suggest a strong sterculiaceous and lauralean component (Hayes 1996, 1999), alongside woods with lauraceous (Poole *et al.* 2000*c*), cunoniaceous (Poole *et al.* 2000*a*), illiciaceous (Poole *et al.* 2000*b*), atherospermataceous (Poole & Francis 1999; Poole & Gottwald 2001) and winteraceous (Poole & Francis 2000) affinity (Fig. 4). All these elements, with the exception of the illiciaceous, lauraceous and *Sassafrasoxylon* Poole *et al.*, have adisjunct distribution between North America and Asia, and are characteristic of cooler temperate biomes. The presence of the illiciaceous and sassafrasaceous elements could suggest a somewhat warmer temperate biome, or perhaps a more recent adaptation of these plants to warmer latitudes.

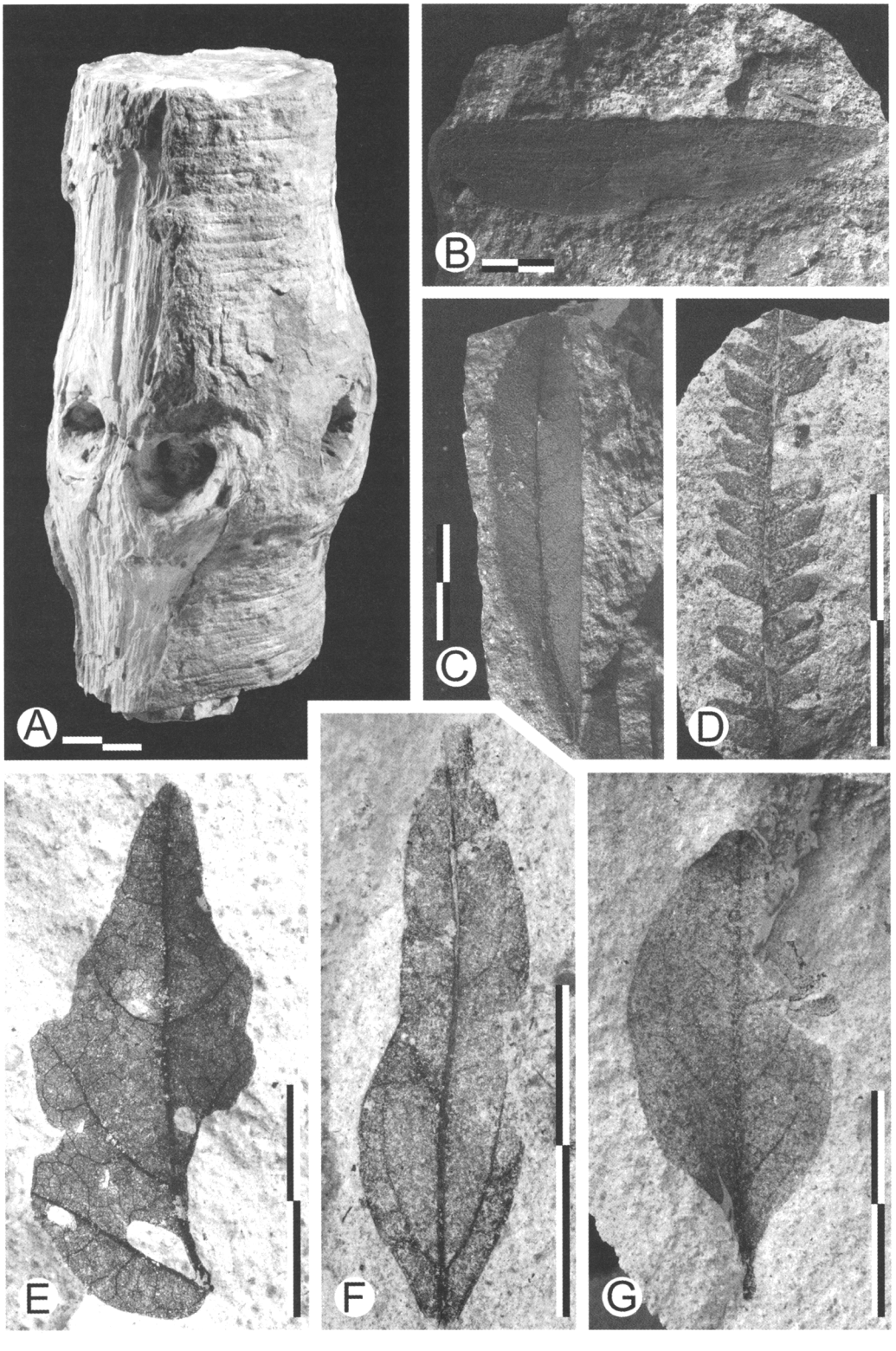
Precursors to the changes in vegetation seen in the Campanian–Maastrichtian are present in the Coniacian and Santonian. The first records of *Nothofagidites* Erdtman ex Potonié (Baldoni & Medina 1989; Keating 1992), *Proteacidites* Cookson ex Couper (Dettmann & Thomson 1987; Baldoni & Medina 1989; Barrera *et al.* 1999) and Myrtaceae (Dettmann & Thomson 1987; Baldoni & Medina 1989) occur, although the rare occurrence of these grains indicates the plants were of minor importance in the vegetation. This is supported by the lack of wood from these groups.

Campanian–Maastrichtian interval

Between the Santonian and Campanian there is an unmistakable turnover in pollen taxa that is also reflected in the wood (Fig. 4) and other macro-floras (Dettmann 1989; Askin 1992). Within the angiosperm wood flora the more 'primitive' wood types with affinities to the 'Magnoliidae, Hamamelidae and Rosidae' (Poole & Cantrill 2001) do not continue through to the Campanian. The only primitive types of wood occurring in the Coniacian flora, that also appear in the Campanian, are the cunoniaceous *Weinmannioxylon* Petriella and the monimiaceous *Hedycaryoxylon* Süss (but these xylotypes, *W. ackamoides* Poole et Cantrill and *H. tambourissoides* Poole et Gottwald, both disappear during the Campanian). *Hedycaryoxylon* is replaced by other anatomically different, monimiaceous taxa, whereas the *Weinmannioxylon nordenskjoeldii* Poole *et al.* xylotype continues through until the Eocene (Fig. 4).

Perhaps the most dramatic change is the increase in importance of the Nothfagaceae. The Nothofagaceae is a typical, and one of the most important elements, of the relictual Southern Hemisphere temperate floras today (Manos 1997). Nothofagaceae in the Antarctic pollen floras is first represented by the ancestral *Nothofagidites senectus* Dettmann et Playford, notably distinct from extant *Nothofagus* Blume pollen (Dettmann *et al.* 1990). Importantly, *Nothofagus* pollen is extremely common and its absence can be regarded as evidence for the lack of the genus in areas where it has not been found (Swenson & Hill 2001). This family is only rarely recorded prior to the Campanian, as pollen analyses from Santonian strata (Baldoni & Medina 1989; Keating 1992). Despite the sparse occurrences in the Santonian no wood is known until the Campanian when this group becomes important in both the fossil wood and pollen record (Poole 2002). These changes are supported by an increase in abundance and/or diversity of other taxa including pollen of *Dacrydium* Sol. Ex G. Forst., Proteaceae and Myrtaceae, and a variety of other angiosperms also evidence the changes occurring at, or just prior to, the mid-Campanian (Dettmann & Thomson 1987).

In the Maastrichtian of Vega and Seymour islands on the Antarctic Peninsula the oldest known occurrences of *Nothofagus* subgenera *Fuscospora*, *Lophozonia* and *Brassospora* have been found in the pollen record (Dettmann *et*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al. 1990) alongside wood of the *Fuscospora* type (Poole 2002) (Fig. 4). Manos (1997) and Swenson *et al.* (2000) recognize the subgenus *Lophozonia* as the most basal clade within Nothofagaceae, with the pollen record extending back to the late Campanian in Antarctica (Dettmann *et al.* 1990) and appearing only slightly later in the wood flora (Poole 2002). By the Maastrichtian all but the *Brassospora* subgenus are represented in the wood flora, whereas all four subgenera are represented in the pollen flora. The lack of wood allied to *Brassospora* is not surprising as this group, although a copious pollen producer today, is often confined to montane areas. We can confidently assume that by the mid-Campanian the Nothofagaceae had now become an important and diverse component of the Antarctic ecosystem having substantially changed the face of the flora relative to the ancestral Coniacian–Santonian vegetation.

By the Maastrichtian the wood floras continued to increase in abundance and diversity, with other angiospermous taxa appearing and Nothofagaceae diversifying further (Poole *et al.* 2003). Wood anatomical characters, coupled with good preservation of these now prolific angiosperms, provide us with important indications pertaining to the local environment, as well as the vegetational composition and dynamics. The Antarctic material is comprised predominantly of aerial organs (branches or trunks – only one specimen could be confidently identified as having a root origin), possibly dominated by sap-wood remains (cf. Wheeler & Manchester 2002 and their inferences drawn from the Eocene Clarno Formation woods). The dominance of sap wood is evidenced from preserved fungal hyphae associated with the ray parenchyma and vessel lumens or tracheids, suggesting that these fungi are sap-staining fungi restricted to sap wood. The detachment from the parent plant may have occurred during the Antarctic polar winter or at least during the dormant phase of the year as many of the angiosperm woods have vessels filled with well-developed tyloses, but with no evidence of bud-like outgrowths of parenchyma into the vessel lumen, which mark the beginning of tylose formation (cf. Chattaway 1949; Wheeler & Manchester 2002). The woods probably resided, for a time at least, in a damp, but not waterlogged, aerobic environment. Moist conditions probably prevailed on the magmatic arc adjacent to the James Ross Island Basin, encouraging fungal growth within the woody debris covering the forest floor. This woody debris was probably then transported, by streams or rivers during times of storms or flash floods, to the coast where the material was finally deposited offshore in the shallow-marine environment.

At this time podocarps and angiosperms were the main canopy elements of the perhumid, tall open forests (Askin 1988; Specht *et al.* 1992). Palynofloras suggest the Myrtaceae were present along with diverse species of *Nothofagus*, *Gunnera* L., Proteaceae, Aquifoliaceae, Olacaceae, Loranthaceae and Sapindaceae accompanied by a rich fern component including the Osmundaceae and Gleicheniaceae (e.g. Askin 1989, 1990). At the end of the Maastrichtian the warmer temperate elements, *Sassafrasoxylon* and Illiciaceae, disappeared (Fig. 4), whilst the abundance of fern taxa also decreased (Askin 1988, 1990), possibly in response to a cooling in the climate, leaving a floral composition very similar to that which occurs today in the cool temperate rainforests of South America. In previous publications (Poole *et al.* 2001, 2003) the vegetational composition of the Antarctic Peninsula during the Late Cretaceous and early Tertiary has been likened to the extant low- to mid-altitudinal Valdivian rainforests under the 'Valdivian model'. Indeed the similarities in terms of environmental dynamics in addition to vegetational composition are remarkably similar. Along the Andean margin of South America stratovolcanic activity is a major source of disturbance along with associated events such as landslides, earthquakes and the flooding of lake systems. Glacial erosion and deposition contribute to the general disturbance especially at altitude. The Antarctic Peninsula region during the Cretaceous and Tertiary was a vegetated active volcanic arc and thus would have been subject to similar ecological disturbances. There is no doubt that climate change influenced vegetational composition, although evolving palaeoenvironments in the Antarctic

Fig. 5. Late Cretaceous and Cenozoic floras. (A)–(D) Palaeogene plant fossils from the James Ross Island Basin. (**A**) *Araucaria marenssi* Cantrill et Poole, a petrified araucarian trunk from the Eocene La Meseta Formation, DJ.1057.53. (B)–(D) Leaf fossil from the Palaeocene Cross Valley Formation. (**B**) *Araucaria nathorstii*, DJ.1111.14. (**C**) Angiosperm leaf, D.523.1. (**D**) Fern frond, DJ.1113.134. (E)–(G) Coniacian leaf fossil from the Hidden Lake Formation. (**E**) sterculiaceous taxon, D.8754.8.1a. (**F**) lauraceous taxon, D.8754.8.57a. (**G**) Unidentified angiosperm, D.8754.45a. Scale bar divisions are 1 cm.

Peninsula region probably contributed in equal, if not greater, importance. One good example of environmental dynamics, rather than climate, accounting for vegetation change can be seen in Late Cretaceous–Palaeocene strata on King George Island lying to the north of the James Ross Island Basin. The Late Cretaceous–Early Palaeocene strata is lava-dominated, suggesting that stratovolcanic activity was high and the centre of activity was proximal (Smellie *et al.* 1984; Shen 1994, 1999; Orton 1996). By the Palaeocene epiclastic deposits including tuffaceous rocks indicate that the volcanic dynamics had changed, lowering the rate of disturbance. Late Cretaceous floras of this region also document ecological disturbances: low-density vegetation is dominated by ferns such as *Thyrsopteris* Kunze and *Dacrydium*, and a relatively small percentage of angiosperms with nothofagaceous, sterculiaceous, lauraceous and myrtaceous affinity (Dutra & Batten 2000; Poole *et al.* 2001), whereas post-disturbance vegetation in proximal volcanic settings is characterized by gymnosperms such as cycads and podocarps (Cao 1992; Dutra & Batten 2000; Poole *et al.* 2001).

Palaeocene–Eocene interval

The Valdivian-type ecosystem continues over the Cretaceous–Tertiary boundary, with no suggestion of catastrophic environmental devastation, into the Eocene where the last evidence for this Valdivian-type ecosystem can be found in the palynological record of Seymour Island (Askin 1997) and the wood record of King George Island (Poole *et al.* 2001). Palaeocene and Eocene volcanic activity was still prevalent across the Antarctic Peninsula with terrestrially deposited fossil floras (Fig. 5B, D) providing evidence for ecological disturbance similar to that observed in the Valdivian region today (Hunt 2001; Poole *et al.* 2001 and references therein; Hunt & Poole 2003). Frequent disturbance in the lower part of the sequence on King George Island is characterized by low-diversity flora consisting only of *Nothofagus* and podocarps overlying a coarse volcanic debris flow. Floras more distal from the centre of volcanic activity probably experienced lower levels of disturbance and this is again supported by the floral composition. The presence of myrtaceous, eucryphiaceous and nothofagaceous angiosperms alongside podocarps and Cupressaceae suggest that the flora was relatively diverse and had experienced low or relatively moderate levels of disturbance (Askin 1997; Poole *et al.* 2001). Higher up the sequence and in more distal locations floral diversity increases with pteridophytes (such as Cyatheaceae, Dicksoniaceae and Osmundaceae), conifers (including Araucariaceae, Cupressaceae and Podocarpaceae) and angiosperms (e.g. Nothofagaceae, Proteaceae, Myrtaceae, ?Araliaceae, Anacardiaceae and Cunoniaceae) representing low levels of disturbance, i.e. climax or pre-eruption vegetation. Interestingly, there are no records of *Chusquea* Kunth. (bamboo), a characteristic understorey element of the Valdivian ecosystem today. Poole *et al.* (2001) have suggested that ferns, ubiquitous at this time (Zhou & Li 1994; Mohr 2001), may have filled this niche in these Antarctic forests. By the Late Eocene, angiosperm leaf floras at a palaeolatitude of approximately 62°S show evidence of both deciduous and possible evergreen habits (Hunt & Poole 2003), whereas the wood floras suggest an overriding deciduous habit (Poole *et al.* 2001).

Although this Valdivian-type ecosystem may have persisted for longer, into the Late Eocene, the sudden widespread glaciation of Antarctica and the associated shift towards cooler temperatures at the Eocene–Oligocene boundary (*c.* 34 Ma) (DeConto & Pollard 2003) would have had a detrimental effect on the prevailing vegetation. The cool temperate rainforests would have become less diverse, possibly becoming more analogous to the extant Magellanic subpolar *Nothofagus*- (evergreen and deciduous) dominated forests mixed with conifers (*Podocarpus* L'Her. Ex Pers., *Pilgerodendron* Florin) growing south of approximately 47°S across the southern Aysén and Magallanes regions of Chile and Tierra del Fuego in Argentina (Moore 1983; Veblen *et al.* 1996). Here permanent snow, ice caps and glaciers are present at altitude, cold temperate conditions (MAT 3–6 °C) prevail with high levels of precipitation (MAP 1000–4000 mm) and strong permanent winds (Hoffmann 1975). Indeed, Late Eocene Antarctic fossil assemblages from Seymour Island and McMurdo Sound consist of podocarpaceous and araucariaceous conifers, *Nothofagus* (both deciduous and evergreen) with at least three other angiosperm types and ferns (Dusén 1908; Case 1988; Doktor *et al.* 1996; Askin 1997, 2000; Cantrill 2001*b*; Francis 2000; Pole *et al.* 2000).

Neogene

The cooling climate across the Eocene–Oligocene boundary (e.g. Zachos *et al.* 2001) is attested to both by a more fragmentary Antarctic plant record and also shifts in leaf size classes

(Cantrill 2001*b*). These changes are also seen in the palynological record, with a dramatic decrease in diversity, occurrence and abundance of terrestrial palynomorphs (Raine 1998; Askin & Raine 2000; Raine & Askin 2001). Within the James Ross Basin post-Eocene floras are lacking, due in part to a lack of strata from the latest Eocene until the Miocene (Hobbs Glacier Formation: Pirrie *et al* 1997; Jonkers *et al.* 2002). The overlying James Ross Island Volcanic Group (late Miocene–Pliocene) and the Pliocene Cockburn Island Formation (Jonkers 1998*a*, *b*; Jonkers & Kelley 1998) also lack plant material, and a terrestrial palynoflora has not been documented. Elsewhere in the Antarctic Peninsula the post-Eocene record of macroplants is contentious. In the South Shetland islands the age of a series of Oligocene glacial and interglacials (Birkenmajer 1987, 1990, 1997) has been questioned (Dingle *et al.* 1997; Dingle & Lavelle 1998; Hunt 2001) so that all the fossil floras are now considered to be Eocene in age (Hunt 2001). What is clear from the Oligocene and Miocene strata on King George Island (e.g. Polonez Cove Formation and Cape Melville Formation), and the Miocene and Pliocene units in the James Ross Basin (Hobbs Glacier Formation, James Ross Island Volcanic Group and Cockburn Island Formation), is that conditions for plant growth were extremely unfavourable and a cyclical glacial–interglacial environment prevailed.

The impact of this climate regime on plant communities is best seen in a recent series of cores from offshore Cape Roberts in the Ross Sea (Raine 1998; Askin & Raine 2000; Raine & Askin 2001). Although sedimentation patterns have influenced the accumulation of palynomorphs, the pattern is one of low diversity and abundance interspersed with periods of higher diversity and abundance presumably in response to cold and warm climate periods. By the Early Oligocene the Antarctic flora had become species depauperate with *Nothofagus* and podocarpaceous conifers probably dominating the canopy, and with lycophytes and some bryophytes, and ferns contributing to the understorey (Askin 2000; Pole *et al.* 2000; Cantrill 2001b; Mohr 2001). The flora has analogies with today's Magellanic tundra (*c.* 48°S and the southern tip of Tierra del Fuego and across the Chilean archipelago) which supports predominantly bog communities (Moore 1983; Ruthsatz & Villagran 1991) under a regime of high precipitation (2000–6000 mm year^{-1}) and low temperatures (MAT 5–6 °C). In some sheltered, less unfavourable areas of this tundra small stands of evergreen forest can be found dominated by *Nothofagus* (*N. antarctica* (G. Forst.) Oerst. and *N. betuloides* (Mirb.) Blume), *Drimys* J.R. Forst. Et G. Forst., *Pilgerodendron* and occasional *Maytenus* Molina, elements that have been associated with past Antarctic vegetation. At higher elevations a belt of low 'krumholz' vegetation comprising *Nothofagus* occurs (Moore 1983; Veblen *et al.* 1996). Changes to the Antarctic Neogene vegetation due to cooling of the continent probably resulted in a transition of the vegetation from low forest to krumholz forms and ultimately to tundra. The exact timing of these transitions is unclear, but the terrestrial succession from Cape Roberts (Raine 1998; Askin & Raine 2000; Raine & Askin 2001) shows a general decline in diversity and abundance through the Oligocene and into the Miocene, with fewer abundance spikes in Nothofagaceae. This suggests that, although the vegetation survived successive glaciations presumably in refugia, the ability to recover progressively diminished. The Late Pliocene Meyer Desert Formation (Sirius Group) from East Antarctica contains prostrate, gnarled deciduous *Nothofagus* (as evidenced from leaves, wood and pollen from glacial sediments of the Sirius Formation *c.* 1.8–5.3 Ma: Carlquist 1987; Francis & Hill 1996). Some of the fossil woods show evidence of traumatic events and scarring (Francis & Hill 1996), which is also a common feature in other prostrate species, such as the magellanic *Nothofagus*, to which the habit of these *Nothofagus* fossils can be likened. *Nothofagus* probably had a deciduous habit with single seasonal leaf falls attested to by the strong plicate vernation of fossil *Nothofagus* leaves coupled with dense accumulation of leaves within a single layer (Hill *et al.* 1996). More recent investigations of this flora reveal a surprising floral diversity including conifers, cushion plants, ranunculids, possible grasses and chenopods, and a variety of moss taxa (some cushion forming) growing in a subglacial tundra-like environment (Hill & Truswell 1993; Ashworth & Cantrill 2004). Fossil plant material suggests mean annual temperatures of approximately –20 °C, but possibly colder without snow cover to protect the dormant plants, and growing seasons of up to 3 months with temperatures reaching only about 5 °C in the growing season (Francis & Hill 1996; Hill & Jordan 1996). This evidence lends further support to a magellanic subpolar forest–tundra-type ecosystem.

The change from true magellanic subpolar forest to true tundra in Antarctica at the end of the Tertiary would probably have been punctuated rather than gradual with the flora

responding to pulses of glaciations, surviving in refugia during the severest of climates and only making a transitory comeback during the interglacials. Finally, these last remaining plants also succumbed to the deteriorating climates brought about by declining atmospheric CO_2, continental separation and widescale glaciation (Exon *et al.* 2000; DeConto & Pollard 2003) such that today only two species of vascular plant, *Colobanthus quietensis* (Kunth) Bartl. and *Deschampsia antarctica* Desv., along with a few species of lichens and mosses, survive in today's extreme southern high-latitude environments.

Summary

Four stages of vegetation development associated with taxonomic turnover and canopy development are recognized from the Aptian through to the Tertiary across much of the Antarctic Peninsula.

- Early–mid-Cretaceous vegetation was conifer dominated, ranging from forests with lower storeys comprising ginkopsids, spehnopsids, ferns, liverworts alongside extinct taxa, such as bennettites and taeniopterids, to dispersed clumps of individuals more akin to open woodland. The forests had stand densities of approximately 600 stems per hectare, with productivity estimates and taxon composition similar to the warm temperate araucarian–podocarp vegetation of North Island, New Zealand (Falcon-Lang *et al.* 2001; Falcon-Lang & Cantrill 2001*a*). The Alexander Island floras are the only known *in situ* fossil forests to be found in or near the James Ross Island Basin and therefore are taken as a general guide for the ensuing angiosperm-dominated vegetation of the Peninsula region.
- Middle–early Late Cretaceous floras reflect the arrival of the angiosperms at the expense of the bryophytes/hepatophytes, gymnosperms such as bennettites, and, initially, ferns and lycophytes. The initially herbaceous angiosperms had become arboreal by the Coniacian and invaded the conifer-dominated canopy, giving rise to new understorey niches that ferns and liverworts subsequently exploited. By the Santonian angiosperms were an important component of the overstorey, and families including the Sterculiaceae, Lauraceae, Cunoniaceae, Monimiaceae, Atherospermataceae and Winteraceae progressively replaced more 'primitive' forms. Taxonomic similarity with the Vadivian rainforests of Chile was beginning to develop, although the Antarctic vegetation retained some more warm temperate taxa such as the Illiciaceae and *Sassafras*-like plants. The expansion of *Nothofagus* and the replacement of the warm temperate elements in the Campanian changed the vegetation once more. It became similar to the cool temperate rainforests of Valdivia in South America today (Poole *et al.* 2001, 2003).
- The similarities to the Valdivian rainforests strengthened through the Maastrichtian to become dominant up until the Eocene. Vegetation changes reflected environmental disturbances due to volcanic activity that were occurring at this time. Climate deterioration associated with the onset of glaciation in Antarctica led to a further change in the vegetation.
- Diversity decreased towards the Eocene–Oligocene boundary until the forests probably became more similar to the Magellanic subpolar forests of southern South America today where communities are dominated by *Nothofagus* mixed with conifers. The flora became more depauperate during the Oligocene and Miocene, such that by the Miocene–Pliocene it was probably more similar to the Magellanic tundra of southern South America, supporting local stands of *Nothofagus* and a few other angiosperm and conifer taxa. *Nothofagus* decreased in stature as a result of the deteriorating climate conditions. It is likely that the vegetation went through a krumholtz phase in habit prior to becoming low prostrate shrubs in the Pliocene tundra. By the end of the Tertiary, with glaciation widespread and temperatures plummeting, widespread vegetation had been wiped from Antarctica such that only two species of vascular plants occur there today.

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