

A Fossil Wood Flora from King George Island: Ecological Implications for an Antarctic Eocene Vegetation

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Early Tertiary sediments of the Antarctic Peninsula region continue to yield a rich assemblage of well-preserved fossil dicotyledonous angiosperm wood. The wood flora under consideration is from the Collins Glacier region on Fildes Peninsula, King George Island and is derived from tuffaceous sediments of the Middle Unit of the Fildes Formation. These deposits accumulated in a volcanic setting adjacent to a basic-intermediate stratocone. The fossil assemblage provides further evidence for the existence of cool temperate forests, similar in composition to those found today in New Zealand, Australia and, in particular, southern South America. This paper describes two conifer and five angiosperm morphotypes, four of which are new additions to the Antarctica palaeoflora records. *Cupressinoxylon* Goeppert, which is the dominant conifer in terms of numbers, and *Podocarpoxylon* Gothan represent the conifers. The angiosperm component includes two species of *Nothofagoxylon* and two previously undescribed wood morphotypes that exhibit greatest anatomical similarity to woods of *Luma* A. Gray (Myrtaceae) and *Eucryphia* Cav. (Cunoniaceae). These morphotypes are described and assigned to the organ genera *Myrceugenelloxylon* Nishida, and *Weinmannioxylon* Petriella, respectively. A model based on the extant cool temperate Valdivian rainforests is proposed and ecological reconstructions based on palaeobotanical and geological evidence suggest that changes in the palaeovegetation reflect natural dynamics following volcanic disturbances. © 2001 Annals of Botany Company

Key words: Fossil wood, Antarctica, Myrtaceae, *Eucryphia*, Nothofagaceae, Eocene, Valdivia, Tertiary.

INTRODUCTION

Fossil floras from the Antarctic Peninsula region play an integral role in understanding the biodiversity and palaeoecology of high latitude forests that existed during the Late Cretaceous and Early Tertiary. Moreover, these plant records are crucial for studies of biogeographic trends during the final phases of the break-up of Gondwana, which in turn has important implications for phylogenetic studies. During the Late Cretaceous and Early Tertiary, the climate of the Antarctic Peninsula is suggested to have been relatively mild and moist with a lack of significant ice at high latitudes (Truswell, 1990; Askin, 1992; Francis, 1996). A cooling event occurred between the Late Cretaceous, with mean annual temperatures of 8–15 °C and a frostless climate, and the mid-Palaeocene (Askin, 1992; Zachos *et al.*, 1993; Ditchfield *et al.*, 1994; Dingle and Lavelle, 1998). Foliar evidence from King George Island (Birkenmajer and Zastawniak, 1986) and Seymour Island (Dusén, 1908; Case, 1988) suggests that during the Palaeocene a cool to warm temperate climate with mean annual temperatures of 10–12 °C and high rainfall (1000–4000 mm year⁻¹) prevailed. Based on shallow marine palaeotemperature data, the temperature reached its peak in the Early Eocene and subsequently declined during the Late Eocene (Ditchfield

et al., 1994; Dingle and Lavelle, 1998 and references cited therein).

The composition of the vegetation on King George Island reflects the postulated warm to cool, moist climates. Palaeocene to Eocene leaf, wood and pollen floras (see Fig. 1 and Table 1) record elements associated with modern temperate austral forests such as Araucariaceae, Podocarpaceae, Nothofagaceae, Cunoniaceae, Lauraceae and some Proteaceae (e.g. Torres and Lemoigne, 1988; Askin, 1992; Li, 1992, 1994; Zhou and Li, 1994a; Markgraf *et al.*, 1996). Warm temperate, alongside relatively tropical, taxa such as Gunneraceae, Monimiaceae and Sterculiaceae, are also recognized in these floral assemblages (Orlando, 1964; Dettmann, 1989; Askin, 1992). These southern polar forests experienced a unique growth regime with long periods of winter darkness and near-continual low-angle incident sunlight during the summer months.

The tectonic setting of King George Island at a palaeolatitude of 62°S (approximately coincident with that of today; Lawver *et al.*, 1992) during the Early Tertiary comprised eastwards subduction of the Pacific Ocean floor beneath the Antarctic Peninsula. This resulted in uplift and active volcanism in the form of stratovolcanoes (Pankhurst and Smellie, 1983; Smellie *et al.*, 1984). Agglomerate and fossiliferous tuff deposits, intercalated with lavas in the Late Cretaceous to Early Tertiary strata on King George Island, are typical of the mixed effusive-explosive style of volcanism associated with these landforms (Shen, 1994; Xue *et al.*,

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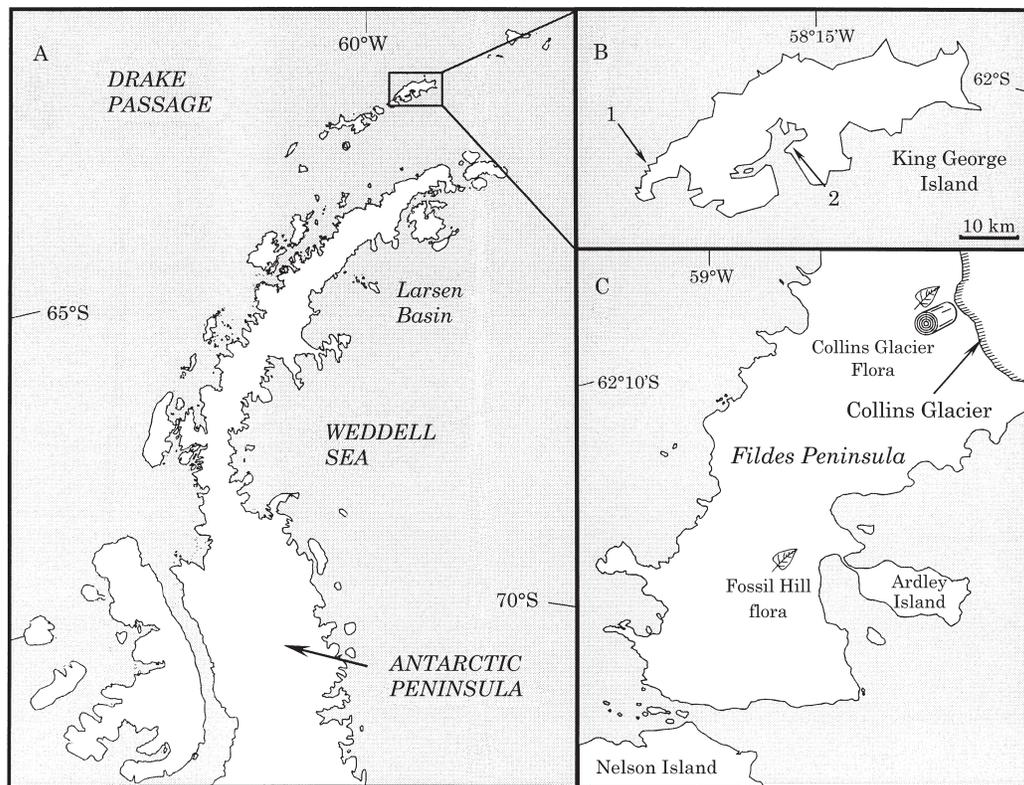


FIG. 1. Map of the Antarctic Peninsula region showing macrofossil localities mentioned in the text. **A**, Antarctic Peninsula region. **B**, King George Island showing the position of the Fildes Peninsula (1) and the Palaeocene-Eocene fossil plant locality, Point Hennequin (2) mentioned in the text. **C**, Fildes Peninsula showing the position of the Collins Glacier Flora, Fossil Hill flora and Ardley Island.

1996). Volcanism has important implications for the development of local and regional floras since it modifies pre-existing terrains and can destroy vegetation over a wide area, which in turn can lead to successional changes in the vegetation (Burnham and Spicer, 1986; Burnham, 1994).

This paper describes seven fossil wood morphotypes from the Collins Glacier Flora on Fildes Peninsula, King George Island. Four of these morphotypes are new records to the Antarctic palaeoflora. Using contemporaneous macrofossil records and comparisons with the ecosystem of southern South America today, the biogeographic and ecological implications of the flora are discussed in the context of the stratovolcanic setting.

MATERIALS AND METHODS

The wood material examined in this study was collected during the British Antarctic Survey expedition to the northern Antarctic Peninsula region during the 1999 field season. The details for repository, (type) locality and lithostratigraphic horizon are applicable to all wood material described below and have therefore not been repeated throughout the text. The material is associated with tuffaceous rocks from the Middle Unit of the Fildes Formation, Fildes Peninsula, King George Island 62°10'S 59°04'W (Fig. 1). The age of this formation has been dated as Eocene (i.e. 49–43 Ma; Smellie pers. comm., 2000; Smellie *et al.*, 1984; Fensterseifer *et al.*, 1988; Soliani *et al.*,

1988). This is in agreement with Shen (1999) who included the outcrop in the Middle Eocene Rocky Cove Member of the Fossil Hill Formation.

The Collins Glacier Flora (Fig. 1C) consists of silicified wood fragments less than 40 cm long and approx. 30 cm in diameter found in an ochre coloured, modern clay outwash, which overlies green tuffaceous deposits of the Middle Unit, Fildes Formation. Some of the wood fragments retain pieces of the original fossiliferous lithology that weathers identically to the underlying tuffaceous sediments. This suggests that the wood has weathered from the same unit and may have been displaced only a short distance spatially and stratigraphically from its original position. Silicified wood specimens generally display a high degree of anatomical preservation, although some samples show evidence of crushing and localized degradation prior to petrification.

Wood specimens were thin-sectioned using standard techniques employed for petrified plant fossil material (e.g. Hass and Rowe, 1999). Systematic affinities of the fossils were initially determined by consulting reference literature such as Cutler and Gregory (1998), Metcalfe and Chalk (1950, 1989), Metcalfe (1987), Ilic (1991) and searching the computerized OPCN (Wheeler *et al.*, 1986; LaPasha and Wheeler, 1987) and CSIRO Family Key (Ilic, 1987) wood databases. Subsequent comparisons were made with extant wood samples housed in the Jodrell Laboratory, Royal Botanic Gardens Kew, UK; the Wood

TABLE 1. Comparison of Myrcogenelloxylon antarcticus with its closest anatomical analogue *Luma apiculata*, and Weinmannioxylon eucryphioides with its closest anatomical analogue *Eucryphia lucida*

	<i>Luma apiculata</i> ¹	<i>Myrcogenelloxylon antarcticus</i> sp. nov.	<i>Eucryphia lucida</i> ²	<i>Weinmannioxylon eucryphioides</i> sp. nov.
Ecological range	Below 700 m above sea level in both Andean and Coastal mountains of S. America	Unknown	Cool temperate rainforests of Tasmania, up to 1000 m above sea level	Unknown
Habit	Small tree in north, up to 25 m in southern part of its range	Unknown	Trees of moderate height	Unknown
Porosity	Diffuse; solitary, rarely in clusters; circular to elliptic	Diffuse; solitary, paired; circular to elliptic	Diffuse; solitary, paired, few in radial files and clusters; circular to angular, weakly elliptic	Diffuse to weakly semi-ring; solitary or paired, rarely in radial files and clusters; circular to slightly elliptic
Vessels				
Number per mm ²	175–220	77–102	105–133	62–179
VTØ µm range (mean)	15–38 (29)	37.5–67.5 (54)	27.5–65 (47)	25–105 (49)
VRØ µm range (mean)	15–57 (40)	50–122.5 (84)	32.5–67.5 (55)	17.5–95 (64)
VEL µm range (mean)	425–800 (587)	620–1160 (714)	520–1030 (720)	620–1160 (714)
Perforation plate (n° bars)	Scalariform (21–37)	Scalariform (numerous)	Scalariform (up to 38), rarely simple	Scalariform (up to 55), rarely simple
Spiral thickening	Absent	Absent	Present	?Absent
Intervessel pitting	Circular to horizontally elongate, scalariform	Circular mainly horizontally elongate and scalariform	Opposite to horizontally elongate, scalariform	Opposite to horizontally elongate, scalariform
Tyloses	Present	Absent	Present*	Present
Ray				
Width	Uniseriate and 2–3 seriate	Biseriate	Uniseriate, locally biseriate	Uniseriate, locally biseriate
Cell characteristics	Procumbent body cells and upright marginal cells	Procumbent body cells and upright marginal cells	Square/procumbent body cells, square/upright marginals; thickened walls	Square/procumbent body cells, square/upright marginals; thickened walls
Height (µm)	80–915	50–400	90–520	120–910
Ray-vessel pitting	Opposite to scalariform	Elongate to scalariform	Occasionally circular, mainly elongate to scalariform	Occasionally circular, mainly elongate to scalariform
Fibre-tracheid				
Radial Ø (µm)	12–22	10–30	15–30	7.5–27.5
Wall thickness (µm)	2.5–6.2	2.5–4	5–7.5	2–5
Axial parenchyma	Diffuse	?Diffuse	Diffuse, diffuse in aggregate	?Diffuse

Data from ¹Rancusi *et al.*, 1987; ²Hill, 1991; Read and Brown, 1996; Dickison, 1978 and supplemented with personal observations of *Eucryphia lucida* (WC006 deposited in the Wood Anatomy Section, Utrecht). V, Vessel; R radial; T, tangential; EL, element length; Ø, diameter, *not observed in WC006.

Anatomy Section in The National Herbarium, Utrecht University, The Netherlands; and the Federal Research Centre for Forestry and Forest Products, Hamburg, Germany. Wood measurements were taken in accordance with IAWA recommendations wherever possible (IAWA Committee, 1989) except in the case of vessel element length which was measured in thin sections of both fossil and modern wood samples, as maceration of the fossil material is not possible. The specimens are deposited at the British Antarctic Survey, Cambridge, UK.

SYSTEMATIC PALAEOBOTANY

Order: Coniferales

Family: Cupressaceae

Organ genus: *Cupressinoxylon* Goeppert

Type species: *Cupressinoxylon subaequale* Goeppert, 1850
Cupressinoxylon sp.

Material: P. 3023-81, P. 3023-82, P. 3023-83, P. 3023-84, P. 3023-89

Description: This description is based on five specimens: P. 3023-81 is a 16-year-old branch 4 cm in diameter; P. 3023-82 is branch wood at least 30 years old and 7 cm in diameter; P. 3023-83 is trunk wood at least 64 years old, no diameter could be estimated; P. 3023-84 is trunk wood at least 12 cm in diameter; and P. 3023-89 is branch wood 16–19 years old and 6 cm in diameter.

Growth rings: Distinct, ring boundary markedly defined by a narrow late wood zone (one–three cells wide) (Fig. 2). False rings present in P. 3023-83 and P. 3023-84 usually occurring in the latter part of the growth cycle. *Tracheids:* In transverse section 9 to 40 (mean 24) μm in radial diameter. *Pitting:* In radial walls uniseriate, rarely biseriate (Fig. 3). Pit rows short, one to eight pits tall. Pits circular, bordered, apertures elliptical to slit-like, oblique (cupressoid) (Figs 3, 6). Rare tangential pits were observed in one specimen (P. 3023-84). Crossfield regions with one or rarely two cupressoid pits (Fig. 6). *Rays:* Uniseriate, one to 14 (median three) cells tall; approx. 12 rays per tangential millimetre (Fig. 4). *Pith:* Up to 800 μm in diameter containing thick-walled (up to 12 μm thick) sclerids with a diameter of up to 48 μm .

Comparison: The walls of the medullary ray cells, particularly the tangential walls, are predominantly smooth, and crossfield regions are characterized by cupressoid pits. This combination of characters defines the form genus *Cupressinoxylon*. Although records of leaves (e.g. Zhou and Li, 1994a) confirm the presence of the Cupressaceae in King George Island floras (Table 2), wood has only been described from Suffield Point (Torres et al., 1984; Torres, 1990). This wood material, referred to as *C. parenchymatosum*, is

poorly preserved and the name has not been properly formalized. It is, however, anatomically similar to the material described here, but with slightly shorter rays (one–ten) and more abundant axial parenchyma. No other cupressaceous wood has been recorded from King George Island sequences. Until detailed studies of the King George Island fossil conifer wood assemblages have been made following the discovery of more specimens, we feel that it is better to leave this material assigned to generic level only.

Family: Podocarpaceae

Organ genus: *Podocarpoxylon* Gothan, 1908

Type species: *Podocarpoxylon juniperoides* Gothan, 1908
Podocarpoxylon fildesense Zhang & Wang, 1994

Material: P. 3023-51

Description: This description is based on branch material that is at least 15 years old and over 7 cm in diameter.

Growth rings: Distinct slightly asymmetric, ring boundary subtle with a narrow late wood zone that is only two to three cells thick (Fig. 7). False rings absent. *Tracheids:* In transverse section 8 to 36 (mean 31) μm in radial diameter. *Pitting:* In radial walls of the tracheids circular, pits bordered, typically podocarpoid, tangential walls with rare scattered pits (Figs 5, 10). Crossfield regions with one to four pits, pits also podocarpoid (Fig. 8). *Rays:* Uniseriate, one to five (median two) cells tall, approx. 19 rays per tangential millimetre (Fig. 9).

Comparison: This material is almost identical to *Podocarpoxylon fildesense* including the black resinous rays in tangential section (Zhang and Wang, 1994) (Fig. 9). The only major difference is ray height: Zhang and Wang (1994) reported rays ranging from one to 16 cells, but generally two to eight cells tall. In this material the ray height is substantially less (one–five cells) than that reported by Zhang and Wang (1994), but branch wood tends to have shorter rays (cf. Carquist, 1988).

Class: Magnoliopsida

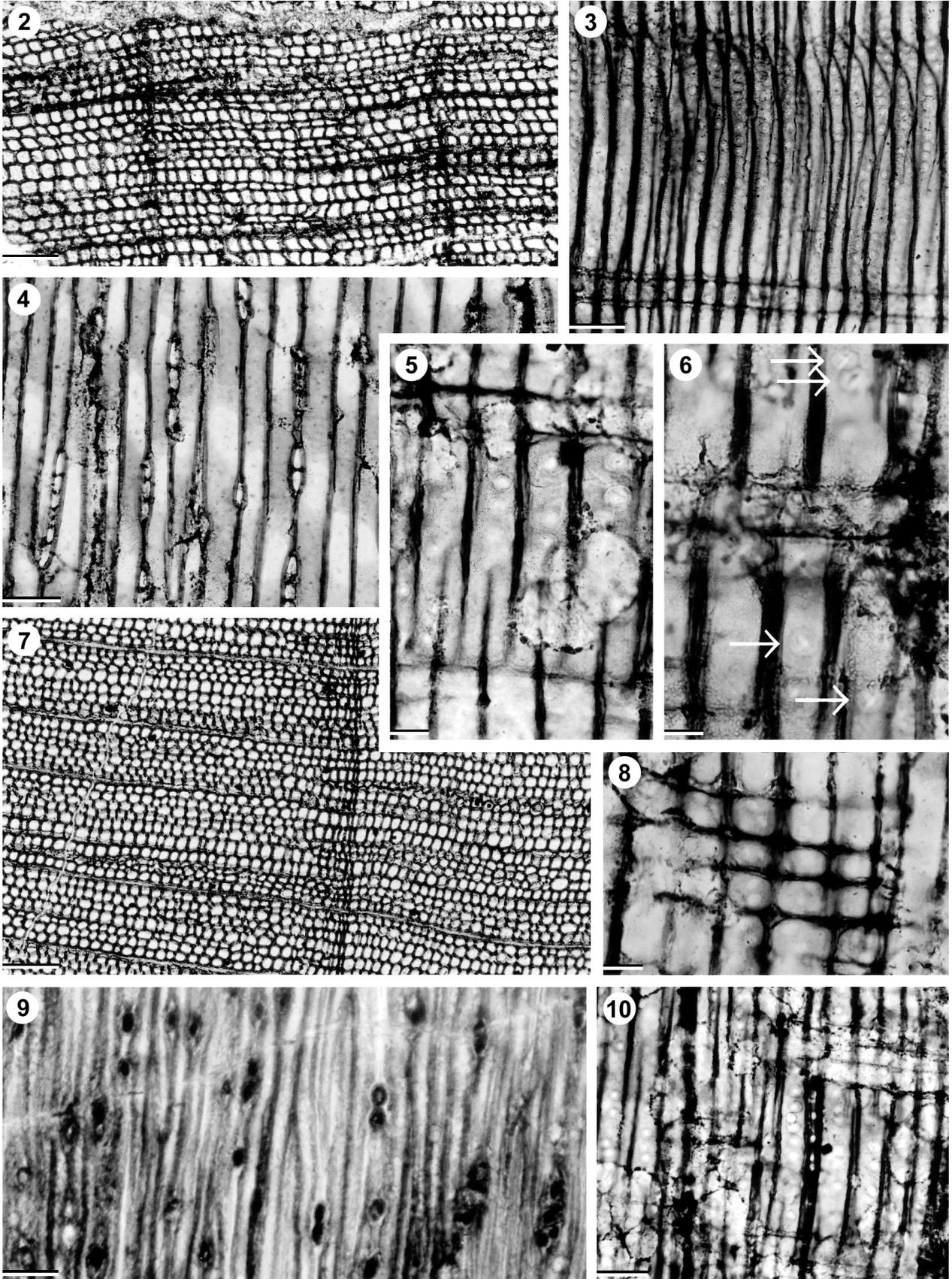
Order: Fagales

Family: Nothofagaceae

Organ genus: *Nothofagoxylo*n Gothan, 1908

Emended generic diagnosis: Fossil wood usually with distinct growth rings. Diffuse to semi-ring porous. Vessels solitary, in radial rows, sometimes small groups. Vessel outline circular, radially elongate, sometimes more angular. Intervessel pitting opposite, scalariform, sometimes alternate. Tyloses present. Ray vessel pitting circular, oval, horizontally elongate to scalariform, usually simple, sometimes bordered. Perforation plates predominantly simple, although scalariform perforation plates can be present in late wood vessels. Axial parenchyma rare. Rays heterocellular,

FIGS 2–10. Light micrographs of the fossil coniferous wood *Cupressinoxylon* sp. (Figs 2–4, 6) and *Podocarpoxylon fildesense* (Figs 5, 7–10). Fig. 2. Transverse section (TS) of P. 3023-82 showing the narrow late wood zone; bar = 100 μm . Fig. 3. Radial longitudinal section (RLS) of P. 3023-83 showing uniseriate pitting in the tracheid walls, note the cupressoid pit type; bar = 50 μm . Fig. 4. Tangential longitudinal section (TLS) of P. 3023-83 showing the short uniseriate rays; bar = 50 μm . Fig. 5. RLS of P. 3023-51 showing uniseriate rows of podocarpoid pits; bar = 25 μm . Fig. 6. RLS of P. 3023-83 showing cupressoid pits (arrowed) in the crossfields; bar = 25 μm . Fig. 7. TS of P. 3023-51 showing the narrow late wood zone; bar = 100 μm . Fig. 8. RLS of P. 3023-51 showing up to four podocarpoid pits per crossfield; bar = 25 μm . Fig. 9. TLS of P. 3023-51 showing the short rays one to three cells high; bar = 50 μm . Fig. 10. RLS of P. 3023-51 showing uniseriate rays of pits in the radial walls; bar = 50 μm .



composed of procumbent body cells and upright marginal cells; generally uniseriate, biseriate and triseriate. Fibres with simple pits, either septate or non-septate.

Type species: *Nothofagoxylon scalariforme* Gothan, 1908

Nothofagus scalariforme Gothan, 1908

Material: P. 3023·12, P. 3023·14, P. 3023·19, P. 3023·24, P. 3023·26

Description: This description is based on five pieces of branch-, stem- or trunk wood. P. 3023·19, P. 3023·12, P. 3023·24 and P. 3023·26 each have a minimum estimated diameter of 3, 6, 6 and 8 cm, respectively, based on growth ring curvature. P. 3023·14 originated from the outer portion of a branch or trunk as the outer cortical layers are present but no diameter can be estimated.

Growth rings: Distinct and weakly distinct demarcated by a change in fibre and vessel diameter (Fig. 11). *Vessels:* Semi-ring to ring porous, mainly solitary or in pairs but can be grouped into radial files of up to four pores (Figs 11 and 13). In cross section, vessels are thin-walled and generally circular to radially elliptic. The mean vessel tangential diameter is 64 µm (range: 20–130 µm), mean vessel radial diameter is 83 µm (range: 25–165 µm) and mean vessel element length is 598 µm (range: 160–850 µm). On average there are 88 vessels per mm² [range: (35) 68–116 mm⁻²]. *Perforation plates:* Simple in the large early wood vessels and scalariform in the narrower late wood vessels (Fig. 14). Abundant thin-walled tyloses within the vessel obscure vessel end walls making the determination of simple perforation plates difficult. *Intervessel pitting:* Mainly scalariform (Fig. 15), occasionally transitional, with pit diameters of up to 30 µm. *Ray-vessel pitting:* Mainly scalariform, occasionally oval-horizontally elongate (Fig. 12), up to 18 µm in diameter. *Fibres:* Thin-walled, non-septate and organized into regular radial files in cross section; no fibre pitting was observed. Mean fibre tangential diameter is 16 µm (range: 10–25 µm) and mean fibre radial diameter is 15.5 µm (range: 10–25 µm). *Axial parenchyma:* None observed. *Rays:* Uniseriate, occasionally part biseriate or biseriate, composed of square and occasionally square-upright or more procumbent cells; ray height ranges from 130–960 µm. There are six–16 rays per tangential millimetre.

Comparison: The combination of small vessels solitary or in groups and circular to elliptic in cross section, mainly simple, occasionally scalariform perforation plates, narrow rays and opposite to scalariform intervessel pits are characteristic of extant *Nothofagus* and fossil *Nothofagoxylon* wood (e.g. Patel, 1986; Rancusi et al., 1987). On this basis, these wood specimens are assigned to *Nothofagoxylon* which includes approximately 15 species in Antarctica and South America. These Antarctic woods exhibit anatomical characters consistent with *Nothofagoxylon scalariforme* and have thus been assigned to the type

species. However, the vessel distribution in transverse section is also very similar to the specimen illustrated by Pons and Vicente (1985) for *Nothofagoxylon aconguaense* from South America. The Antarctic material differs from *Nothofagoxylon aconguaense* in that it lacks the characteristic multiseriate rays and alternate intervessel pitting. From comparisons with modern *Nothofagus* material, these fossil specimens share greatest anatomical similarity to *Nothofagus betuloides* Blume and *N. gunnii* Oerst.

Nothofagoxylon neuquense Cozzo, 1950

Material: P. 3023·41

Description: This description is based on one piece of fossil wood originating from a branch or trunk which has undergone some compression.

Growth rings: Distinct and demarcated by a change in fibre and vessel diameter (Fig. 16). *Vessels:* Semi-ring porous, mainly elliptical in cross section, solitary and paired (Fig. 16). Vessel diameter and abundance could not be measured accurately due to the compressed nature of the specimen. Thin-walled tyloses occur within the vessels. *Perforation plates:* Simple, although difficult to determine because of the abundant tyloses, and scalariform. *Intervessel pitting:* Mainly bordered, closely packed, opposite, horizontally elongate and subopposite to alternate with polygonal outlines (Fig. 17). Pit diameters range from 12 to 26 µm. *Ray-vessel pitting:* Simple, circular to almost square with a diameter of approx. 5 µm. *Fibres:* Compressed in tangential section, ?non-septate; no fibre pitting was observed. *Axial parenchyma:* Indeterminable in cross-section due to preservation; none observed in longitudinal section. *Rays:* Uniseriate (Fig. 18) some part biseriate, heterocellular, composed mainly of square-procumbent body cells becoming less procumbent (i.e. more square) towards the margins. Rays are 150–530 µm tall.

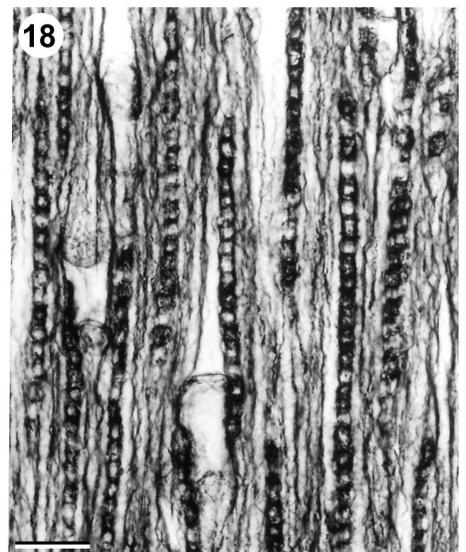
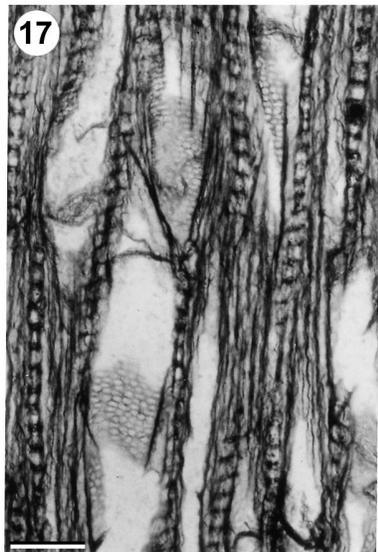
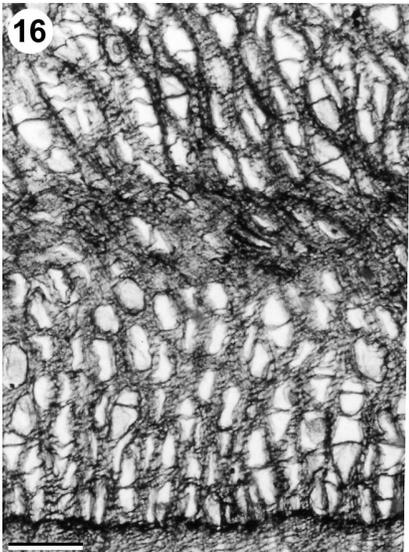
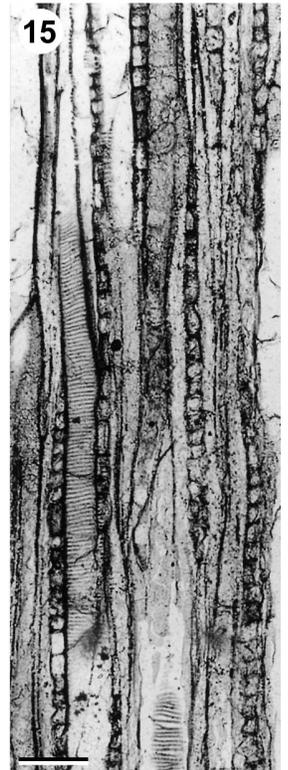
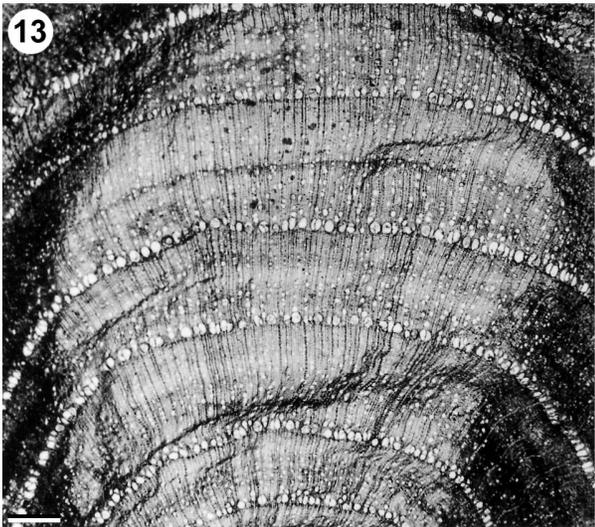
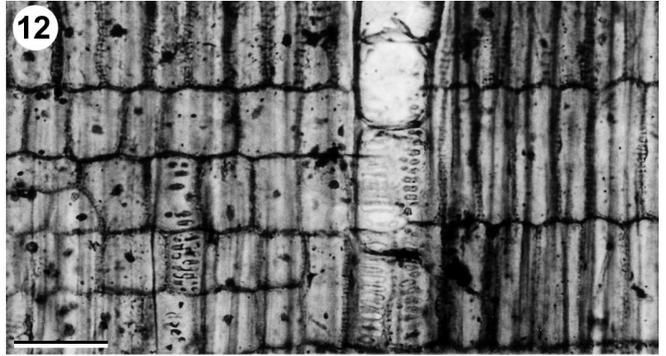
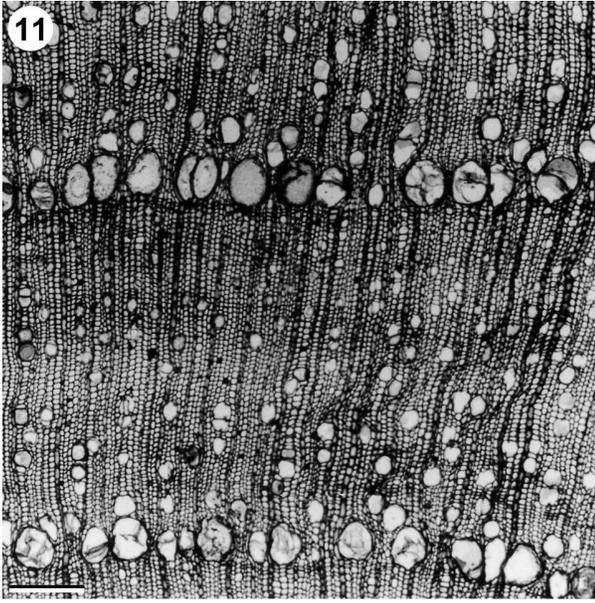
Comparison: This specimen from King George Island has undergone a degree of compression but all observable characters agree with those described by Cozzo (1950) for *Nothofagoxylon neuquenense* from the Tertiary of Neuquen, Santa Cruz in Argentina. This specimen differs from those assigned to *Nothofagoxylon scalariforme* in that the intervessel pits are predominantly alternate to opposite and ray-vessel pits are round-elliptic compared with the predominantly scalariform intervessel and ray-vessel pitting in *Nothofagoxylon scalariforme*. When compared with modern *Nothofagus* woods, the greatest similarity is shared with *Nothofagus procera*.

Nothofagoxylon corrugatus sp. nov.

Holotype: P. 3023·9

Etymology: After the Latin ‘corrugatus’ referring to the characteristic undulated appearance of the wood in cross section.

FIGS 11–18. Light micrographs of *Nothofagoxylon scalariforme* (Figs 11–15) and *Nothofagoxylon neuquenense* (Figs 16–18). Fig. 11. Transverse section (TS) of P. 3023·19; bar = 200 µm. Fig. 12. Radial longitudinal section (RLS) of P. 3023·19 showing ray structure and vessel ray pitting; bar = 50 µm. Fig. 13. TS of P. 3023·19 illustrating vessel arrangement; bar = 500 µm. Fig. 14. RLS of P. 3023·24 showing simple and scalariform perforation plates; bar = 50 µm. Fig. 15. Tangential longitudinal section (TLS) of P. 3023·14 showing uniseriate rays; bar = 75 µm. Fig. 16. TS of P. 3023·41 showing the vessel arrangement; bar = 200 µm. Fig. 17. Oblique TLS of P. 3023·41 showing the characteristic alternate-opposite intervessel pitting; bar = 75 µm. Fig. 18. TLS of P. 3023·41 showing the uniseriate rays; bar = 75 µm.



Other material: P. 3023-3, P. 3023-5, P. 3023-13, P. 3023-21, P. 3023-50

Species diagnosis: Growth rings distinct and deeply undulating. Semi-ring to weakly diffuse porous. Vessels solitary, paired, radial files of up to eight pores, predominantly radially elliptical, and more or less circular in cross section. Perforation plates simple in the early wood and scalariform in the late wood. Intervessel pitting scalariform. Ray vessel pitting horizontally elongate to scalariform. Rays heterocellular uniseriate (>70%), occasionally part biseriata (<30%); crystals absent. Fibres thin-walled, non-septate, in regular radial files. Axial parenchyma rare.

Description: This description is based on six pieces of branch-, stem- or trunk wood. P. 3023-5, P. 3023-3, P. 3023-9, P. 3023-13 and P. 3023-21 are probably derived from stem material with minimum estimated diameters of 5, 7, 8 and 10 cm, respectively, based on growth ring curvature. P. 3023-50 probably originated from a branch or trunk and no diameter can be estimated.

Growth rings: Distinct and naturally undulating (Fig. 19) demarcated by a change in fibre and vessel diameter (Fig. 20). *Vessels:* Semi-ring to weakly diffuse porous, mainly solitary or in pairs (Fig. 20) but can be grouped into radial files of up to eight pores. In cross section they appear radially elliptic and circular, with thin vessel walls. The mean vessel tangential diameter is 53.5 µm (range: 25–92.5 µm), mean vessel radial diameter is 73 µm (range: 25–150 µm) and mean vessel element length is 671 µm (range: 320–980 µm). There are, on average, 112 vessels per mm² (range: 84–142 mm⁻²). *Perforation plates:* Simple in the large early wood vessels and scalariform in the narrower late wood vessels (Figs 21 and 25). Thin-walled tyloses within the vessel obscure the vessel end walls thus making the determination of simple perforation plates difficult (Fig. 21). *Intervessel pitting:* Mainly scalariform (Fig. 23), occasionally transitional, with pit diameters of up to 30 µm. *Ray-vessel pitting:* Mainly scalariform, occasionally oval-horizontally elongate (Fig. 24); up to 25 µm in diameter. *Fibres:* Thin-walled, non-septate and organized into regular radial files in cross section; no fibre pitting was observed. Mean fibre tangential diameter is 13.5 µm (range: 7.5–17.5 µm) and mean fibre radial diameter is 15 µm (range: 7.5–25 µm). *Axial parenchyma:* None observed. *Rays:* Uniseriate, rarely part biseriata (Figs 22 and 23), entirely biseriata in P. 3023-13; composed of square-procumbent and occasionally square-upright and upright cells (Fig. 21); ray height ranges from 100–920 µm. There are nine–16 rays per tangential millimetre.

Comparison: The Antarctic woods can be distinguished from other species of *Nothofagoxylon* in having a combination of simple and scalariform perforation plates, scalariform intervessel and vessel ray pits, entirely uniseriate rays and a characteristic undulating appearance of the wood in

cross section. Closest anatomical similarity is with the Miocene/Pliocene Sirius Formation woods, *Nothofagus* sp., described by Carlquist (1987) from the Transantarctic Mountains, and *Nothofagoxylon scalariforme* (Gothan, 1908) from the Cretaceous of Seymour Island. *Nothofagus* sp. differs in that the King George Island material lacks the characteristic change from transitional early wood intervessel pits to scalariform intervessel pits in early and late wood, respectively, and the Sirius *Nothofagus* material is not described as having undulations in transverse section (Carlquist, 1987). Specimens assigned to *Nothofagoxylon corrugatus* differ from *Nothofagoxylon scalariforme* in the presence of distinct undulations in transverse section. This feature is readily identifiable in the fossil wood with the naked eye, and we believe that this distinct feature supports the erection of the new anatomical species.

These Antarctic woods are similar in transverse section to extant *Nothofagus solandri* Oerst. and *Nothofagus fusca* Oerst. from New Zealand, both of which have the characteristic undulating appearance. Moreover, simple perforation plates in the early wood and scalariform perforation plates in the late wood characterize New Zealand *Nothofagus* (Patel, 1986; Carlquist, 1987) and the fossil material. However, New Zealand species tend to have only opposite, occasionally alternate intervessel pits (Patel, 1986; Carlquist, 1987) thus distinguishing them from the fossil species described here. The longitudinal anatomy of the fossils is more similar to South American *N. antarctica* (Forst.) Oerst., *N. pumilio* Reiche, *N. nitida* Reiche and *N. betuloides*, and the Tasmanian *N. gunnii*. *Nothofagus antarctica* can exhibit some transectional undulations (Ilic, 1991) but does not have scalariform perforation plates in the narrow vessels, and ray vessel pitting can be irregular (Rancusi et al., 1987). *Nothofagus pumilio* and *N. nitida* differ from the fossil material in that the extant material has simple perforation plates and diffuse porous wood (Rancusi et al., 1987; Ilic, 1991). *Nothofagus betuloides* and *N. gunnii* are most similar anatomically, exhibiting the characteristic change from transitional intervessel pitting to scalariform intervessel pitting seen in early and late wood, respectively (Carlquist, 1987), but both lack the obvious undulations in transverse section.

Order: Rosales

Family: Cunoniaceae

Organ genus: *Weinmannioxylon* Petriella, 1972

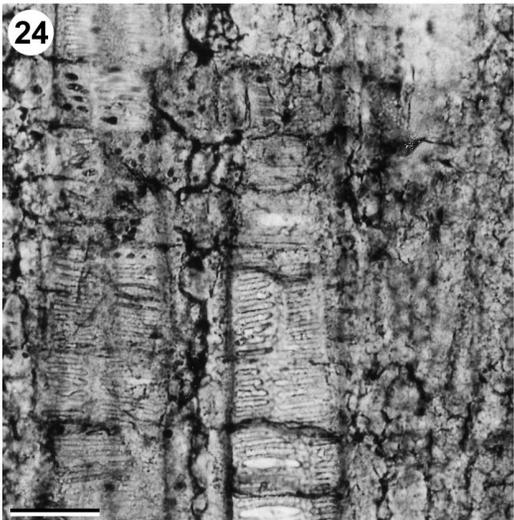
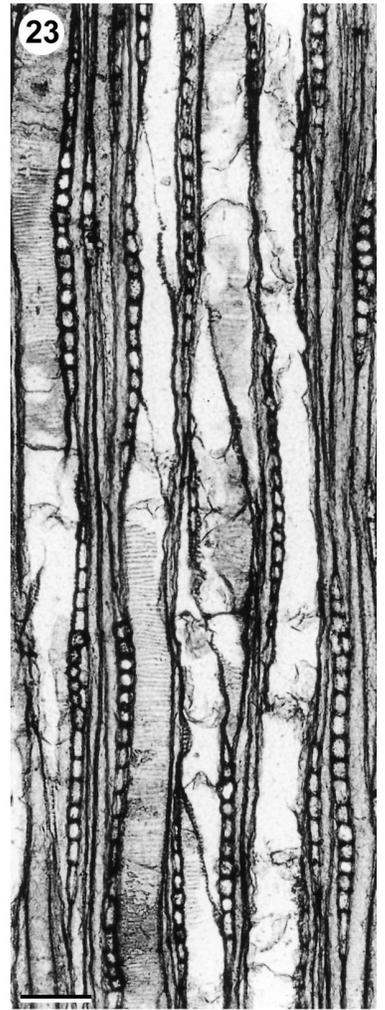
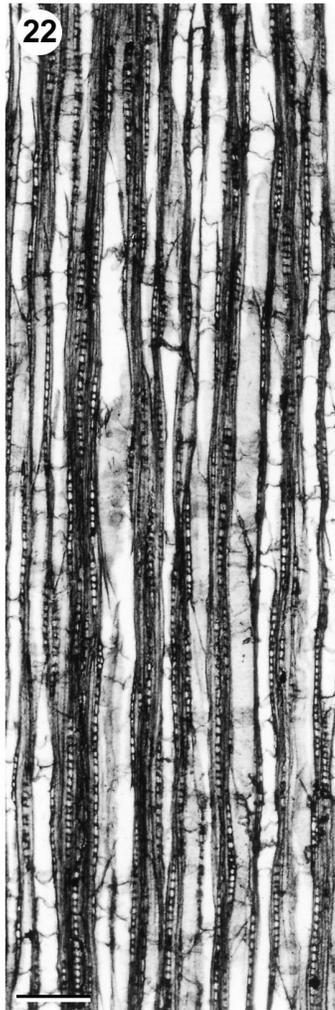
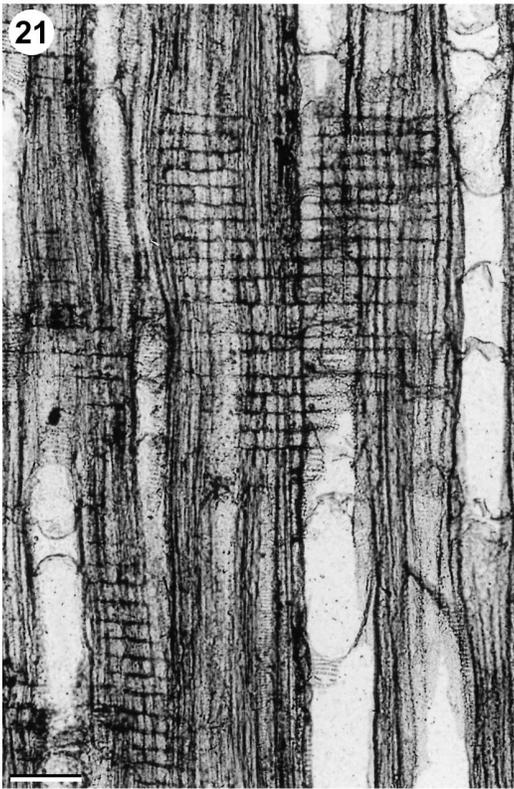
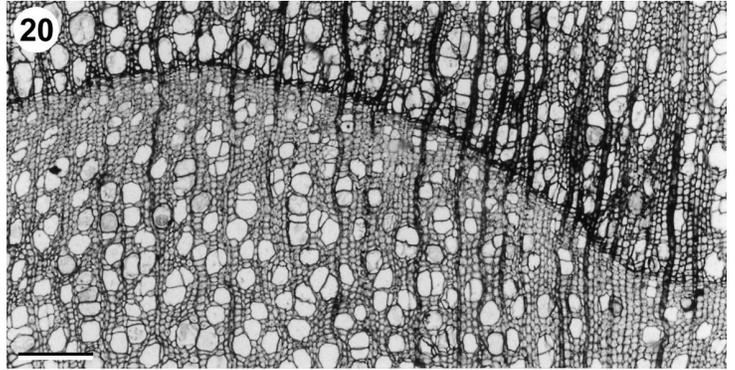
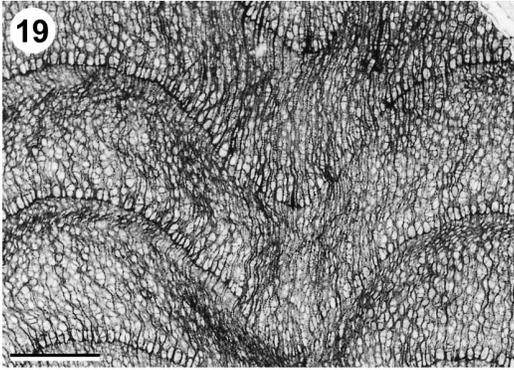
Type species: *Weinmannioxylon multiperforatum* Petriella, 1972

Weinmannioxylon eucryphioides sp. nov.

Holotype: P. 3023-11

Etymology: After *Eucryphia* with which the fossils show good similarity

FIGS 19–25. Light micrographs of *Nothofagoxylon corrugatus* sp. nov. Fig. 19. Transverse section (TS) of P. 3023-3 showing the characteristic undulations; bar = 1 mm. Fig. 20. TS of P. 3023-9 showing the vessel arrangement; bar = 200 µm. Fig. 21. Radial longitudinal section (RLS) of P. 3023-5 showing ray structure and simple perforation plate in a large diameter vessel; bar = 75 µm. Fig. 22. Tangential longitudinal section (TLS) of P. 3023-9 showing uniseriate rays in the early wood; bar = 200 µm. Fig. 23. TLS of P. 3023-5 showing scalariform intervessel pitting and tyloses; bar = 75 µm. Fig. 24. RLS of P. 3023-5 showing scalariform vessel ray pits; bar = 50 µm. Fig. 25. TLS of P. 3023-9 showing scalariform perforation plate; bar = 75 µm.



Other material: P. 3023-6, P. 3023-10, P. 3023-31, P. 3023-32, P. 3023-54

Species diagnosis: Vessels numerous, mainly solitary, paired, rarely grouped; mean tangential diameter approx. 50 μm ; mean element length 700 μm . Perforations plates scalariform with numerous bars, rarely simple. Intervessel and vessel ray pitting opposite to scalariform. Rays heterocellular; uniseriate, locally biseriate; up to 1000 μm in height.

Description: This description is based on five pieces of branch-, stem- or trunk wood. P. 3023-54, P. 3023-32, P. 3023-31 and P. 3023-11 each have a pith present and have a minimum estimated diameter of 5, 6, 6.5 and 8 cm respectively. P. 3023-10 and P. 3023-6 probably originated from larger branch or trunk organs of unknown diameter.

Growth rings: Distinct and demarcated by a decrease in the radial diameter of one–four rows of fibres and overall vessel diameter (Fig. 26). *Vessels:* Semi-ring to weakly diffuse porous, mainly solitary or in pairs but can be grouped into short radial files of up to five pores; clusters of up to five vessels are also present. In cross section they appear more or less circular with thin vessel walls. The mean vessel tangential diameter is 49.5 μm [range: 25–105 (200) μm], mean vessel radial diameter is 63.5 μm [range: 17.5–95 (187.5) μm] and mean vessel element length is 714 μm (range: 620–1160 μm). There are, on average, 103 vessels per mm^2 (range: 62–179 mm^{-2}) with fewer vessels occurring in the larger diameter material. *Perforation plates:* Scalariform (Fig. 37) with up to 55 bars, very rarely simple (Fig. 32). Thin-walled tyloses are present in specimens P. 3023-11 and P. 3023-6. *Intervessel pitting:* Mainly scalariform (Fig. 38), occasionally transitional, circular and opposite with pit diameters ranging from 6–17 μm . *Ray-vessel pitting:* Occasionally circular, mainly elliptical (Fig. 30), horizontally elongate to scalariform (Fig. 31), with pit diameters of up to 15 μm , mainly horizontal but occasionally tend towards a diagonal orientation. *Fibres:* Thin-walled, non-septate and organized into regular radial files in cross section. No fibre pitting was observed. Mean fibre tangential diameter is 17 μm (range: 10–30 μm) and mean fibre radial diameter is 15 μm (range: 7.5–27.5 μm). *Axial parenchyma:* None observed. *Rays:* Relatively short, uniseriate (Figs 36 and 37), rarely partly biseriate (Fig. 36), composed of mainly square, square-procumbent and procumbent body cells and one or two rows of more upright marginal cells (Fig. 28). Some ray cells have thickened walls. Range in height from 120–910 (1400) μm . There are seven–15 rays per tangential millimetre.

Comparison: The combination of predominantly uniseriate rays, scalariform, rarely simple, perforation plates,

scalariform intervessel pitting and transitional to scalariform vessel ray pitting is characteristic of *Eucryphia* Cav. of the Cunoniaceae (or Eucryphiaceae according to some authorities e.g. Taylor and Hill, 1996; Figs 27, 29, 33–35). The fossil material differs from *Eucryphia* in general in that there are no obvious helical thickenings, and fibres with slit-like apertures to the pits were not observed (both possibly due to preservation); in addition, *Eucryphia* generally has a greater predominance of biseriate rays. Greatest anatomical similarity within *Eucryphia* is shared with *E. lucida* Druce from Tasmania, Australia (see Table 1 for a summary and Figs 27, 29, 33–35). The preponderance of highly oblique scalariform perforation plates in the fossil, and uniseriate as opposed to uniseriate-, biseriate- and triseriate rays, in conjunction with simple and scalariform (as opposed to a dominance of scalariform) perforation plates, distinguishes this fossil specimen from the South American species of *Eucryphia* [i.e. *E. cordifolia* Cav. and *E. glutinosa* (Poepp. & Endl.) Baillon]. Interestingly, helical thickenings (not observed in the fossil) are less conspicuous or entirely absent in *E. cordifolia* and *E. glutinosa* (Dickison, 1978).

Torres (1985) noted the presence of eucryphiaceous wood in the Antarctic flora. She illustrated a cross section (with solitary and grouped vessels at a growth ring boundary) and a tangential section (showing obvious biseriate to triseriate rays), presumably from the same specimen as the cross section, but no description or further illustrations were provided. The wood illustrated by Torres is anatomically distinct from *Weinmannioxylon eucryphioides*, but without a detailed description and more illustrations no determination of validity or further comparisons with modern *Eucryphia* or *Weinmannioxylon eucryphioides* can be made. The fossil specimens described here differ from other species assigned to the organ genus *Weinmannioxylon* (i.e. Petriella, 1972; Poole et al., 2000; Poole and Cantrill, 2001) in that the other species have relatively short, entirely uniseriate rays, predominantly scalariform vessel ray pitting and entirely scalariform perforation plates. In the light of the close anatomical similarity to *Eucryphia* and the apparent differences when compared with other cunoniaceous fossils, we feel that this justifies the erection of the new species, *Weinmannioxylon eucryphioides*.

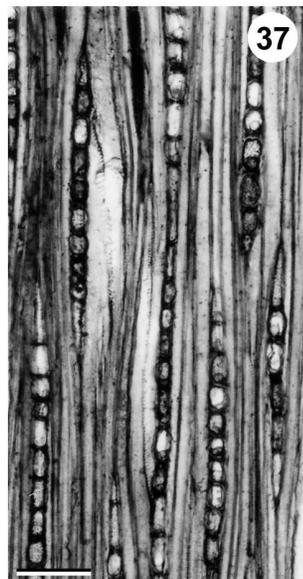
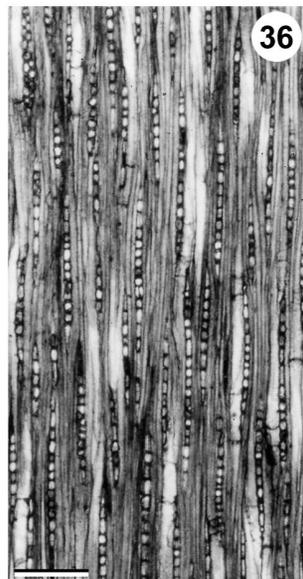
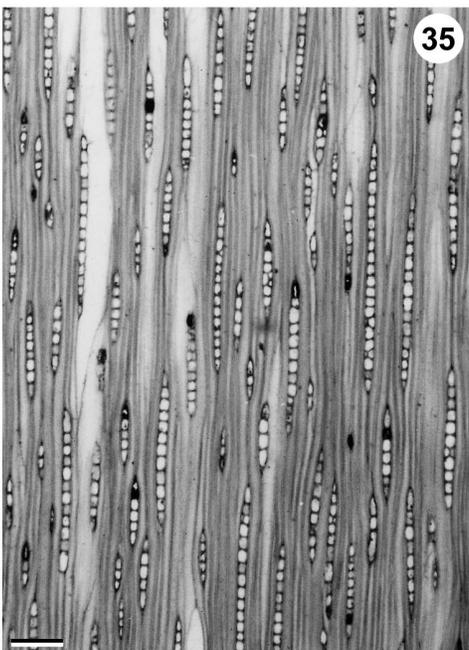
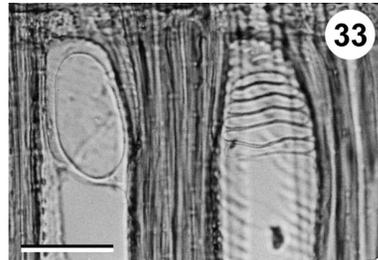
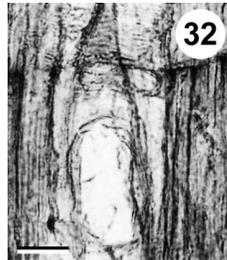
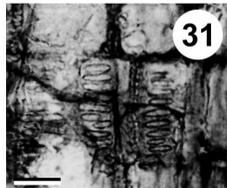
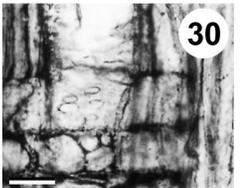
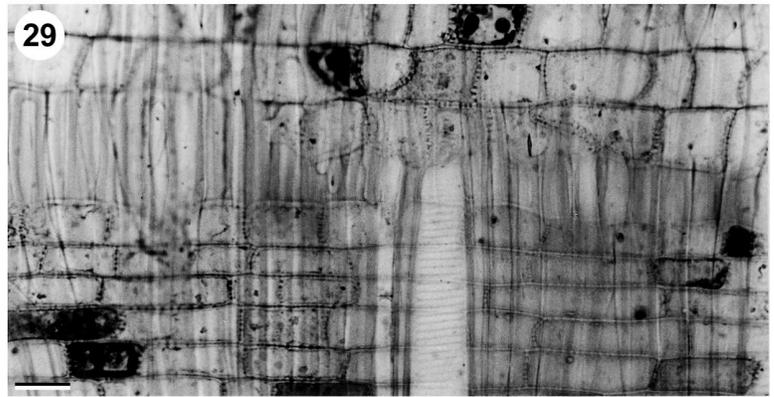
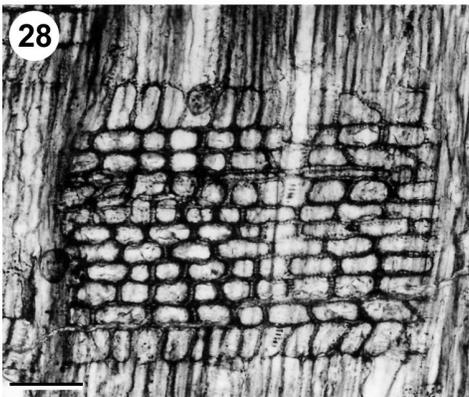
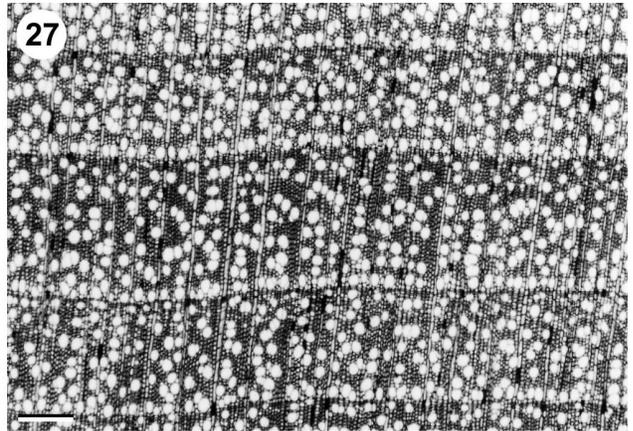
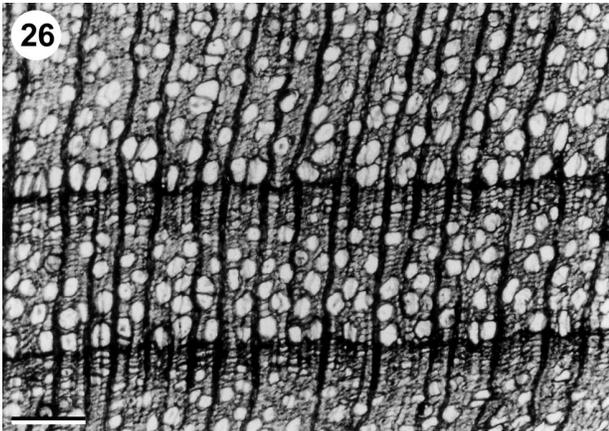
Order: Myrtales

Family: Myrtaceae

Organ genus: *Myceugenelloxylon* Nishida, 1984

Emended generic diagnosis: Wood diffuse porous. Pores generally solitary, multiple pores often two–three, evenly scattered throughout the wood. Perforation plates scalariform with few to many bars. Intervessel pits opposite to

FIG. 26–38. Light micrographs of *Weinmannioxylon eucryphioides* sp. nov. (Figs 26, 28, 30–32, 36–38) and extant *Eucryphia lucida* (Figs 27, 29, 33–35) for comparison with the fossil. Fig. 26. Tangential section (TS) of P. 3023-11 showing vessel distribution; bar = 200 μm . Fig. 27. TS of *Eucryphia lucida* (Kew: *E. billardieri* IFI.11156 Australia); bar = 250 μm . Fig. 28. Radial longitudinal section (RLS) of P. 3023-6 showing ray cell composition; bar = 75 μm . Fig. 29. RLS of *Eucryphia lucida* (Kew: *E. billardieri* IFI.11156 Australia) showing ray cell composition and scalariform vessel ray pits; bar = 50 μm . Fig. 30. RLS of P. 3023-6 showing elliptical vessel ray pits; bar = 25 μm . Fig. 31. RLS of P. 3023-6 showing scalariform vessel ray pits; bar = 25 μm . Fig. 32. RLS of P. 3023-6 showing simple perforation plate; bar = 25 μm . Fig. 33. RLS of *Eucryphia lucida* (Utrecht: WC006) showing simple and scalariform perforation plates; bar = 50 μm . Fig. 34. RLS of *Eucryphia lucida* (Utrecht: WC006) showing elliptical and scalariform vessel ray pits; bar = 25 μm . Fig. 35. Tangential longitudinal section (TLS) showing of *Eucryphia lucida* (Kew: *E. billardieri* IFI.11156 Australia) showing the predominance of uniseriate rays; bar = 250 μm . Fig. 36. TLS of P. 3023-54 showing uniseriate rays; bar = 200 μm . Fig. 37. TLS of P. 3023-54 showing scalariform perforation plate and uniseriate rays; bar = 75 μm . Fig. 38. TLS of P. 3023-10 showing scalariform intervessel pitting; bar = 75 μm .



scalariform, occasionally alternate. Vessel ray pits circular to horizontally elongated. Rays uni- to triseriate, rarely quadriseriate; multiseriate rays heterocellular with upright cells forming marginal rows which axially unite some multiseriate rays.

Type species: *Myceugenelloxylon pseudoapiculatum* Nishida, 1984

Other taxa: *Myceugenelloxylon maytenoides* (Nishida Nishida et Nasa) Poole Hunt Cantrill comb. nov

Myceugenelloxylon antarcticus sp. nov.

Holotype: P. 3023-4

Etymology: After Antarctica where the material was found.

Species diagnosis: Vessels abundant, mainly solitary, paired, rarely grouped; mean element length approx. 715 μm . Perforations scalariform with numerous bars. Intervessel and vessel ray pitting opposite to scalariform. Rays biseriate with uniseriate wings almost as wide as the biseriate body; heterocellular, composed of procumbent body cells and up to six rows of upright marginal cells; up to 500 μm in height; sometimes two or three rays fused axially.

Description: This description is based on one piece of fossil wood, P. 3023-4, from the inner portion of a branch or trunk with a minimum estimated diameter of 8 cm.

Growth rings: Distinct and demarcated by a change in the radial diameter of one to three rows of fibres and a slight change in vessel diameter (Fig. 39). *Vessels*: Weakly diffuse porous, mainly solitary or paired, and circular to radially elliptic in cross section (Fig. 39). Vessels are thin walled. The mean vessel tangential diameter is 54 μm (range: 37.5–67.5 μm) and mean vessel radial diameter is 84 μm (range: 50–122.5 μm); mean vessel element length is 1540 μm (range: 1300–1875 μm). Tyloses are absent. There are, on average, 88 vessels per mm^2 (range: 77–102 mm^{-2}). *Perforation plates*: Scalariform (Fig. 41) with numerous bars per perforation plate (exact number indeterminable due to preservation and fineness of bars). *Intervessel pitting*: Mainly horizontally elongate to scalariform, sometimes more circular and oppositely arranged. *Ray-vessel pitting*: Small circular to horizontally elliptic (Fig. 42), opposite very rarely more transitional. *Fibres*: Non-septate; no fibre pitting was observed. Mean fibre tangential diameter is 20 μm (range: 12.5–27.5 μm), mean fibre radial diameter is 20 μm (range: 10–30 μm) and thin walls have a radial thickness of 2.5–4 μm . *Axial parenchyma*: Rare and ?diffuse. *Rays*: Heterocellular and biseriate with up to eight upright marginal rows of cells which can axially unite neighbouring rays (Fig. 45), very rarely uniseriate. The biseriate portion tends to be as wide, in tangential longitudinal section, as the uniseriate portions (Fig. 45). Rays are composed of more or less procumbent cells

forming the body and usually three, but up to six rows of tall (i.e. 30–130 μm) upright marginal cells (Fig. 41). Some of the ray cells have thickened walls (Fig. 41). Rays are short, ranging from 300 to 500 (–700) μm when ununited. There are four to nine rays per tangential millimetre.

Differential description and affinity: The two organ genera for myrtaceous fossil wood with closest anatomical similarity to the specimen described above are *Myceugenelloxylon* (Nishida, 1984) and *Myceugenellites* (Nishida et al., 1988) from South America. According to Nishida et al. (1988), the genus *Myceugenelloxylon* is distinguished from *Myceugenellites* by vessel density and number of bars per perforation plate only. In modern material, quantitative differences are variable among specimens of the same taxon; therefore, these differences are not considered great enough to warrant a separate organ genus and the organ genus *Myceugenellites* is thus considered a junior synonym of *Myceugenelloxylon*.

Myceugenelloxylon antarcticus differs from the two species of *Myceugenelloxylon* from South America, i.e. *M. pseudoapiculatum* and *M. maytenoides*, in that the Antarctic specimens have fewer vessels per mm^2 , rays that are predominantly biseriate (as opposed to predominantly biseriate and triseriate), and a greater abundance of scalariform ray vessel pits. *Myceugenelloxylon pseudoapiculatum* (Nishida, 1984) lacks axially fused rays and *M. maytenoides* (Nishida et al., 1988) has frequent reticulate areas in the scalariform perforation plates. Other myrtaceous fossil woods (i.e. Gottwald, 1966; Kramer, 1974; Ragonese, 1980) can be distinguished from the Antarctic specimen in that they have entirely simple perforation plates. The anatomical similarity shared with extant *Luma apiculata* (DC) Burret and the differences seen when compared with other myrtaceous fossils from South America justifies the erection of the new species *Myceugenelloxylon antarcticus* for this specimen.

Myceugenelloxylon antarcticus shows greatest similarity to extant *Luma* and, in particular, *Luma apiculata* [previously *Myceugenella apiculata* (DC) Kaus; Myrtaceae; Figs 40, 43, 44 and 46] from temperate South America. *Luma apiculata* has predominantly biseriate rays, scalariform intervessel- and vessel ray pits, as shared with the fossil, but differs in having a greater number of bars per perforation plate and more uniseriate rays than the fossil. In all other characters, the fossil and *L. apiculata* compare favourably (see Table 1 and Figs 40, 43, 44 and 46).

DISCUSSION

The palaeoforests that grew on King George Island during the Eocene are similar in composition to the extant cool temperate Valdivian rainforests of Chile which lie between

FIGS 39–46. Light micrographs of *Myceugenelloxylon antarcticus* sp. nov. (P. 3023-4; Figs 39, 41, 42, 45) and *Luma apiculata* (Figs 40, 43, 44, 46) for comparison with the fossil. Fig. 39. Transverse section (TS) showing the vessel arrangement; bar = 1 mm. Fig. 40. TS showing vessel arrangement; bar = 200 μm . Fig. 41. Radial longitudinal section (RLS) showing the thickened ray cells and ray composition and scalariform perforation plate; bar = 50 μm . Fig. 42. RLS showing ray cell pitting; bar = 15 μm . Fig. 43. RLS showing ray cell pitting; bar = 25 μm . Fig. 44. RLS showing ray cell composition and scalariform perforation plate; bar = 75 μm . Fig. 45. Tangential longitudinal section (TLS) showing axially united biseriate rays and occasional uniseriate ray (emerging from bottom middle); bar = 75 μm . Fig. 46. TLS showing axially united biseriate rays and relatively abundant uniseriate rays; bar = 75 μm .

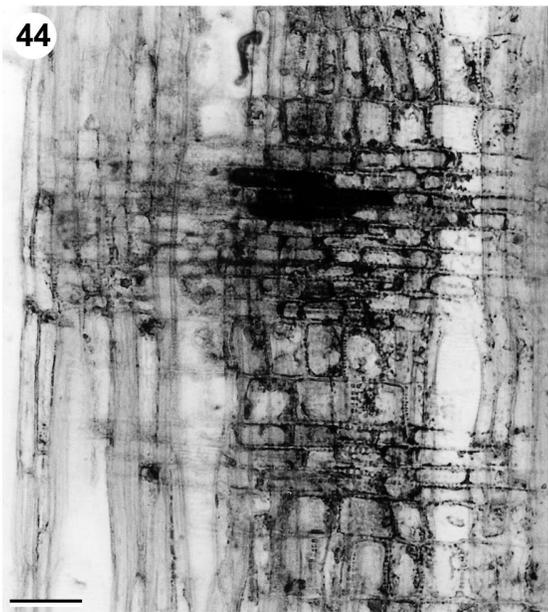
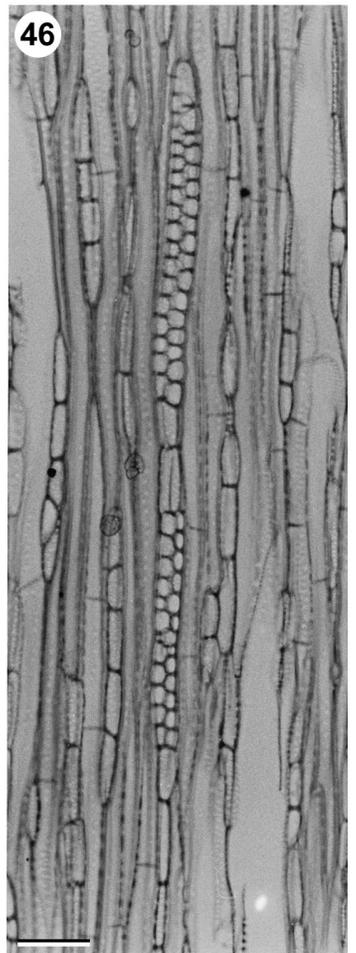
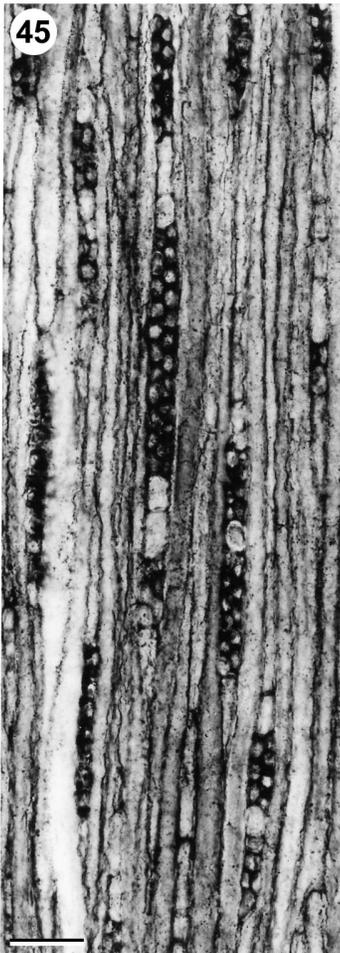
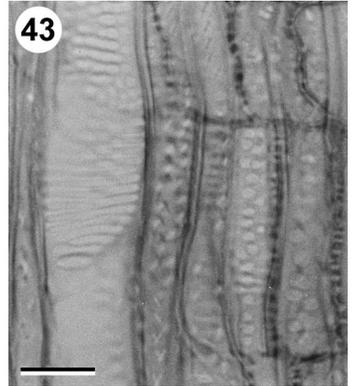
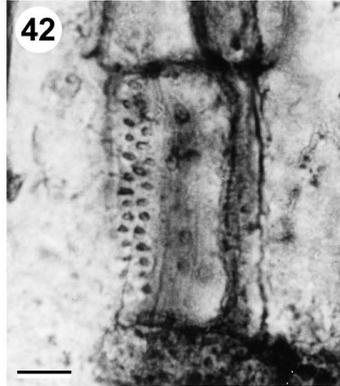
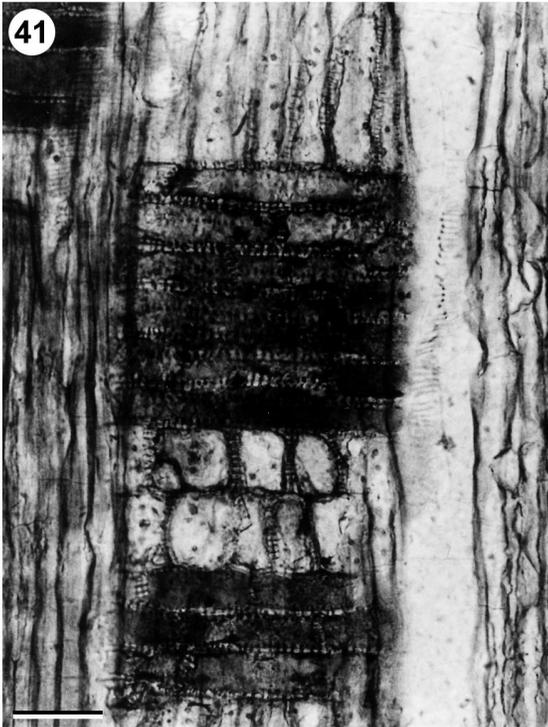
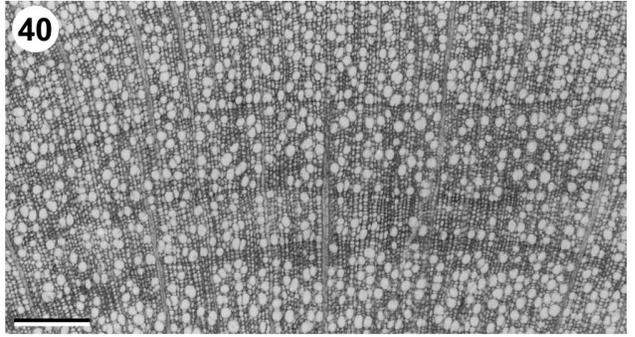
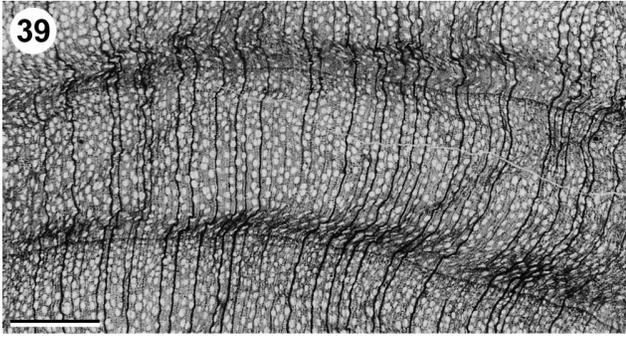


TABLE 2. Table illustrating the high level (84%) of similarity between the Late Cretaceous to Eocene/Oligocene King George Island palaeofloral composition and that of the cool temperate Valdivian rainforests of South America

Families found on King George Island	Present in Valdivian rainforest?	Reference to palaeobotanical literature
Sphenophytes	Present	Barton, 1964; Dutra, 1989a; R.J. Hunt (work in progress)
<i>Equisetum</i>		Cao, 1992
Pteridophytes	Present	Troncoso, 1986; Li and Shen, 1989
Adiantaceae	Present	Troncoso, 1986; Birkenmajer and Zastawniak, 1989
Aspleniaceae	Present	Lyra, 1986; Torres and Meon, 1990; Cao, 1992; Li, 1992; Zhou and Li, 1994b; Duan and Cao, 1998
Blechnaceae	Present	Stuehlik, 1981
Cyatheaceae	Present	Troncoso, 1986; Li and Shen, 1989; Cao, 1992; Li, 1992; Zhou and Li, 1994b
Dennstaedtiaceae	Present	Stuehlik, 1981; Li and Shen, 1989; Cao, 1992, 1994; Li, 1994; Zhou and Li, 1994b; Duan and Cao, 1998
Dicksoniaceae	Present	Stuehlik, 1981
Gleicheniaceae	Present	Torres and Meon, 1993; R.J. Hunt (work in progress)
Hymenophyllaceae	Present	Li and Shen, 1989; Li, 1992; Cao, 1992, 1994; Zastawniak, 1994; Zhou and Li, 1994b
Lophosoriaceae	Present	Stuehlik, 1981; Cao, 1992, 1994; Duan and Cao, 1998; Hunt and Page (work in progress)
Osmundaceae	Present	Stuehlik, 1981
Polypodiaceae	Present	Stuehlik, 1981
Salviniaceae	Present	Stuehlik, 1981
Schizaceae	Present	Cao, 1992
Lycophytes	Present	Li, 1994; Zhou and Li, 1994a
Selaginellaceae	Absent	
Cycadophytes	Present	Barton, 1964; Lucas and Lacey, 1981; Davies, 1982; Torres, 1985; Troncoso, 1986; Palma-Heldt, 1987; Torres and Lemoigne, 1988; Torres and Meon, 1990; Hee and Soon, 1991; Cao, 1992, 1994; Zastawniak, 1994; Zhou and Li, 1994a
Zamiaceae	Absent	
Coniferophytes	Present	Orlando, 1963, 1964; Torres <i>et al.</i> , 1984; Torres, 1985; Czajkowski and Rosler, 1986; Li and Shen, 1989; Li, 1992; Zhou and Li, 1994a
Araucariaceae	Present	Zastawniak, 1981; Zastawniak <i>et al.</i> , 1985; Torres, 1985; Lyra, 1986; Troncoso, 1986; Palma-Heldt, 1987; Torres and Lemoigne, 1988; Torres and Meon, 1990; Li and Shen, 1989; Li, 1992; Zhang and Wang, 1994; Cao, 1992, 1994; Zastawniak, 1994; Zhou and Li, 1994a; Duan and Cao, 1998
Cupressaceae	Present	
Podocarpaceae (including <i>Phyllocladus</i>)	Present	

Angiosperms	
?Araliaceae	Li, 1992, 1994
?Caesalpiniaceae	Troncoso, 1986; <i>Birkenmajer and Zastawniak</i> , 1986
?Hydrangeaceae	Czajkowski and Rosler, 1986
?Malvaceae	Dutra and Batten, 2000
?Poaceae	Stuehlik, 1981; Birkenmajer and Zastawniak, 1986; Troncoso, 1986; Palma-Heldt, 1987
Anacardiaceae	<i>Zastawniak, 1981</i> ; Czajkowski and Rosler, 1986; Li and Shen, 1989; Li, 1992, 1994
<i>Chusquea</i>	Stuehlik, 1981
Cochlospermaceae	Zastawniak <i>et al.</i> , 1985; <i>Birkenmajer and Zastawniak</i> , 1986
Cunoniaceae (including Eucryphiaceae)	Torres, 1985; Czajkowski and Rosler, 1986; Li and Shen, 1989; Zhang and Wang, 1994 but see Poole <i>et al.</i> , 2000
Dilleniaceae	Orlando, 1964; <i>Birkenmajer and Zastawniak</i> , 1986; Zastawniak, 1994
Gunneraceae	Torres and Meon, 1990
Icacinaeae	Troncoso, 1986
Lauraceae	Orlando, 1964; Del Valle <i>et al.</i> , 1984; <i>Birkenmajer and Zastawniak</i> , 1986; Troncoso, 1986
Loranthaceae	Cao, 1992
Melastomataceae	Li and Shen, 1989; Li, 1992, 1994
Monimiaceae	Orlando, 1964; Del Valle <i>et al.</i> , 1984; Troncoso, 1986; Birkenmajer and Zastawniak, 1989
Myricaceae	<i>Czajkowski and Rosler</i> , 1986; Troncoso, 1986; <i>Dutra, 1989a</i>
Myrtaceae	Orlando, 1964; Czajkowski and Rosler, 1986; Palma-Heldt, 1987; Cao, 1992; Li, 1994; Zastawniak, 1994
Nothofagaceae	Barton, 1964; Zastawniak, 1981; Del Valle <i>et al.</i> , 1984; Torres, 1984, 1985; Zastawniak <i>et al.</i> , 1985; Czajkowski and Rosler, 1986; Lyra, 1986; Troncoso, 1986; <i>Tokarski et al.</i> , 1987; Torres and Lemoigne, 1988; Dutra 1989 <i>a, b</i> ;
	Li and Shen, 1989; Cao, 1992, 1994; Li, 1992, 1994; Zastawniak, 1994; Zhang and Wang, 1994; Duan and Cao, 1998; Dutra and Batten, 2000
Proteaceae	Orlando, 1964; Czajkowski and Rosler, 1986; <i>Troncoso, 1986</i> ; Dutra, 1989 <i>b</i> ; Li and Shen, 1989; Torres and Meon, 1990; Cao, 1992; Li, 1992, 1994
Rhamnaceae	Stuehlik, 1981; Zastawniak <i>et al.</i> , 1985; Dutra, 1989 <i>a, b</i>
Sapindaceae	<i>Zastawniak, 1981</i> ; Troncoso, 1986; Dutra, 1989 <i>a</i>
Sterculiaceae	Orlando, 1964; Del Valle <i>et al.</i> , 1984; Czajkowski and Rosler, 1986; Birkenmajer and Zastawniak, 1986; Li and Shen, 1989; Shen, 1994
?Verbenaceae	Birkenmajer and Zastawniak, 1986

“?” in front of the family name indicates tentative assignment to that family; author and/or date in italics indicates tentative assignment to that family by the author indicated.

approx. 37°45' and 43°20'S (see Table 2). Some similarities can also be found with the broad-leaved temperate forests of Tasmania and New Zealand (see Hill and Scriven, 1995 and references therein). However, the Valdivian rainforests occur in a geological setting most similar to that seen on King George Island in the Tertiary; that is, oceanic crust being subducted beneath a convergent continental margin. This activity resulted in the formation of mountains (Antarctic Peninsula and the Andes, respectively) and crustal melting at depth that in turn led to volcanism and the development of large stratovolcanoes. Furthermore, both areas are on the eastern side of the Pacific where trade winds provide strong orographic rainfall. The structure of the Valdivian rainforest is governed by high rainfall (mean annual precipitation >3000 mm), altitude, and disturbance largely as a result of volcanic activity (Veblen and Ashton, 1978). Since similar floristic composition, postulated high rainfall and volcanic disturbance characterize the King George Island setting, the structure and ecology of the Valdivian forests provides a working model for the interpretation of fossil assemblages from Fildes Peninsula.

The Valdivian Model

Along the Andean margin of South America where the Pacific plate is being subducted beneath the South American continent, stratovolcanic activity is a major cause of disturbance along with associated events such as landslides, earthquakes, damming and flooding of lake systems and lahars. Glacial erosion and deposition also contribute to the general disturbance, especially in the high altitudes of the Andes. Volcanic activity is especially important in the maintenance of plant community structure and the composition of the cool temperate Valdivian rainforests. Vegetation close to the vent becomes buried or flattened (Spicer, 1989). With decreasing altitude, vegetation is partially buried or succumbs to forest fire, resulting in complete to partial dieback of stand vegetation. Ash and lava often defoliate and/or bury plants and cause widespread tree-fall. Fires and poisoning by noxious gases also result in plant death. In more distal locations the effects of volcanism may be less severe with limited fire and defoliation rather than death of the forest trees. Secondary effects of the eruptions can be equally disruptive: inundation of lakes leads to temporary damming of drainage systems, drowning valley bottom floras.

Climax (pre-eruption) vegetation. The Valdivian rainforests occur most extensively along the Coastal Range to the western flanks of the Andes. The higher, more xeric slopes above the broadleaved tree zone in the northern (i.e. approx. 38°S) part of the Valdivian rainforest support stands of Araucariaceae which give way to a more podocarpaceous cool-adapted, Nothofagaceae-dominated vegetation at slightly lower altitudes. Here *Nothofagus* forms the emergent tree stratum and the podocarps, which are more diverse in height, contribute to both the dominant and subdominant strata (Veblen et al., 1996). On poorly drained sites, e.g. along ridge flanks at all elevations, and xeric sites, some members of the Cupressaceae (e.g. *Fitzroya*

Hook f. ex. Lindl., *Pilgerodendron* Florin and *Austrocedrus* Florin et Boutelje) contribute to the *Nothofagus* emergent tree stratum. On the lower slopes, *Nothofagus* is joined by emergent *Eucryphia* with other Cunoniaceae, Monimiaceae, Podocarpaceae (e.g. *Podocarpus nubigenus* Lindl., *Saxegothaea* Lindl.) and some Cupressaceae (e.g. *Pilgerodendron*) forming a mixture of dominant and subdominant trees (Veblen et al., 1983, 1995). *Luma* and *Eucryphia* occur as canopy vegetation in low to mid-altitude positions (e.g. <700 m in the case of *Luma*). The understorey of these forests contains shade-tolerant tree species such as members of the Araliaceae, Lauraceae, Monimiaceae, Proteaceae and Myrtaceae, along with tree ferns, other ferns and members of the Hydrangeaceae which contribute to the scrambling, climbing element of the vegetation. The bamboo, *Chusquea* Kunth., tends to dominate the modern understorey vegetation in South America (Veblen et al., 1983) but is absent from similar forests in New Zealand and Tasmania. Cyatheaceae, Dicksoniaceae and possibly some Osmundaceae are also found in these lower altitudinal regions where the humidity is relatively high, such as alongside streams. *Equisetum* also grows in these damp habitats. In undisturbed stands, young or small trees of shade-intolerant species, such as *Nothofagus*, *Eucryphia* and some Cunoniaceae are scarce but appear when light penetrates the canopy as a result of fine scale gap dynamics. Such gap dynamics open up the canopy and allow shade-tolerant understorey species to gradually replace senescing emergent trees (such as *Nothofagus*), and they may, in turn, ultimately become dominant in the absence of any further disturbance (Veblen et al., 1996). The fern component occurs in a number of different ecological niches. For example, in well-illuminated sites such as forest margins Gleicheniaceae, Schizaeaceae and some Aspleniaceae predominate; whereas Dennstaedtiaceae dominates in similar localities at higher altitude. Blechnaceae, Hymenophyllaceae and other Aspleniaceae favour places with relatively low light regimes.

Post-disturbance vegetation. After widescale disturbances the ensuing plant succession is governed by complex interlinked factors. These include the degree of damage sustained by the forest, initial taxonomic composition of the affected areas, time of year, presence or absence of a nearby regenerative flora, the stability of newly formed slopes, the degree of exposure, and distance from the vent (Veblen et al., 1977; Spicer, 1989). Ferns of light-demanding genera, such as members of the Cyatheaceae and Gleicheniaceae, are good colonizers of ash. Initially, *Gumera* also dominates exposed sites in areas subject to relatively high precipitation, along with *Equisetum* (Spicer, 1989; Veblen et al., 1996). Later, however, the pioneer taxa give way to *Nothofagus* in areas where conditions of constant disturbance favour pure stand *Nothofagus* growth. Most *Nothofagus* spp. regenerate well after disturbance which removes the pre-existing vegetation and exposes bare soil. Fires promote vigorous resprouting of certain *Nothofagus* species, thus enabling them to capitalize on the available light, resulting in even-aged cohorts of shade-intolerant *Nothofagus* (Veblen and Lorenz, 1987; Burns, 1993). Further away from the volcano, elements of the flora

suffering from mass or partial defoliation will releaf and continue to grow.

In South America, in substrates formed by recent glacial deposits such as moraines, supraglacial landslide debris and in-transit moraines, patches of temperate *Nothofagus*-dominated rainforest can establish (Veblen *et al.*, 1989). *Nothofagus* spp. are the initial colonizers of these new deposits along with, or succeeding, the nitrogen-fixing *Gunnera*, and some Ericaceae (*Pernettya* Gaudich) on well-drained sites (Heusser, 1964). *Nothofagus* ultimately becomes dominant in the successional forests, although instability of the in-transit moraines helps prevent canopy closure. This *Nothofagus* colonization is consistent with the ability of certain *Nothofagus* species (e.g. *Nothofagus dombeyi*) to establish on weathered volcanic ash surfaces exposed by landslides in the mid-elevations of the Chilean Andes (Veblen *et al.*, 1989).

Fossil and geological evidence in support of the Valdivian model. Disturbance in the Valdivian environment is largely driven by volcanic activity, with eruptions decreasing in severity and frequency further away from any volcanic edifice. Therefore, we would expect vegetation closer to the vent to have a greater abundance of taxa associated with early stages of secondary succession, while vegetation further away would show a higher percentage of climax species. Although glacial activity may have had an overriding effect on floras found in later, i.e. younger, deposits, the Eocene King George Island fossil floras can be constrained to vent proximal or vent distal positions both in time and space by the rock record. This provides a qualitative measure of predicted disturbance frequency and, if the King George Island palaeovegetation is responding to landscape processes in the same way as the Valdivian rainforest, this allows us to predict the types of fossil assemblages that should occur in each palaeoenvironmental setting (Table 3).

On King George Island, stratovolcanic activity is recorded by a thick sequence of lavas (indicative of proximal locations and high disturbance) with intercalated tuffaceous and epiclastic volcanic sediments (indicative of more distal locations and low disturbance). Temporal changes in the rock record appear to relate to either a migration of the stratovolcanic centre, or a shift in the focus of volcanic activity. On Fildes Peninsula, the Late Cretaceous to Early Palaeocene lava dominated strata suggest that the stratovolcano activity was nearby (Smellie *et al.*, 1984; Shen, 1994; Orton, 1996). These are overlain by Palaeocene to Eocene tuffaceous and epiclastic deposits, suggesting that the volcanic centre was either further away or that the focus of the erupting lava had changed (Smellie *et al.*, 1984; Orton, 1996). During the Eocene, King George Island was still a focus for pyroclastic activity and epiclastic sedimentation which gave rise to extensive tuffaceous deposits in which the Collins Glacier Flora was preserved. Forest fires, which could have been associated with volcanic activity, are known to have occurred on King George Island, but to date charcoalified specimens have only been recovered from Point Hennequin and Fossil Hill (Fig. 1) (R.J.H. work in progress).

Migration of either the centre of volcanic activity or a change in the focus of volcanism, such as on Fildes Peninsula, has important implications for vegetational succession since forest stands closer to the site of activity should experience a higher frequency of disturbance than their distal counterparts. The palaeoflora can provide further evidence of a disturbed environment as leaves and pollen are commonly preserved in the Palaeocene-Eocene volcanoclastic sediments of King George Island, although well-preserved fossilized wood is comparatively rare (Birkenmajer and Zastawniak, 1988, 1989).

Ecological disturbance can be inferred from Late Cretaceous floras from this region where the low-density vegetation is dominated by ferns and a relatively small percentage of angiosperms; gymnosperms generally characterize post-disturbance vegetation in proximal volcanic settings (Table 3; Cao, 1992; Dutra and Batten, 2000). On Fildes Peninsula, stratigraphically and geographically preserved vegetation distribution patterns occur. Using the Valdivian Model in relation to the palaeobotanical and geological evidence outlined above, Palaeocene-Eocene ecological disturbance consistent with evidence for fluctuating volcanic activity can be found at Fossil Hill (Shen, 1994), Ardley Island (Orlando, 1964) and in the Collins Glacier Flora described herein (Fig. 49). The sequence at Fossil Hill is 12 m thick and probably represents one single eruptive phase, thus providing evidence for a stratigraphically/temporally changing environment. A low diversity flora consisting only of *Nothofagus* and podocarps, characteristic of high disturbance, represents the lower part of the sequence, overlying a coarse volcanic debris flow (Fig. 47C). Higher up the sequence, the floral diversity increases, with pteridophytes, conifers—including Araucariaceae, Cupressaceae, Podocarpaceae—and angiosperms, including *Nothofagus*, Proteaceae, Myrtaceae, ?Araliaceae, Anacardiaceae and Cunoniaceae (Fig. 47A). From the Valdivian Model these latter angiosperm taxa would represent environments of low disturbance. In the uppermost part of the sequence the low diversity *Nothofagus* assemblages suggest a return to high disturbance environments (Cao, 1994; Li, 1994; Fig. 47B). The Collins Glacier Flora of Middle Eocene age is either contemporaneous or slightly older than the Fossil Hill flora. It is preserved in thick tuffaceous and epiclastic sediments characteristic of a more distal location relative to the volcanic centre. As such, it should have experienced lower levels of disturbance than the Fossil Hill flora, and this is supported by the floral composition. The presence of *Luma* and *Eucryphia* alongside *Nothofagus*, podocarps and Cupressaceae suggests that the flora was relatively diverse and had experienced low or relatively moderate levels of disturbance (Fig. 47A). Based on the modern altitudinal range of *Luma* and *Eucryphia* associations, the palaeoforest probably grew at low- to mid-altitudes on the flanks of the volcano. On Ardley Island, a flora probably coeval with the Fossil Hill flora includes leaves belonging to the Cupressaceae, Lauraceae, Monimiaceae, Sterculiaceae, Myrtaceae and Proteaceae (Orlando, 1964), and can therefore also be interpreted as a low disturbance vegetation (at least until the time of preservation), probably further from the volcanic activity

TABLE 3. Theoretical key to palaeovegetation composition based on the modern vegetation relationships in the Valdivian rainforests and the sequences of restoration observed in modern eruptions

R.D.F.	Geological indicators	Plant associations	Predicted fossil assemblages
Low	Lacustrine and fluvial epiclastic sediments common, few primary volcanic sediments and low proportion of lava.	Diverse mixed forest resembling undisturbed all-aged Valdivian forests, with a low proportion of <i>Nothofagus</i> and a high proportion of other angiosperms e.g. Lauraceae, Monimiaceae and Myrtaceae, <i>Chusquea</i> and fern understory and subordinate <i>Nothofagus</i> .	High diversity assemblages preserved in lacustrine or fluvial epiclastic sequences. Low proportions of <i>Nothofagus</i> to other shade tolerant angiosperms.
Moderate	Epiclastic and primary volcanic sediments with low to moderate proportion of lavas.	Moderately diverse mixed or patchy forest stands with some shade-tolerant vegetation in parts of the canopy e.g. even-aged senescent <i>Nothofagus</i> , <i>Eucryphia</i> and some members of the Cunoniaceae. Some shade-tolerants including members of the Lauraceae, Monimiaceae and Myrtaceae. <i>Chusquea</i> and fern understory.	Single bedding planes with mixed character that may show distinct patchy variations in diversity over a wide area.
High	High volume of lava with low proportion of primary volcanic sediments.	Fire/disturbance adapted angiosperms and conifers. Even-aged <i>Nothofagus</i> stands with <i>Araucaria</i> , podocarps and ferns. Shade-intolerants including <i>Eucryphia</i> and some members of the Cunoniaceae. Some shade-tolerant angiosperm taxa, <i>Gunnera</i> , <i>Equisetum</i> , light loving ferns, <i>Chusquea</i> .	Basal sequences containing pre-disturbance vegetation (potentially disturbed or possibly undisturbed). Overlain by <i>Gunnera</i> , <i>Equisetum</i> and fern rich 'opportunistic colonization' horizon. Upper sequences containing low diversity even-aged <i>Nothofagus</i> dominated assemblages with <i>Araucaria</i> , conifers and ferns.

R.D.F., Relative disturbance frequency.

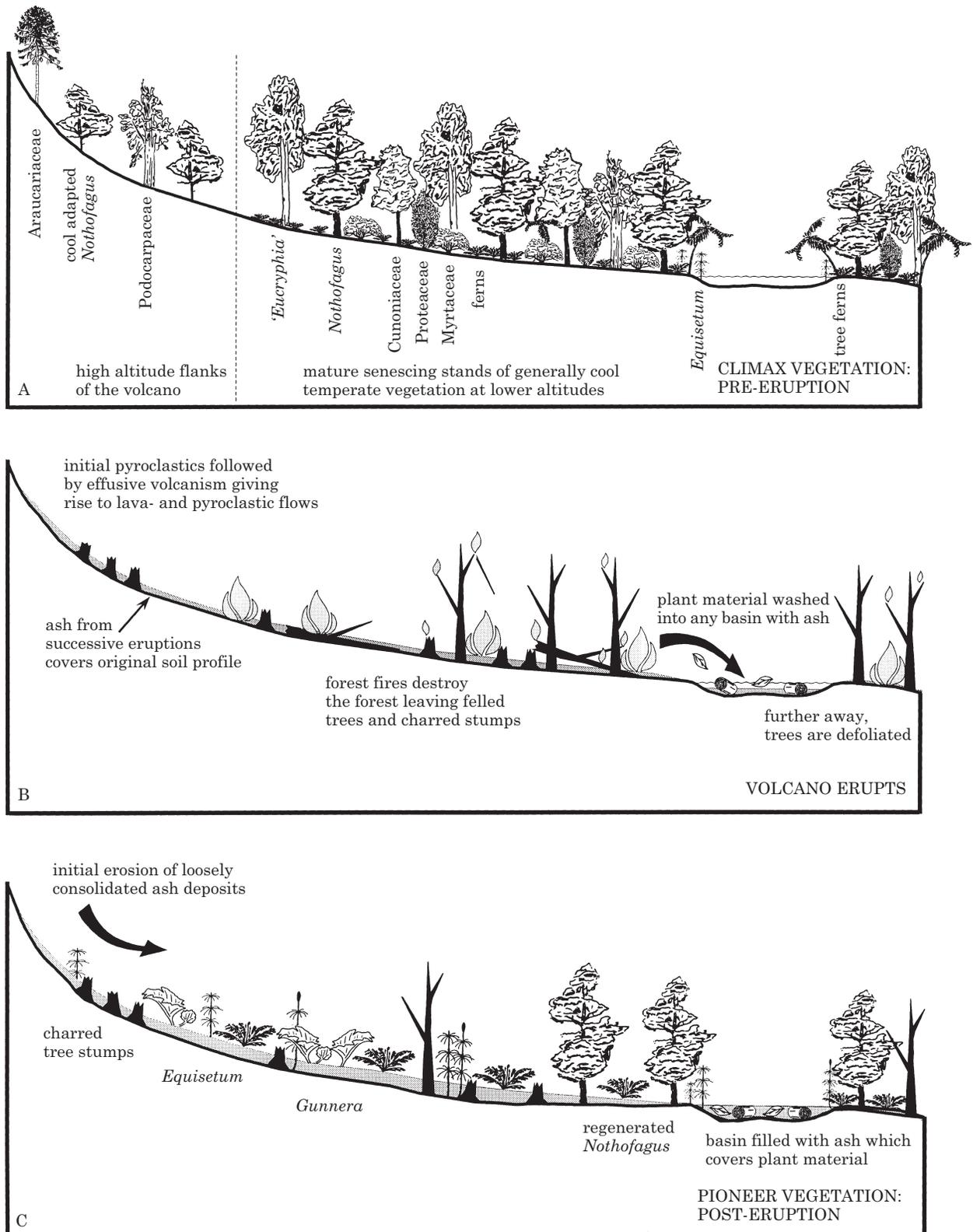


FIG. 47. Reconstructions of the vegetational succession along a transect of Fildes Peninsula from the high altitudinal (proximal) flanks of the volcanoes to the lower (more distal) altitudes derived from the palaeoflora and the Valdivian Model. **A**, climax vegetation composed mainly of cool temperate elements but some warmer temperate elements, such as Proteaceae, present; **B**, immediately post-disturbance, for example, a volcanic eruption with ash deposits, fires and tectonic movements which devastate the surrounding landscape; **C**, post-eruption pioneer vegetation of ferns, *Gunnera*, *Equisetum* and resprouting *Nothofagus* which will, in time, return to the climax vegetation. See text for further details.

than either the Fossil Hill flora or the Collins Glacier Flora (Fig. 47A). Cyatheaceae, Dicksoniaceae and some Osmundaceae all occur in the micro- and macrofossil records on Fildes Peninsula at this time and these probably formed an understorey with shrubby angiosperms such as the Proteaceae. Interestingly, fossil evidence for *Chusquea* on King George Island is limited to one Oligocene pollen record (Stuchlik, 1981). Therefore, perhaps ferns, ubiquitous in the palaeoflora (Zhou and Li, 1994b), filled this niche as they do in the *Nothofagus*-dominated forests of New Zealand and Tasmania, if indeed an ecological equivalent exists today.

CONCLUSIONS

Seven morphotypes of fossil wood have been found on Fildes Peninsula, King George Island. *Cupressinoxylon* represents the dominant conifer, in terms of number of specimens, with a subsidiary podocarp component. Two new records of *Nothofagoxylon* have been documented: a new species, *Nothofagoxylon corrugatus*, and *Nothofagoxylon neuquenense* previously only found in the Tertiary flora of South America. Fossil wood with closest anatomical similarity to *Eucryphia* (today found in South America and Tasmania) and *Luma* (found only in South America) are the first records of these wood types in Antarctica. This paper documents the first fossil evidence for nothofagaceous material occurring in association with eucryphiaceous and myrtaceous woods in Antarctica.

Elements within the Collins Glacier Flora have a disjunct distribution across the Southern Hemisphere, but in terms of overall vegetational similarity, the closest modern analogue is the low- to mid-altitudinal cool temperate Valdivian rainforests of southern Chile. Past dominance of *Nothofagus* could have indicated a shift towards a less favourable climate for other tree species (cf. occurrence of *Nothofagus* in drier sites east of the Andes such as those at high elevations, or with poor drainage; Veblen *et al.*, 1996); but the Valdivian Model has been put forward to explain the ecological changes seen in the Palaeocene-Eocene King George Island floras as the geological and palaeobotanical evidence supports volcanic disturbance in equable, favourable habitats dominated by taxa found in modern Valdivian rainforest ecosystems. Some care must be taken when applying this model, since accurate interpretations of vegetational succession require fine-scale bedding plane, or at least time-equivalent, observations of the fossil floras, which are currently lacking. Climatic or taphonomic interpretations, often used to explain changes in floral composition and diversity, can now be refined in light of this model of vegetation dynamics. With greater understanding and application, the model will allow Antarctic floras to be used as a tool for more precise interpretation of the palaeoclimate, vegetational succession and frequency of disturbance. As more fossils are uncovered and identified, and with further clarification of the stratigraphy, ideas concerning Antarctic vegetation and the Valdivian Model can be refined as this unique ecosystem becomes more fully understood.

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