Antarctica: Cretaceous cradle of austral temperate rainforests?

MARY E. DETTMANN

Department of Botany, University of Queensland, St Lucia, Qld 4067, Australia

Abstract: Although it is well known that certain Gondwanic elements of present-day austral temperate rainforests occurred on Antarctica during latest Cretaceous to early Tertiary times, there has been insufficient factual evidence for pinpointing the cradle of these forests. Fossil evidence from Antarctica and closely associated regions in the Createaceous southern Gondwanan assembly confirms that Antarctica was a Cretaceous origination and dispersal region of certain elements of today's southern hemispheric humid and perhumid forests. Antarctic origins are indicated for the fern *Lophosoria*, the podocarp gymnosperms *Lagarostrobus* and *Dacrydium*, *Nothofagus*, *Ilex*, and several lineages of the Proteaceae; migration to their present regions of distribution was probably step-wise. Antarctica also served as a Cretaceous dispersal corridor for other angiosperms represented today in mid to low latitude austral regions. These include *Ascarina* (or its stock), Myrtaceae, Gunneraceae, and Winteraceae, all of which had earlier histories in northern Gondwana or southern Laurasia. Origination and dispersal appears to be related to changing environmental circumstances associated with fragmentation of Gondwana and opening and enlargement of the southern oceans.

The concept of Antarctica as the source for plants now widely distributed in southern regions is not new. Both Darwin (1859) and Hooker (1847) suggested that Antarctica must have, in the past, supported a flora containing elements now restricted to southern perhumid forests. Many of these elements are now confined to southern South America, New Zealand, and the frontal arc from eastern Australia to the Indo-Malaysian region (Fig. 1). Although extending into the tropics, the plants there occur in upland rainforests and fringing communities and have mesothermal, not megathermal, requirements (e.g. Webb & Tracey 1981). They include southern conifers (the podocarps and araucarians), *Nothofagus*, rainforest to sclerophyllous members of the Proteaceae, and Winteraceae, *Ilex*, *Gunnera*, Myrtaceae, and several cryptogams.

Knowledge of the Cretaceous vegetation of Antarctica is mainly from the Antarctic Peninsula and nearby islands where a near-complete Cretaceous sequence is exposed (Ineson *et al.* 1986; Farquharson 1982); diverse plant megafossil and spore–pollen assemblages reported from these sequences provide a broad perspective of the contemporaneous floral succession (Truswell in press, and references cited therein). Evidence of the Cretaceous vegetation in the vicinity of the Ross and Weddell seas comes from recycled spores and pollen believed to have been sourced from subglacial Cretaceous sequences and redeposited in Recent marine muds (Truswell 1983; Truswell & Drewry 1984).

Recent marine muds from a range of localities off the coast of George V Land and Wilkes Land, Eastern Antarctica, have also yielded data on the Antarctic Cretaceous flora (Truswell 1983). The recycled palynomorphs were probably sourced from Antarctic counterparts of Cretaceous sequences in southern marginal basins of Australia. Remnants of one of those sequences, near the coast of George V Land, have yielded palynofloras comparable to those of Early Cretaceous age in the Otway and Gippsland basins, southeastern Australia (Domack *et al.* 1980). Plant fossil evidence from the Cretaceous of southern Australia, New Zealand, and southern South America is also relevant as these areas were associated with Antarctica for most of the Cretaceous. India and southern Africa were also closely aligned with Antarctica at the close of the Jurassic and their Cretaceous floras may be expected to reveal evidence of floral exchange and migration pathways between northern and southern Gondwana.

Cretaceous vegetation of southern high latitude regions: a perspective

From the latest Jurassic to the close of the Cretaceous, Antarctica's land vegetation comprised a series of evergreen coniferous rainforests (Jefferson 1983; Truswell 1983, in press; Dettmann 1986*a*; Dettmann & Thomson 1987; Askin 1988). Similar forests occurred in high latitude regions of adjacent land masses of the southern Gondwana assembly, but from the Antarctic Peninsula northwards to Patagonia, floral zonation was steep with an interfingering of austral podocarp and northern Gondwanan

From Crame, J. A. (ed.), 1989, *Origins and Evolution of the Antarctic Biota*, Geological Society Special Publication No. 47, pp. 89–105.

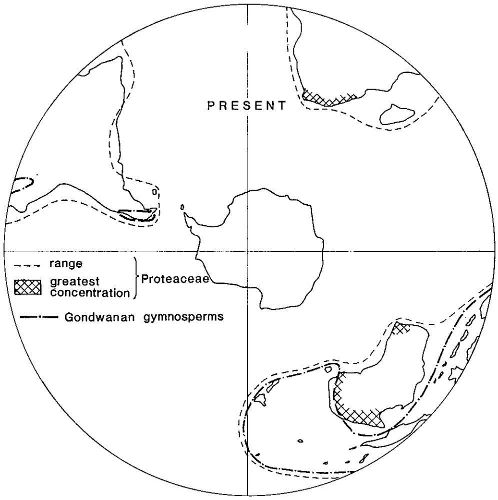


Fig. 1. Present distribution ranges of Proteaceae and Gondwanan gymnosperms including the Podocarpaceae. Map is South Polar Lambert equal-area (adapted from Smith *et al.* 1981).

cheirolepidacean communities (Figs 2 and 3). The geographical limits of the Antarctic-type vegetation fluctuated during opening and enlargement of the South Atlantic, Indian, and Southern oceans. With progressive opening of these oceans austral planktonic dinocyst floras (Helby *et al.* 1987) achieved circumpolar distribution in mid- to high latitude regions (Fig. 2).

The Antarctic Early Cretaceous forests were rich in podocarps and araucarians. Associated with them were ginkgos, taeniopterids, and bennettitaleans together with understorey and ground communities of ferns, lycopods, and bryophytes; angiosperms, of chloranthaceous stock, appeared no later than the early Albian and may have been represented by Barremian–Aptian times (Dettmann 1986*b*). There was marked regionalism in understorey associations between the Antarctic Peninsula and the eastern Antarctic–Australasian area (Dettmann & Thomson 1987). Exchange of floral elements between these and neighbouring areas of southern Gondwana was probably step-wise and mostly west to east (Fig. 2a, b).

The open-canopied forests of the northern Antarctic Peninsula region (for full locality map see Francis 1986, text. fig. 1) were of high productivity and climates were equable, wet, and temperate (Creber & Chaloner 1985; Francis 1986). To the south, on Alexander Island, growth rings in wood suggest marked seasonality or trees growing at the limits of their ecological range (Jefferson 1982). The abrupt zonation in vegetation from the Antarctic Peninsula to southern South America and the Falkland Plateau implies a steep climatic gradient (Dettmann 1986*a*) which appears to have decreased during enlargment of the South Atlantic Ocean. The vegetation fringing this ocean on the Falkland Plateau and in southern South Africa retained its cheirolepidacean character for much of the Early Cretaceous (Figs 2b and 3).

The Early Cretaceous climate of the eastern Antarctic–southeastern Australian region is also considered to have been cool to warm temperate, (Dettmann 1981; Douglas 1986) and was favourable for forest and peat swamp growth. Evidence for ice rafting in sediments of Early Cretaceous age in South Australia has been advanced by Frakes & Francis (1988), but they note that summer temperatures were probably warm.

During the Late Cretaceous, Antarctica and southern Australasia were vegetated by podocarp-rich coniferous forests that extended into southern South America and over the Falkland Plateau (during Campanian–Maastrichtian times; Fig. 2d, e). In the Turonian, *Lagarostrobus*, early Proteaceae, and *Ilex* were introduced into these forests, and in the Campanian *Dacrydium* and *Nothofagus* were established. As for the Early Cretaceous, there was marked regionalism involving both cryptogams and angiosperms (Dettman & Thomson 1987). Angiosperm pollen is neither common nor diverse in Cenomanian–Turonian palynofloras, reflecting a flora rich in cryptogams; however, during the Campanian–Maastrichtian there was considerable turnover of taxa with the loss of many of the cryptogam elements and the introduction of angiosperms. Amongst the latter were Myrtaceae, Gunneraceae, probable Epacridaceae, Winteraceae, Trimeniaceae, and an array of Proteaceae including probable *Macadamia*, *Gevuina*/*Hicksbeachia*, *Knightia*, *Xylomelum*, and *Beauprea* (Dettmann & Jarzen in press). Some were emigrants from northern Gondwana, but others almost certainly evolved in Antarctica (see later discussion). Migration between eastern and western Antarctica may have been bidirectional and there was exchange with northern Gondwana, possibly via South America.

Late Cretaceous climates are thought to have been cool to warm temperate with little or no seasonality and high moisture levels (Dettmann 1986*a*; Askin 1988), and are therefore similar to those of the Early Cretaceous.

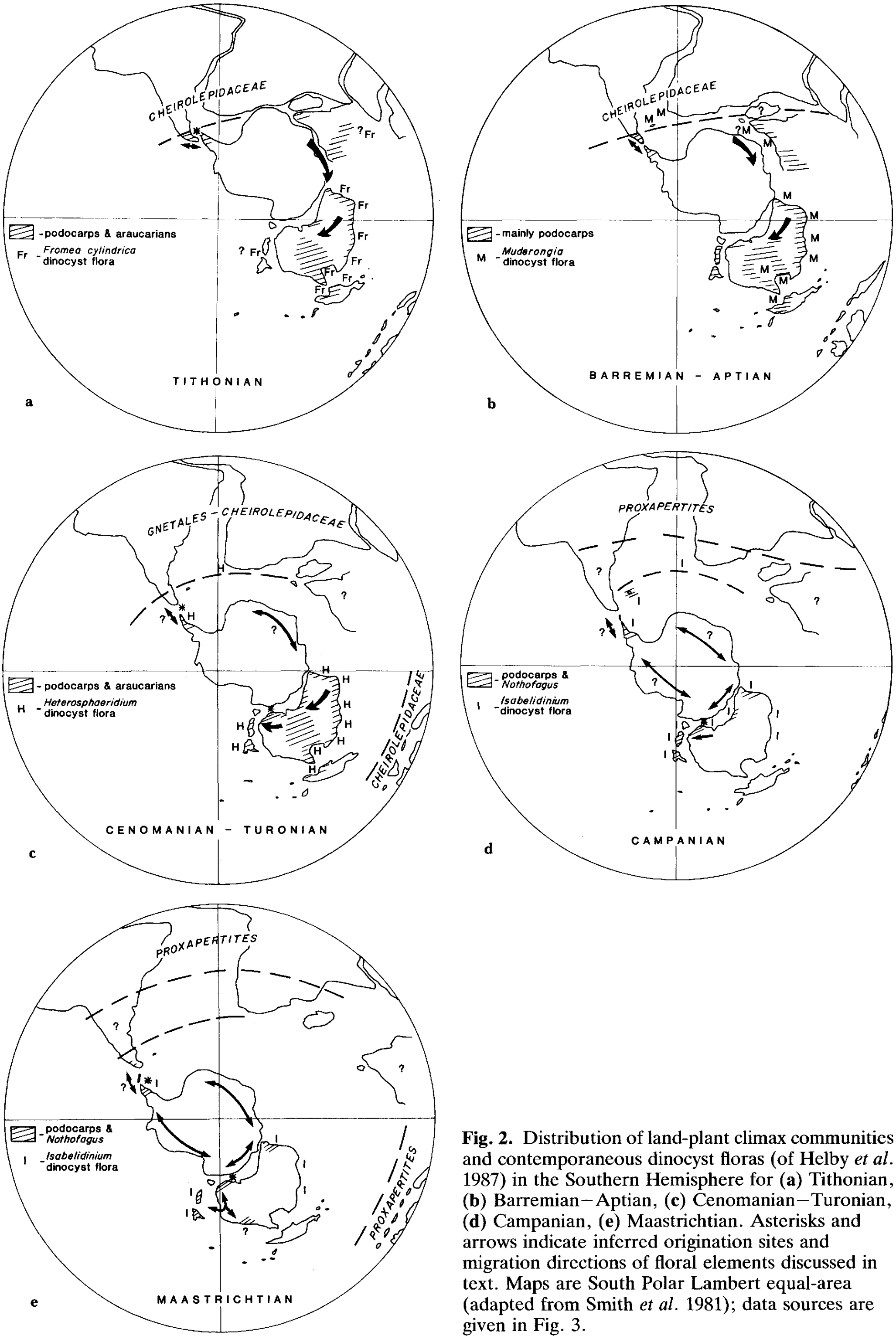


Fig. 2. Distribution of land-plant climax communities and contemporaneous dinocyst floras (of Helby *et al.* 1987) in the Southern Hemisphere for (**a**) Tithonian, (**b**) Barremian–Aptian, (**c**) Cenomanian–Turonian, (**d**) Campanian, (**e**) Maastrichtian. Asterisks and arrows indicate inferred origination sites and migration directions of floral elements discussed in text. Maps are South Polar Lambert equal-area (adapted from Smith *et al.* 1981); data sources are given in Fig. 3.

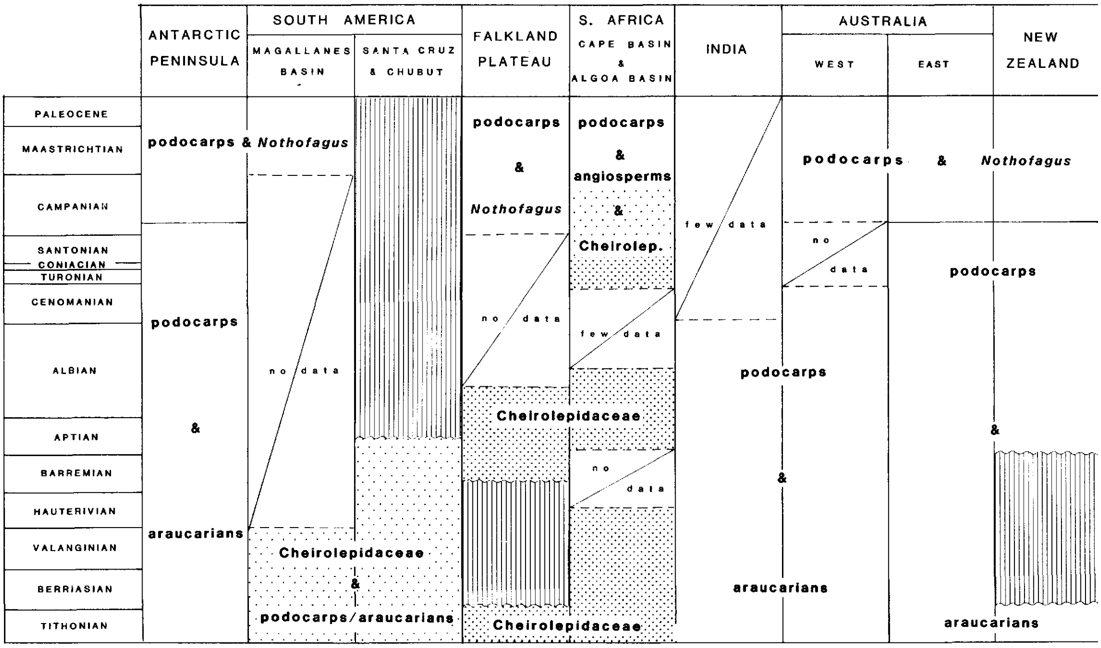


Fig. 3. Chronostratigraphic and geographic distributions of latest Jurassic to earliest Tertiary land-plant climax communities of southern Gondwanic regions. Vertical hatching denotes hiatuses within sedimentary sequences from regions specified. Principal sources of data are: Antarctic Peninsula, Askin (1983, 1989), Dettmann & Thomson (1987); Magallanes Basin, Baldoni & Archangelsky (1984), Archangelsky *et al.* (1984); Santa Cruz and Chubut, Archangelsky *et al.* (1981, 1984), Volkheimer *et al.* (1977); Falkland Plateau, Harris (1977), Hedlund & Beju (1977), Kotova (1983); South Africa, McLachlan & Pieterse (1978); India, Varma *et al.* (1984), Venkatachala (1974), Venktachala *et al.* (1980); Australia, Dettmann (1981), Helby *et al.* (1987 and references cited therein); New Zealand, Couper (1953, 1960), Raine *et al.* (1981), Raine (1984).

Selected floristic elements in the Cretaceous of Antarctica

Although many are preliminary accounts, palaeobotanical and palynological studies have provided a wealth of information on the character and composition of Antarctica Cretaceous floras. Represented in the vegetation were affiliates of extant cryptogams and phanerogams, many of which are important in today's austral floras.

Selected taxa identified amongst Antarctic Cretaceous plant fossils are summarized in Table 1 and discussed below with reference to their early histories in and beyond southern Gondwana.

Bryophyta

Anthocerotaceae, *Phaeoceros/Nothylas*-type (Figs 4, 5a; Table 1): Both *Foraminisporis dailyi* (Cookson & Dettmann) Dettmann 1963 and *Foraminisporis wonthaggiensis* (Cookson & Dettmann) Dettmann 1963 have been allied to the hornworts genera *Phaeoceros* and *Nothylas* (Dettmann 1963, 1986*b*; Jarzen 1979). *F. dailyi* occurs in Berriasian–Cenomanian sediments on the Antarctic Peninsula, and although unreported in situ from eastern Antarctic sequences, has a Berriasian–Campanian range in the Otway Basin. Morphologically similar spores of *Nevesisporites* attest to a history dating back to the Early Jurassic in Australia and South America. *F. wonthaggiensis* has Valanginian first appearances in the Otway Basin and occurs in probable remnants of that sequence in eastern Antarctica (Domack *et al.* 1980). However, it is not known from the Antarctic Peninsula region.

Ricciaceae/Riellaceae (Fig. 4; Table 1): Described species of *Triporoletes* are believed to represent spores borne by aquatic and terrestrial members of these families. A ricciaceous affinity for *T. reticulatus* (Pocock) Playford 1971 is strengthened by its association with the plant macrofossil *Hepaticites discoides* Douglas 1973 in Early Cretaceous sediments of the Otway Basin. Here *T. reticulatus* appears in the

Table 1. *Cretaceous range and appearance in the Antarctic region of selected plant groups as indicated by spore and pollen evidence.*

Plant family/genus	Spore/pollen taxa	Cretaceous range			Appearances older (younger) elsewhere	Present distribution
		Antarctic Peninsula	New Zealand/ Campbell Plat.	E. Antarctica S. Australia		
MUSCI						
Sphagnaceae	*Stereisporites* spp.	ranges	throughout	Cretaceous		cosmopolitan
HEPATICEAE						
Anthocerotaceae:						
Phaeoceros	*Foraminisporis dailyi* (Cookson & Dettmann)	Berrias.–Cenoman.	Albian–Cenoman.	Berrias.–Campan.	Berrias.; Queensland	cosmopolitan
Nothylas	*F. wonthaggiensis* (Cookson & Dettmann)	–	–	Valangin.–Maastr.	Valangin.; Queensland	cosmopolitan
Ricciaceae/Riellaceae:						
Riccia, Riella	*Triporoletes reticulatus* (Pocock)	Albian–Maastr.	Albian–Maastr.	Barrem.–Maastr.	Valangin.; Queensland	cosmopolitan
LYCOPODIOPSIDA						
Lycopodium (Lycopodium)	*Retitriletes* spp.	ranges	throughout	Cretaceous		cosmopolitan
FILICOPSIDA						
Cyatheaceae/Dicksoniaceae:	*Cyathidites* spp.	ranges	throughout	Cretaceous		tropical & temperate regions
Dicksoniaceae:	*Dictyophyllidites* spp.	ranges	throughout	Cretaceous		mainly topical
	Trilites tuberculiformis Cookson	Cenom.–Maastr.	–	Albian–Maastr.	Valangin.; Queensland	
Gleicheniaceae:						
Gleichenia, Dicranopteris	*Gleicheniidites* spp.	ranges	throughout	Cretaceous		tropical & subtropical regions
	Clavifera spp.	l. Maastr.	Campan.–Maastr.	Turon.–Maastr.	Albian; Queensland	
Lophosoriaceae:						
Lophosoria	*Cyatheacidites annulatus* Cookson	Berrias.–Campan.	–	Cenom. Santon.	Albian; Queensland	South & central America
Marsilaceae (?):	*Crybelosporites striatus* (Cookson & Dettmann)	late Albian	Albian–Cenom.	early Albian–Santon.	late Aptian; Falkland Plat.	tropical & temperate regions
Osmundaceae:	*Baculatisporites* spp. *Osmundacidites* spp.	ranges	throughout	Cretaceous		tropical & temperate regions
Parkeriaceae:						
Ceratopteris	*Cicatricosisporites australiensis* (Cookson)	Berrias.–Albian	Aptian–Cenom.	Berrias.–Campan.	Tithonian; India	tropical & subtropical regions

Table 1. *cont.*

Plant family/genus	Spore/pollen taxa	Antarctic Peninsula	Cretaceous range New Zealand/ Campbell Plat.	E. Antarctica S. Australia	Appearances older (younger) elsewhere	Present distribution
Schizaeaceae:						
Anemia (Anemirhiza), *Mohria*	*Cicatricosisporites hughesii* Dettmann	early Albian	–	Barrem.–Campan.	Berrias.; Queensland	tropical America, Africa
Anemia (Anemia)	*Nodosisporites* spp.	middle Albian	–	–	Barrem.–Apt; Patagonia	mainly tropical America
Anemia (Coptophyllum)	*Appendicisporites* spp.	middle Albian	–	late Albian	Barrem.; Queensland, Patagonia	tropical America, Africa, Madagascar, India.
GYMNOSPERMAE						
Araucariaceae:						
Araucaria	*Araucariacites australis* Cookson	ranges	throughout	Cretaceous		mainly Southern Hemisphere
Brachyphyllum irregulare	*Balmeiopsis limbata* (Balme)	Albian–Cenom.	–	Barrem.–Cenom.	Late Jurassic; N. Africa	extinct
Podocarpaceae:						
Microcachrys	*Microcachryidites antarcticus* Cookson	Berrias.–Maastr.	Apt.–Maastr.	Berrias.–Maastr.	Late Jur.; India N. Aust.	Tasmania
Trisacocladus tigrensis	*Trichotomosulcites subgranulatus* Couper	Alb.–Maastr.	Alb.–Maastr.	Barrem.–Maastr.	Berrias.–Apt.; S. America	extinct
Lagarostrobus	*Phyllocladidites mawsonii* Cookson	Tur./Con.–Maastr.	Tur.–Maastr.	Tur.–Maastr.	(Campan./ Maastr.); Falkland Plat.	Tasmania
Dacrydium	*Lygistepollenites* spp.	Santon.–Maastr.	Camp.–Maastr.	Santon.–Maastr.	(Mioc.); New Guinea	South America to Malaysia; not in Australia
Dacrycarpus	*Dacrycarpites australiensis* Cookson & Pike	Maastr.	(Eocene)	Maastr.	(Eocene); S. America	New Zealand, E. Australia, New Caledonia, New Guinea, E. Asia
Podocarpus	*Podocarpidites ellipticus* Cookson	ranges	throughout	Cretaceous		as above
ANGIOSPERMAE						
Aquifoliaceae: *Ilex*	*Ilexpollenites* spp.	Maastr.	Camp.–Maastr.	Turon.–Maastr.	(Senon.); Borneo	widespread, not in New Zealand
Chloranthaceae: *Ascarina*	*Clavatipollenites hughesii* Couper	e. Albian–Campan.	l. Albian–Cenom.	Barrem.–Santon.	Aptian; Falkland Plat.	New Zealand, Malaysia, Pacific Isl., Madagascar

Gunneraceae: *Gunnera*	*Tricolpites reticulatus* Cookson	Maastr.	Campan.–Maastr.	Campan.–Maastr.	Turon.; Peru	Southern Hemisphere
Fagaceae: *Nothofagus* Ancestral group	*Nothofagidites senectus* Dettmann & Playford	Campan.–Maastr.	Campan.–Maastr.	Campan.–Maastr.	(Maastr.); S. Amer.	extinct form
N. fusca group	*N. fusca* type	Maastr.	Maastr.	Maastr.	Maastr.; S. Amer.	S. Amer., New Zealand, Tasmania
N. menziesii group	*N. menziesii* type	Maastr.	(Paleocene)	(Eocene)	Maastr.; S. Amer.	S. Amer., New Zealand, E. Aust.
N. brassii group	*N. brassii* type	Maastr.	(Eocene)	Maastr.	Maastr.; S. Amer.	New Caledonia, New Guinea
Myrtaceae:	*Myrtaceidites* spp.	e. Campan.–Maastr.	(Paleocene)	(Paleocene)	Senon.; Borneo, N. Africa	Australia, Polynesia to Malaya, South America
Proteaceae: *Beauprea*	*Beaupreaidites* spp.	l. Maastr.	l. Campan.–Maastr.	e. Campan.–Maastr.	(Eocene); N. Aust.	New Caledonia
Macadamia (?)	*Propylipollis* cf. scaboratus (Couper)	Campan.–Maastr.	Campan.–Maastr.	Campan.–Maastr.	–	Australia to E. Malaysia
Gevuina/*Hicksbeachia*	*Propylipollis reticuloscabratus* (Harris)	Maastr.	–	Campan.–Maastr.	(Oligoc.); Queensland	N. Australia, S. Amer., and tropical Pacific.
Xylomelum (?)	*Propylipollis annularis* (Cookson)	Maastr.	(Paleocene)	(Paleocene)	–	Australia
Winteraceae: *Bubbia, Belliolum*	*Pseudowinterapollis wahooensis* (Stover)	–	Maastr.	Campan.–Maastr.	Similar forms in Apt.–Alb. Israel	New Guinea, E. Australia, New Caledonia

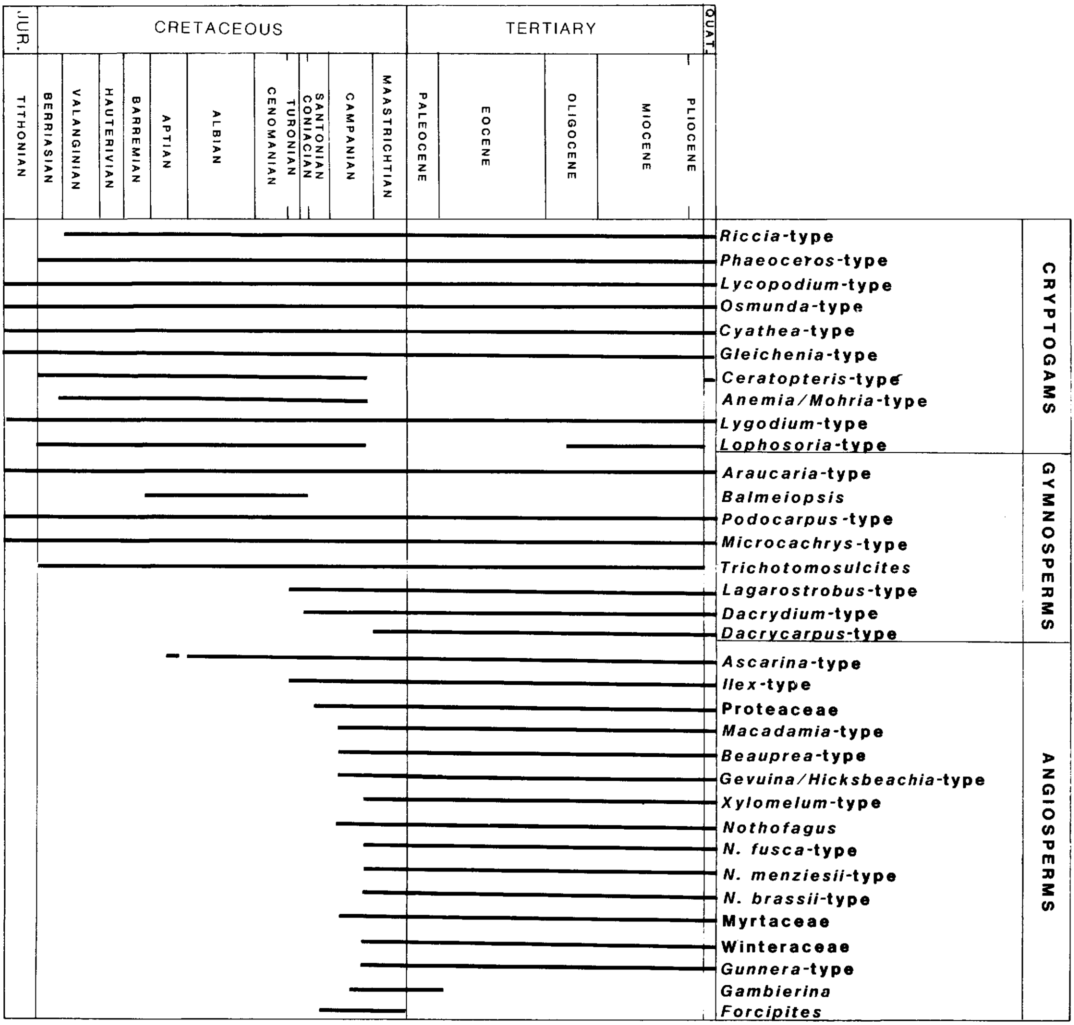


Fig. 4. Known stratigraphic ranges of selected floral elements in Antarctica and Australasia (including New Zealand, New Caledonia, Papua New Guinea, and intervening islands). Based on published data referred to under descriptions of the various groups.

Valanginian and is a common component of low gradient fluviatile/estuarine sediments of Albian–Turonian age. In contrast, the species occurs infrequently in Albian–Maastrichtian fan slope sediments in the James Ross Island region, Antarctic Peninsula (Dettmann & Thomson 1987). It seems likely that the parental source of *T. reticulatus* migrated to Antarctica during the Cretaceous, as older, Late Jurassic, records are known from Laurasia.

Lycopodiopsida

Lycopodiaceae, *Lycopodium*-type (Figs 4, 5b; Table 1): *Retitriletes*, which has cosmopolitan Late Mesozoic–Recent distribution and records that extend into the Triassic, replicates spores of *Lycopodium* (*Lycopodium*). Extant members of this subgenus are mainly terrestrial, occurring on disturbed sites adjacent to rainforests and on moorlands (Øllgard 1979).

Retitriletes species are common and diverse in Early Cretaceous palynofloras of Australia and New Zealand, but less so in coeval sediments of the Antarctic Peninsula region.

Filicopsida

Gleicheniaceae, *Gleichenia*/*Dicranopteris*-type (Fig. 4; Table 1): Dispersed spores included in *Gleicheniidites* verify the widespread distribution of the family during Jurassic–Cenozoic times. *Clavifera* incorporates fossil spores that probably were borne by an extinct alliance of the family which evolved during the Late Jurassic or Early Cretaceous. As discussed by Askin (1989), oldest appearances of *Clavifera triplex* (Bolkhovitina) Bolkhovitina 1966 imply earlier representation in eastern Australia (Albian) than in the Peninsula region of Antarctica (Late Cretaceous).

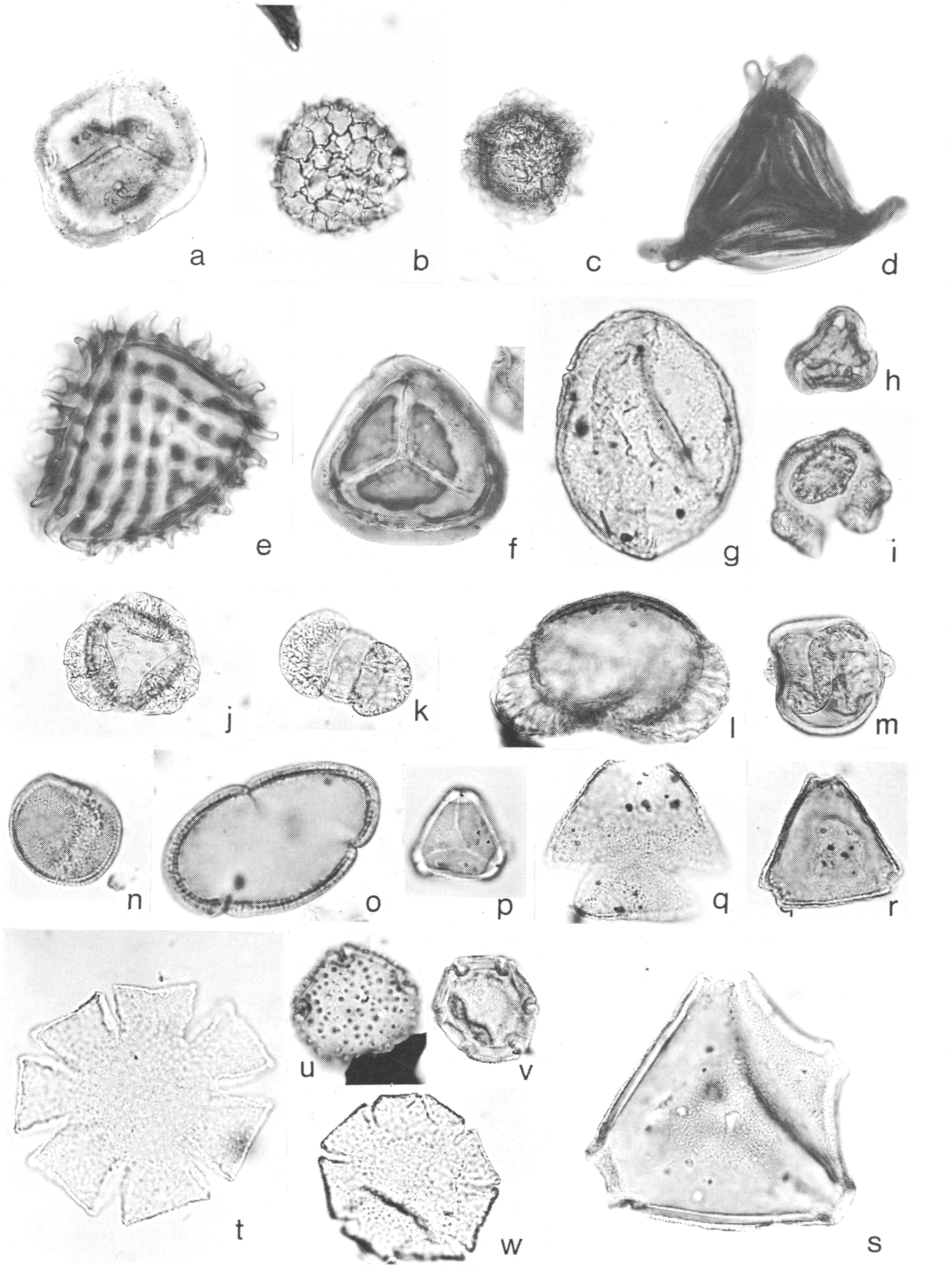
Lophosoriaceae, *Lophosoria*-type (Figs 4, 5; Table 1): This monotypic genus of ferns now restricted to South and central America had wide austral distribution during the Cretaceous and Tertiary as revealed by its unique spores, *Cyatheacidites annulatus* Cookson ex Potonié 1956 (Dettmann 1986*a*). It evolved in the Antarctic Peninsula–southern South America region during earliest Cretaceous times and the spore record suggests further diversification there of allied forms that are now extinct. Migration eastwards to Australia and northwards in South America coincided with environmental changes associated with Early Cretaceous opening of the South Atlantic Ocean. Dispersal across Australia was from west to east and occurred during Albian–Cenomanian phases of rifting between Australia and Antarctica prior to opening of the Southern Ocean.

Marsiliaceae (Fig. 5c; Table 1): *Crybelosporites striatus* (Cookson & Dettmann) Dettmann 1963 includes microspores of hydropteridean, possibly marsiliaceous, affinity. The Albian incoming of *C. striatus* in Australia and Antarctica is later than appearances on the Falkland Plateau (Aptian) and North America (earliest Cretaceous). During Albian–Cenomanian times these aquatic ferns apparently thrived in and about low relief depositional areas of Australia. The rare occurrence of spores in Antarctic Peninsula Cretaceous sediments may be related to the steep terrain on which suitable habitats of standing water may have been lacking (Dettmann 1986*a*).

Parkeriaceae, *Ceratopteris*-type (Fig. 4; Table 1): Species of *Cicatricosisporites* in which the mural sets are in discrete bundles in the equatorial radial regions (Dettmann 1986*b*) are believed to be allied to *Ceratopteris*, an aquatic fern of tropical regions. Earliest records of *Ceratopteris*-like spores are from the Middle Jurassic in the Caribbean and northern African regions, but in Australia and Antarctica it is not recorded until latest Jurassic time. The *Ceratopteris*-like spores represented include *Cicatricosisporites australiensis* (Cookson) Potonié 1956 and *C. ludbrookiae* Dettmann 1963, both of which were widely distributed throughout austral regions during Early–mid Cretaceous times.

Schizaeaceae, *Mohria*/*Anemia*-type (Figs 4, 5d, e; Table 1): Species of *Cicatricosisporites*, *Nodosisporites*, and *Appendicisporites* having mural sets that coalesce in the equatorial radial regions can be allied to the Schizaeaceae. The African genus *Mohria*, and the circum-Caribbean subgenus *Anemia* (*Anemirhiza*) have spores comparable to *Cicatricosisporites hughesii* Dettmann 1963 and *C. pseudotripartitus* (Bolkhovitina) Dettmann 1963. Both occur in Cretaceous sediments of Australia and Antarctica and elsewhere in southern high latitude regions. *C. hughesii* ranges from Barremian–Campanian in the Otway Basin and is known from the early Albian on the Antarctic Peninsula. Older records are unknown from the peninsula although Aptian sediments have yet to be studied. Other forms reminiscent of *Mohria*- and *Anemirhiza*-type spores are known from the Middle Jurassic in northern Gondwana and southern Laurasia, a region that may have been an early radiation centre for these alliances of the Schizaeaceae. Migration into austral areas probably involved India. Available records suggest that introduction in western and northern regions of Australia was earlier (earliest Cretaceous) than in the southeast (Barremian).

Nodosisporites (Fig. 5e) and *Appendicisporites* (Fig. 5d) are morphologically comparable to spores of the subgenera *Anemia* and *Coptophyllum*, respectively, of *Anemia*. Extant members are concentrated in tropical America with ranges that extend to Africa, Madagascar, and India. However, the fossil spore record implies a wider Cretaceous distribution in both the Northern and Southern Hemispheres. Both *Appendicisporites* and *Nodosisporites* are represented in middle Albian–Cenomanian sections of the Antarctic Peninsula sequence, but the latter is unknown from Australia. Earliest appearances of *Appendicisporites* in Australia are markedly heterochronous, with older, Barremian, occurrences in northern and western sequences in contrast to late Albian introduc-


a
b
c
d
e
f
g
h
i
j
k
l
m
n
o
p
q
r
t
u
v
w
s

tions in the southeast. Late Jurassic records of both genera from the Northern Hemisphere confirm a lag in migration to Australasia and Antarctica.

Gymnospermae

Araucariaceae (Figs 4, 5g; Table 1): This family, which has a history that extends into the Triassic, evidently achieved global or near-global distribution during the Cretaceous. *Araucariacites australis* Cookson 1947 probably includes pollen of araucarian origin and is a persistent and sometimes common element of Jurassic–Cretaceous palynofloras of Australasia and Antarctica. The more distinctive *Balmeiopsis limbatus* (Balme) Archangelsky 1979 is less certainly of araucarian derivation. It occurs in pollen sacs of *Brachyphyllum irregulare* Archangelsky 1966 and its first appearances imply radiation from northern Gondwana, southwards to Antarctica and Australasia during the Early Cretaceous. On the Antarctic Peninsula it is known from early Albian–Cenomanian sediments and in Australia has progressively younger incomings from Valanginian in western depositional basins (Backhouse 1988) to Barremian and Albian in central and southeastern areas. Step-wise eastwards migration seems likely.

Podocarpaceae (Figs 4, 5h–m; Table 1): Antarctic Cretaceous palynofloras contain common and diverse podocarpaceous pollen, several morphotypes of which can be allied to extant genera.

The most frequently occurring pollen are the bisaccate *Podocarpidites ellipticus* Cookson 1947 (Fig. 5k), which may represent pollen of *Podocarpus* and certain *Dacrydium* (Pocknall 1981), and trisaccate *Microcachrys*-like *Microcachryidites antarcticus* Cookson 1947 (Fig. 5i). *Microcachrys*, now relict in Tasmania, had widespread southern Gondwana distribution from latest Jurassic–Cretaceous times, but an earlier history in Europe is suggested by the occurrence of *Microcachrys*-like cones in the Middle Jurassic of Poland (Reymanova 1987).

The trisaccate pollen of *Dacrycarpites australiensis* Cookson & Pike 1953 (Fig. 5j) replicates that of *Dacrycarpus*. It has earliest occurrences in Campanian–Maastrichtian sediments of Antarctica and southern Australia, but, thus far, is known only from Eocene and younger sequences in South America and New Zealand (Mildenhall 1980). *Dacrycarpus*-like megafossils from the Jurassic of India (Florin 1940) suggest an earlier history of the genus or its stock outside the Antarctic/Australian region.

Antarctic Cretaceous sequences contain a further distinctive podocarpaceous trisaccate pollen type, *Trichotomosulcites subgranulatus* Couper 1953 (Fig. 5h), which is known from cones of extinct *Trisacocladus tigrensis* Archangelsky 1966. Oldest reported occurrences of the pollen are from the earliest Cretaceous of southern South America. A spread to Antarctica, Australia, and New Zealand was achieved by the Albian and the pollen persists into early Tertiary sediments throughout the Cretaceous distribution area.

Fig. 5. Photomicrographs of fossil cryptogam spores (a–f) and pollen of gymnosperms (g–m) and angiosperms (n–w); magnifications × 375 (j), × 562 (a–i, k–m), and × 750 (n–w). All specimens, except o, r, u, and w, are figured in Dettmann & Thomson (1987) and Dettmann & Jarzen (in press) where locality and repository details are given; specimens in o and w are from sample D.3122.3, Vega Island, and those in r and u from sample 8540, James Ross Island as designated by Dettmann & Thomson. (**a**) *Foraminisporis dailyi* (Cookson & Dettmann) Dettmann 1963 (*Phaeoceros*-type); (**b**) *Retitriletes austroclavatidites* (Cookson) Döring *et al.* 1963 (*Lycopodium*-type); (c) *Crybelosporites striatus* (Cookson & Dettmann) Dettmann 1963 (Marsiliaceae); (d) *Appendicisporites* cf. *insignis* (Markova) Chlonova 1976 (*Coptophyllum*-type); (e) *Nodosisporites* cf. *crenimurus* (Srivastava) Davies 1986 (*Anemia*-type); (**f**) *Cyatheacidites annulatus* Cookson ex Potonié 1956 (*Lophosoria*-type); (**g**) *Araucariacites australis* Cookson 1947 (Araucariaceae); (**h**) *Trichotomosulcites subgranulatus* Couper 1953 (Podocarpaceae); (**i**) *Microcachryidites antarcticus* Cookson 1947 (*Microcachrys*-type); (**j**) *Dacrycarpites australiensis* Cookson & Pike 1953 (*Dacrycarpus*-type); (**k**) *Podocarpidites ellipticus* Cookson 1947 (*Podocarpus*-type); *Lygistepollenites florinii* (Cookson & Pike) Stover & Evans 1973 (*Dacrydium balansae*-type); (**m**) *Phyllocladidites mawsonii* Cookson ex Couper 1953 (*Lagarostrobus*-type); (**n**) *Clavatipollenites hughesii* Couper 1958 (*Ascarina*-type); (**o**) *Tricolpites reticulatus* Cookson 1947 (*Gunnera*-type); (**p**) *Myrtaceidites eugeniioides* Cookson & Pike 1953 (Myrtaceae); (**q**) *Peninsulapollis truswelliae* Dettmann & Jarzen 1988 (?Proteaceae); *Propylipollis* cf. *crassimarginus* Dudgeon 1983 (*Macadamia*-type); (**s**) *Propylipollis* cf. *annularis* (Cookson) Martin & Harris 1974 (*Xylomelum*-type); (**t**) *Nothofagidites asperus* (Cookson) Romero 1973 (*Nothofagus menziesii*-type); (**u**) *Nothofagidites senectus* Dettmann & Playford 1968 (*Nothofagus* ancestral-type); (v) *Nothofagidites lachlaniae* (Couper) Pocknall & Mildenhall 1984 (*Nothofagus fusca*-type); (**w**) *Nothofagidites dorotensis* Romero 1973 (*Nothofagus brassii*-type).

Lagarostrobus, now confined to Tasmania and with bisaccate pollen identical with *Phyllocladidites mawsonii* Cookson 1947 (Fig. 5m), had an Australasian–Antarctic–southern South American distribution during the Late Cretaceous and Tertiary (Playford & Dettmann 1978). Origination was no later than the Turonian, but the southern high latitude radiation centre has not yet been pinpointed from available pollen evidence.

The history of the *Dacrydium balansae*/*D. bidwillii* alliance, which has a distribution range encompassing South America, New Zealand, and Pacific islands to Malaysia, can be traced by the bisaccate pollen genus *Lygistepollenites* (Fig. 5l). Oldest records of the pollen are from Coniacian–Santonian sediments in southeastern Australia and the Antarctic Peninsula (Dettmann & Jarzen in press). The latest Cretaceous–mid Tertiary distribution of the pollen is similar to that of *Phyllocladidites mawsonii* (*Lagarostrobus*); retraction and northwards migration to its present range occurred during and after the Miocene.

Angiospermae

Aquifoliaceae, *Ilex* (Fig. 4; Table 1): *Ilex*, which has cosmopolitan distribution, has a history that extends back to the Late Cretaceous. Oldest indubitable occurrences of *Ilex*-like pollen, *Ilexpollenites*, are in the Turonian of the Otway Basin (Martin 1977). Late Cretaceous migration, with routes involving Antarctica, is implied by respective Campanian and Maastrichtian first occurrences of *Ilexpollenites* in New Zealand (Raine 1984) and on the Antarctic Peninsula. Radiation to Borneo and Africa may have been earlier, in the Senonian (Muller 1981).

Chloranthaceae, *Ascarina* (Figs 4, 5n; Table 1): The oldest angiospermous pollen recorded from Antarctic and Australasian sequences is *Clavatipollenites hughesii* Couper 1958 which is comparable to pollen of *Ascarina*, a shrub now confined to New Zealand, Pacific islands, Malaysia, and Madagascar. Cretaceous records of the pollen suggest origination in northern Gondwana followed by Aptian–Albian radiation worldwide. Australian incomings are not certainly dated but may be as old as Barremian–Aptian (Dettmann 1986*b*) and predate appearances (late Albian) in New Zealand (Raine *et al.* 1981). Elucidation of the timing of introduction in Antartica awaits palynological analyses of Barremian–Aptian sediments that underlie the early Albian sections from which *C. hughesii* has been reported (Dettmann & Thomson 1987).

Fagaceae, *Nothofagus* (Figs 4, 5t–w; Table 1): A southern high latitude evolution of *Nothofagus* during the Late Cretaceous is supported by pollen and leaf evidence (Tanai 1986; Dettmann *et al.* in press). Early Campanian inception of ancestral types, such as *Nothofagidites senectus* (Dettmann & Playford 1968; Fig. 5u) in the Australian/Antarctic region was followed by Maastrichtian diversification and evolution of *brassii* (Fig. 5w), *fusca* (Fig. 5v), and *menziesii* (Fig. 5t) pollen producers on the Antarctic Peninsula and in Tierra del Fuego, South America. The later, staggered appearances of the extant pollen types in New Zealand and Australia imply step-wise migration with routes involving Antarctica (Fig. 6a).

Gunneraceae, *Gunnera* (Figs 4, 5o; Table 1): As indicated by the pollen record, *Gunnera* was established by the Turonian in northern Gondwana (Jarzen 1980) and radiated northwards and southwards during the Late Cretaceous. Its introduction into Antarctica and Australasia during the Late Cretaceous is confirmed by the presence of *Tricolpites reticulatus* Cookson 1947 in Campanian–Maastrichtian sediments of southern Australia, New Zealand, and the Antarctic Peninsula (Dettmann & Jarzen in press).

Myrtaceae (Figs 4, 5p; Table 1): Myrtaceous pollen similar to that of *Szygium* and *Eugenia* of the Myrtoideae occur in early Campanian and Maastrichtian sediments on the Antarctic Peninsula. These records predate earliest occurrences (Paleocene) in Australia and New Zealand, but are younger than the lower Senonian report from Borneo (Muller 1968) and the Santonian of Gabon (Boltenhagen 1976). The pollen evidence is sufficiently persuasive for a Late Cretaceous evolution of the family outside Australia which is now its centre of diversity. Introduction there may have been via Antarctica (Fig. 6b), although migration from Borneo cannot be discounted until Late Cretaceous sequences from intervening regions, including Papua New Guinea, are thoroughly investigated.

Proteaceae (Figs 4, 5r,s; Table 1): Proteaceous pollen represented in Campanian–Maastrichtian sediments of the Antarctica Peninsula confirm the former presence of the Proteoideae and Grevilleoideae (Dettmann & Jarzen in press). Amongst the Proteoideae is the New Caledonian endemic, *Beauprea*, which, as indicated by *Beaupreaidites*, probably evolved adjacent to the seaway between eastern Antarctica and southern Australasia (Pocknall

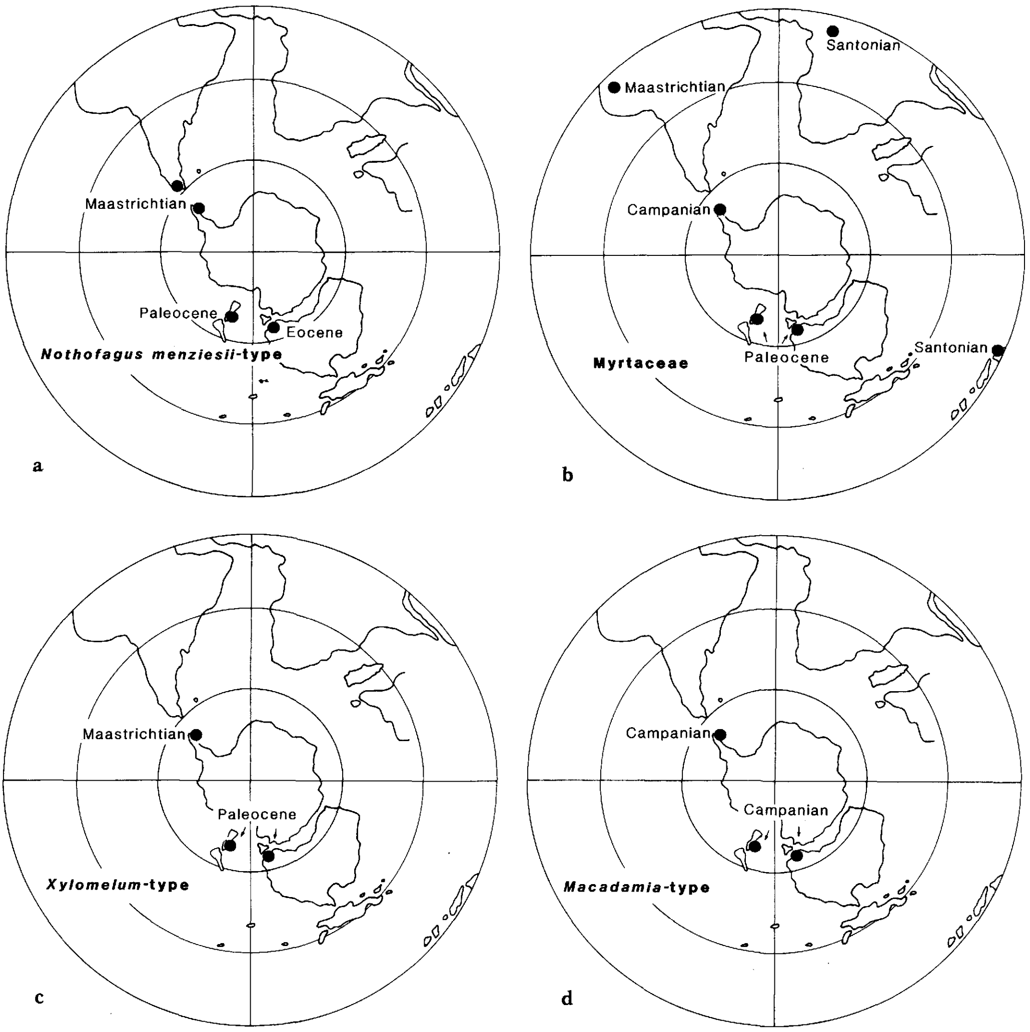


Fig. 6. Time of first appearance of pollen of (**a**) *Nothofagus menziesii*-type, (**b**) Myrtaceae, (**c**) *Xylomelum*-type, (**d**) *Macadamia*-type. Map is South Polar Lambert equal-area for the Santonian (after Smith *et al.* 1981).

& Crosbie 1988; Dettmann & Jarzen 1988). Although *Beaupreaidites* occurs infrequently in the Antarctic Peninsula region, a possible affiliate, *Peninsulapollis* (Fig. 5q), is both common and diverse.

Propylipollis, species of which have been associated with *Gevuina*/*Hicksbeachia*, *Knightia*, *Macadamia*, and *Xylomelum*, occur in Campanian–Maastrichtian sequences or in sediments sourced from those sequences in Antarctica. Pollen of the first two alliances appear in early Campanian sediments in southeastern Australia; this area may have been the site of evolution of the New Caledonian/New Zealand *Knightia* and the *Gevuina*/*Hicksbeachia* alliance (Dettmann & Jarzen in press) which today has a disjunct distribution in northeastern Australia and Chile. But an earlier incoming of *Propylipollis annularis* (Cookson) Martin & Harris 1974 (Fig. 5s) on the Antarctic Peninsula than in southern Australia suggests that possible affiliates of the Australian sclerophyllous *Xylomelum* may have migrated in the reverse direction from western Antarctica to southern Australia (Fig. 6c). The timing and place of origin of *Macadamia*, a northeastern Australian–Malaysian rainforest component, has yet to be ascertained precisely, but pollen evidence suggests introduction in Antarctica and in southern Australasia by the Campanian (Fig. 6d; Dettmann & Jarzen, in press).

Winteraceae (Fig. 4; Table 1): Winteraceous pollen similar to *Belliolum* and *Bubbia* occur in Upper Cretaceous sediments of southeastern Australia and New Zealand, but are as yet unreported from Antarctica. Records of *Drimys* leaves from the early Tertiary on Seymour Island (Dusén 1908) suggest widespread austral distribution of the family during the Tertiary. However, further investigations are required to establish radiation routes from a possible Aptian–Albian source area in Israel (Walker *et al.* 1983).

Phytogeographic implications

Of the elements discussed above, many now have disjunct distributions in the mid- to low latitudes of southern regions. A large number of the phanerogams and certain of the cryptogams have similar or overlapping distribution ranges and are concentrated in rainforests of South America, eastern Australasia, and islands northwards to Malaysia. Some also occur in Africa and/or Madagascar. Not all are Gondwanan in origin as had been postulated from biogeographical studies. The Winteraceae may have had an earlier history in southern Laurasia than in Gondwana, and the same may be true for certain early (Jurassic) Podocarpaceae, including *Microcachrys* (Reymanova 1987), and for many of the cryptogams. Radiation into the Antarctic region was not synchronous and may have involved separate routes through northern Gondwana.

Another group of immigrant taxa probably had origins in northern Gondwana. Amongst these are early chloranthaceous angiosperms, Gunneraceae, Proteaceae, and Myrtaceae. The last-mentioned seems to have occurred in Antarctica prior to introduction in Australia; migration from a northern distribution centre may well have been via a South American–Antarctic route. Floristic evidence for a northern Gondwanan origin of early Proteaceae (Johnson & Briggs 1975) is supported by pollen evidence. This large family is now concentrated in South Africa and Australia and with a distribution range that encompasses South America, and the southwestern Pacific region to Malaysia. Several of its alliances probably evolved in areas fringing the Late Cretaceous seaway between eastern Antarctica and southern Australasia. Amongst these are *Beauprea*, *Gevuina/ Hicksbeachia*, and *Knightia*, all of which date from the Campanian. *Ilex* also probably originated in the region, but at an earlier, Turonian, date.

Antarctica and closely associated areas of southern South America and southern Australasia was almost certainly the site of origin of other floral elements including *Lagarostrobus*, certain *Dacrydium*, *Nothofagus*, and the fern *Lophosoria*. The radiation centre of the last-mentioned was in the vicinity of the Antarctic Peninsula. Evolution occurred in earliest Cretaceous times (Dettmann 1986*a*) during initial opening of the South Atlantic Ocean. The same general region was the site of Maastrichtian diversification of *Nothofagus* (Dettmann *et al.* in press). Pollen evidence also indicates evolution of early *Nothofagus* in southern high latitudes, but the precise centre in Antarctica or contiguous regions has not been delineated as its pollen, which may have been widely disseminated by wind, had synchronous early Campanian appearances in western Antarctica, New Zealand, and southern Australia. The same holds true for the Turonian inception of *Lagarostrobus* and the *Dacrydium* allies that shed *Lygistepollenites*.

Many of the taxa discussed above now occur in mid- to low latitudes and are there concentrated in upland perhumid rainforests or on oceanic islands. They mostly prefer habitats influenced by equable, humid climatic conditions that can be classed as temperate (Webb & Tracey 1981). Some, including *Lagarostrobus*, *Microcachrys*, and the *fusca* and *menziesii* pollen producers of *Nothofagus*, occur in perhumid temperate forests of South America and/or southern Australasia. None of the evidence conflicts with a temperate humid climate.

Implications for origination and dispersal of plants

From the above discussion it is evident that Antarctica was most likely a source area and served as a dispersal corridor during the Cretaceous for certain floral elements now with disjunct distribution in austral mid to low latitude regions. Several phases of floral inception and migration are delineable from the fossil record (Figs 2, 6). They are contemporaneous with opening and enlargement of oceans and fragmentation of the southern Gondwana assembly. Causative factors may well be related to environmental disturbances and climatic changes resulting from volcanic and tectonic activity concurrent with rifting, drifting, and opening of oceans.

Western Antarctica was most likely the source region of *Lophosoria* and extant groups of *Nothofagus*. Inception of the former in earliest Cretaceous times was on a magmatic arc during a phase of considerable volcanic and tectonic activity associated with early opening of the South Atlantic Ocean (e.g. Farquharson 1983). Migration northwards to South America and the Falkland Plateau occurred as this ocean opened progressively from south to north; floral changes recorded there are believed to reflect alterations to terranes and climatic moderation (Dettmann 1986*a*). Migration eastwards to and within Australia coincided with phases of rifting and early drifting between Antarctica and Australia, and with depocentre displacements in intracratonic basins of Australia. Dispersal patterns of other floral elements indicate eastwards migration from western Antarctica and southern South America to Australia during the Early Cretaceous (Fig. 2a, b).

Near the close of the Cretaceous there was renewed volcanism in the Peninsula region (Farquharson 1983) and resultant environmental disturbances may have triggered evolution of primordial *Nothofagus* groups. Dispersal of these groups in a westwards direction to New Zealand and Australia must have involved trans-Antarctic routes (Fig. 6a). The same routes may have been utilized by the Myrtaceae and *Gunnera* after the radiation from northern Gondwana. But other floral elements appear to have migrated in the opposite direction during the Late Cretaceous (Fig. 2c–e). Certain Proteaceae have later inceptions in western Antarctica than in southern Australasia and probably evolved in the embryonic Southern Ocean region (Dettmann & Jarzen, in press). Campanian evolution was contemporaneous with rifting, early drifting, and volcanic activity (Boddard *et al.* 1986; Thompson 1986). Environmental stresses related to these events appear to be mirrored in the spore–pollen assemblages that record turnover of taxa and an expansion of angiosperm communities.

The Transantarctic Association is thanked for facilitating my attendance at the London meeting.

References

ARCHANGELSKY, S., BALDONI, A., GAMERRO, J. C., PALAMARCZUK, S. & SEILER, S. 1981. Palinológia estratigráfica del Cretácico de Argentina Austral. Diagrams del grupos polinicos de Sudroeste de Chubut y Noroeste de Santa Cruz. *Actas VIII Congreso Geologico Argentino, San Luis 1981*, 719–742.

——, ——, —— & SEILER, S. 1984. Palinológia estratigráfica del Cretácico de Argentina Austral. III. Distribucion de las especies y conclusiones. *Ameghiniana*, **21**, 15–33.

ASKIN, R. A. 1983. Tithonian (uppermost Jurassic)–Barremian (Lower Cretaceous) spores, pollen and microplankton from the South Shetland Islands, Antarctica. *In*: OLIVER, R. L., JAMES, P. R. & JAGO, J. B. (eds) *Antarctic earth science*. Australian Academy of Science, Canberra, and Cambridge University Press, Cambridge, 295–297.

—— 1988. Campanian to Paleocene palynological succession of Seymour and adjacent islands, northeastern Antarctic Peninsula. *In*: FELDMAN, R. M. & WOODBURNE, M. O. (eds) *Geology and palaeontology of Seymour Island, Antarctic Peninsula*. Geological Society of America Memoir, **169**, 131–53.

—— 1989. Endemism and heterochroneity in the Seymour Island Campanian to Paleocene palynofloras: implications for origins, dispersal and palaeoclimates of southern floras. *In*: CRAME, J. A. (ed.) *Origins and evolution of the Antarctic Biota*, Geological Society, London, Special Publication, **47**, 107–120.

BACKHOUSE, J. 1988. Late Jurassic and Early Cretaceous palynology of the Perth Basin, Western Australia. *Bulletin of the Geological Survey of Western Australia*, **135**.

BALDONI, A. & ARCHANGELSKY, S. 1983. Palinológia de la Formación Springhill (Cretácico Inferior), subsuelo de Argentina y Chile Austral. *Revista Espanola de Micropaleontologia*, **15**, 47–101.

BODARD, J. M., WALL, V. J. & KANEN, R. A. 1986. Lithostratigraphic architecture of the Latrobe Group, offshore Gippsland Basin. *In*: GLENIE, R. C. (ed.) *Second south-eastern Australian Oil Exploration Symposium, Melbourne, 1985*. Petroleum Exploration Society of Australia, 113–136.

BOLTENHAGEN, E. 1976. Pollen et spores Senoniennes du Gabon. *Revue de Micropaléontologie*, **18**, 191–199.

COUPER, R. A. 1953. Upper Mesozoic and Cainozoic spores and pollen grains from New Zealand. *Paleontological Bulletin New Zealand Geological Survey*, 22.

—— 1960. New Zealand Mesozoic and Cainozoic plant microfossils. *Paleontological Bulletin New Zealand Geological Survey*, 32.

CREBER, G. T. & CHALONER, W. G. 1985. Tree growth in the Mesozoic and early Tertiary and the reconstruction of palaeoclimates. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **52**, 35–60.

DARWIN, C. 1859. *On the origin of species by means of natural selection*. Murray, London.

DETTMANN, M. E. 1963. Upper Mesozoic microfloras from southeastern Australia. *Proceedings of the*

Royal Society of Victoria, **77**, 1–148.

—— 1981. The Cretaceous flora. *In*: KEAST, A. (ed.) *Ecological biogeography of Australia*. Junk, The Hague, 357–375.

—— 1986*a*. Significance of the Cretaceous-Tertiary spore genus *Cyatheacidites* in tracing the origin and migration of *Lophosoria* (Filicopsida). *Special Papers in Palaeontology*, **35**, 63–94.

—— 1986*b*. Early Cretaceous palynoflora of subsurface strata correlative with the Koonwarra Fossil Bed, Victoria. *Memoirs of the Association of Australasian Palaeontologists*, **3**, 79–110.

—— & JARZEN, D. M. 1988. Angiosperm pollen from uppermost Cretaceous strata of southeastern Australia and the Antarctic Peninsula. *Memoirs of the Association of Australasian Palaeontologists*, **5**, 217–237.

—— & —— In press. The Antarctic/Australian rift valley: Late Cretaceous cradle of northeastern Australasian relicts? *In*: TRUSWELL, E. M., BALME, B. E., DETTMANN, M. E. & WILSON, G. J. (eds) *Proceedings of the 7th International Palynological Congress, Brisbane 1988*. Australian Academy of Science, Canberra.

—— & THOMSON, M. R. A. 1987. Cretaceous palynomorphs from the James Ross Island area — a pilot study. *British Antarctic Survey Bulletin*, **77**, 13–59.

——, POCKNALL, D. T., ROMERO, E. J. & ZAMALOA, M. In press. *Nothofagidites* Erdtman ex Potonié 1960; a catalogue of species with notes on the palaeogeographic distribution of *Nothofagus* B1. *Paleontological Bulletin New Zealand Geological Survey*.

DOMACK, E. W., FAIRCHILD, W. W. & ANDERSON, J. B. 1980. Lower Cretaceous sediment from the East Antarctic continental shelf. *Nature*, **287**, 625–626.

DOUGLAS, J. G. 1986. The Cretaceous vegetation, and palaeoenvironments of Otway Group sediments. *In*: GLENIE, R. C. (ed.) *Second southeastern Australia Oil Exploration Symposium, Melbourne*, 1985. Petroleum Exploration Society of Australia, 233–240.

DUSÉN, P. 1908. Uber die Tertiäre Flora der Seymour Insel. *Wissenschaftliche Ergebnisse der Scwedishen Südpolar-expedition 1901–1903*, **3**, 1–127.

FARQUHARSON, G. W. 1982. Late Mesozoic sedimentation in the northern Antarctic Peninsula and its relationship to the southern Andes. *Journal of the Geological Society, London*, **139**, 721–728.

—— 1983. Evolution of Late Mesozoic sedimentary basins in the northern Antarctic Peninsula. *In*: OLIVER, R. L., JAMES, P. R. & JAGO, J. B. (eds) *Antarctic earth science*, Australian Academy of Science, Canberra, and Cambridge University Press, Cambridge, 323–327.

FLORIN, R. 1940. The Tertiary fossil conifers in South Chile and their phytogeographical significance, with a review of the fossil conifers of southern lands. *Kungliga Svenska vetenskapsakademiens handlingar*, **19**, 1–107.

FRAKES, L. A. & FRANCIS, J. E. 1988. Australian Cretaceous ice. *9th Australian Geological Convention, Brisbane 1988, Abstracts*, 144–145.

FRANCIS, J. E. 1986. Growth rings in Cretaceous and Tertiary wood from Antarctica and their palaeoclimatic implications, *Palaeontology*, **29**, 665–684.

HARRIS, W. K. 1977. Palynology of cores from Deep Sea Drilling Sites 327, 328, and 330, South Atlantic Ocean. *In*: BARKER, P. F., DALZIEL, I. W. D. *et al. Initial Reports Deep Sea Drilling Project*, **36**. United States Government Printing Office, Washington, 761–815.

HEDLUND, R. & BEJU, D. 1977. Stratigraphic palynology of selected Mesozoic samples, DSDP Hole 327A and Site 330. *In*: BARKER, P. F., DALZIEL, I. W. D. *et al. Initial Reports Deep Sea Drilling Project*, **36**. United States Government Printing Office, Washington, 817–827.

HELBY, R. J., MORGAN, R. & PARTRIDGE, A. D. 1987. A palynological zonation of the Australian Mesozoic. *Memoirs of the Association Australasian Palaeontologists*, **4**, 1–93.

HOOKER, J. D. 1847. *The botany of the Antarctic voyage of H. M. discovery ships Erebus and Terror in the years 1839–1843. I Flora Antarctica*. Reeve Bros., London. Reprinted 1963, J. Cramer, Weinheim.

INESON, J. R., CRAME, J. A. & THOMSON, M. R. A. 1986. Lithostratigraphy of the Cretaceous strata of west James Ross Island, Antarctica. *Cretaceous Research*, **7**,141–159.

JARZEN, D. M. 1979. Spore morphology of some Anthocerotaceae and the occurrence of *Phaeoceros* spores in the Cretaceous of North America. *Pollen et Spores*, **21**, 211–231.

—— 1980. The occurrence of *Gunnera* pollen in the fossil record. *Biotropica*, **12**, 117–123.

JEFFERSON, T. H. 1982. The Early Cretaceous fossil forests of Alexander Island, Antarctica. *Palaeontology*, **25**, 681–708.

—— 1983. Palaeoclimatic significance of some Mesozoic Antarctic fossil forests. *In*: OLIVER, R. L., JAMES, P. R. & JAGO, J. B. (eds) *Antarctic Earth Science*, Australian Academy of Science, Canberra, and Cambridge University Press, Cambridge, 593–598.

JOHNSON, L. A. S. & BRIGGS, B. G. 1975. On the Proteaceae — the evolution and classification of a southern family. *Botanical Journal of the Linnean Society*, **70**, 83–185.

KOTOVA, I. Z. 1983. Palynological study of Upper Jurassic and Lower Cretaceous sediments, Site 511, Deep Sea Drilling Project Leg 71 (Falkland Plateau). *In*: LUDWIG, W. J., KRASHENINNIKOV, V. A., *et al. Initial Reports of the Deep Sea Drilling Project*, **71**, United States Government Printing Office, Washington, 879–906.

MARTIN, H. A. 1977. The history of *Ilex* (Aquifoliaceae) with special reference to Australia: evidence from pollen. *Australian Journal of Botany*, **25**, 655–673.

MCLACHLAN, I. R. & PIETERSE, R. E. 1978. Preliminary palynological results. Site 361 Leg 40, Deep Sea Drilling Project. *In*: BOLLI, H., RYAN,

W. B. F. *et al. Initial Reports of the Deep Sea Drilling Project* **40**, United States Government Printing Office, Washington, 857–881.

Mildenhall, D. C. 1980. New Zealand Late Cretaceous and Cenozoic plant biogeography: a contribution. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **31**, 197–233.

Muller, J. 1968. Palynology of the Pedawan and Plateau Sandstone Formations (Cretaceous–Eocene) in Sarawak, Malaysia. *Micropaleontology*, **14**, 1–37.

—— 1981. Fossil pollen records of extant angiosperms. *The Botanical Review*, **47**, 1–142.

Øllgard, B. 1977. *Lycopodium* in Ecuador — habits and habitats. *In*: Larsen, L. & Holm–Nielsen, P. (eds) *Tropical Botany*. Academic Press, London, New York, 381–395.

Playford, G. & Dettmann, M. E. 1978. Pollen of *Dacrydium franklinii* Hook.f. and comparable early Tertiary microfossils. *Pollen et Spores*, **20**, 513–534.

Pocknall, D. T. 1981. Pollen morphology of the New Zealand species of *Dacrydium* Solander, *Podocarpus* L'Heritier, and *Dacrycarpus* Endlicher (Podocarpaceae). *New Zealand Journal of Botany*, **19**, 67–95.

—— & Crosbie, Y. M. 1988. Pollen morphology of *Beauprea* (Proteaceae): modern and fossil. *Review of Palaeobotany and Palynology*, **53**, 305–327.

Raine, J. I. 1984. Outline of a palynological zonation of Cretaceous to Paleogene terrestrial sediments in west coast region, South Island, New Zealand. *Reports of the New Zealand Geological Survey*, **109**, 1–82.

——, Speden, I. G. & Strong, C. P. 1981. New Zealand *In*: Reyment, R. A. & Bengtsen, P. (eds) *Aspects of mid-Cretaceous regional geology*. Academic Press, London, 221–267.

Reymanova, M. 1987. A Jurassic podocarp from Poland. *Review of Palaeobotany and Palynology*, **51**, 133–143.

Smith, A. G., Hurley, A. M. & Briden, J. C. 1981. *Phanerozoic paleocontinental maps*. Cambridge University Press, Cambridge.

Tanai, T. 1986. Phytogeographic and phylogenetic history of the genus *Nothofagus* B1. (Fagaceae in the Southern Hemisphere). *Journal of the Faculty of Science Hokkaido University Series 4*, **21**, 505–582.

Thompson, B. R. 1986. The Gippsland Basin — development and stratigraphy. *In*: Glenie, R. C. (ed.) *Second southeastern Australia Oil Exploration Symposium, Melbourne 1985*. Petroleum Exploration Society of Australia, 57–64.

Truswell, E. M. 1983. Recycled Cretaceous and Tertiary pollen and spores in Antarctic marine sediments: a catalogue. *Palaeontographica*, **186B**, 121–174.

—— in press. Antarctica: a history of terrestrial vegetation. *In*: Tingey, B. (ed) *Geology of Antarctica*, Oxford University Press.

—— & Drewry, D. J. 1984. Distribution and provenance of recycled palynomorphs in surficial sediments of the Ross Sea, Antarctica. *Marine Geology*, **59**, 187–214.

Varma, Y., Rao, N. & Ramanujam, G. G. K. 1984. Palynology of some Upper Gondwana deposits of the Palar Basin, Tamil Nadu, India. *Palaeontographica*, **190B**, 37–86.

Ventkatachala, B. S. 1974. Palynological zonation of the Mesozoic and Tertiary subsurface sediments in the Cauvery Basin. *In*: Surange, *et al.* (eds) *Aspects and appraisal of Indian palaeobotany*. Birbal Sahni Institute of Palaeobotany, Lucknow, 476–495.

—— Rawat, M. S., Sharma, K. D. & Jain, A. K. 1980. Aptian-Albian spore and pollen assemblages from the Cauvery Basin, India. *Proceedings of the IV International Palynological Conference, Lucknow 1976*, **2**, 396–402.

Volkheimer, W., Caccavari De Filice, M. A. & Sepulveda, E. 1977. Datos palinologicos de la Formacion Ortiz (Grupo la Amarga). Cretacico inferior de la cuenca nequina (Republica Argentina). *Ameghiniana*, **14**, 59–74.

Walker, J. W., Brenner, G. J. & Walker, A. G. 1983. Winteraceous pollen in the Lower Cretaceous of Israel: early evidence of a magnolialean angiosperm family. *Science*, **220**, 1273–1275.

Webb, L. J. & Tracey, J. G. 1981. Australian rainforest: patterns and change. *In*: Keast, A. (ed.) *Ecological biogeography of Australia*. Junk, The Hague, 605–694.