Structure and floristics of Cretaceous vegetation of southern Gondwana : implications for angiosperm biogeography

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A review of palaeobotanical/palynological data reveals that the vegetation of southern Gondwana was regionalised throughout the Cretaceous. Open forests of high productivity occurred in high southern latitudes whereas woodlands, heathlands and closed forests vegetated mid-latitudinal areas. Angiosperms first entered the region during Barremian-Aptian times from source areas in northern Gondwana. Early immigrants to the Australian-Antarctic assembly were of magnoliid stock, and migration routes involved southern South America. Early angiosperms in India also included non-magnoliid taxa which may have utilised an African/Madagascar corridor. Non-magnoliid angiosperms spread to the Austro-Antarctic landmass during the Albian, some 5-10 Ma after India was isolated from the southern Gondwanan assembly. For the remainder of the Cretaceous southern South America and the Antarctic Peninsula served as an exchange corridor for angiosperms between northern and southern Gondwana. This area was also the cradle of *Nothofagus*, whereas diametrically opposed land adjacent to the embryonic Southern Ocean was a differentiation centre for the Proteaceae. Angiosperm migration was step-wise, and regulated by changing environmental circumstances associated with tectonic/volcanic activity and opening and enlargement of the southern oceans.

Key-words—Gondwana, Angiosperms, Biogeography, Cretaceous, Floral migration.

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सारांश

दक्षिणी गोंडवाना की क्रीटेशी वनस्पति की संरचना तथा वनस्पतिजात : आवृतबीजी जैवभौगोलिकी का महत्व

मैरी ई० डेटमॅन

पुरावनस्पति/परागाणविक आँकड़ों की समीक्षा से व्यक्त होता है कि पूरे क्रीटेशी काल में दक्षिणी गोंडवाना की वनस्पति क्षेत्रीय थी। खुले वन उच्च दक्षिणी अक्षांसों में विकसित हुए जबकि अरण्यभूमि, अजोतभूमि तथा सघन वनों का विकास मध्य-अक्षांसी क्षेत्रों में हुआ। आवृतबीजी पौधों ने पहले उत्तरी गोंडवाना स्रोत क्षेत्रों से बैरेमियन-एप्शियन काल में इस क्षेत्र में प्रवेश किया। आस्ट्रेलियाई-अंटार्कटिक समुच्चय में आरम्भ में प्रवेश करने वाले अवयव मैग्नोलिडी थे और इनका आने का मार्ग दक्षिणी दक्षिण अमेरिका से था। भारत के प्रारम्भिक आवृतबीजी वर्गकों में भी अमैग्नोलिड वर्गक सम्मिलित हैं जो कि सम्भवतः अफ्रीकी/मेडागास्कर मार्ग से आये हैं। आस्ट्रेलियाई-अंटार्कटिक भूभाग पर अमैग्नोलिडी वर्गकों का विस्तार एल्बियन काल में हुआ जिस समय भारत गोंडवानाभूमि से अलग हो चुका था। अन्य स्थानों के लिए क्रीटेशी दक्षिणी दक्षिण अमेरिका तथा अंटार्कटिक प्रायद्वीप से उत्तरी एवं दक्षिणी गोंडवाना में आवृतबीजी पौधों का विस्तार हुआ। यह क्षेत्र **नोथोफेगस** का आश्रय-स्थान था जबकि इसके पीछे दक्षिणी समुद्र से लगी भूमि प्रोटिएसी हेतु विविधता का केन्द्र थी। आवृतबीजी पौधों का विकास शनैः शनैः तथा विवर्तनिक/ज्वालामुखीय गतिविधियों द्वारा नियंत्रित परन्तु बदलते वातावरण में हुआ है।

PALAEOBOTANICAL and palynological data have been crucial to understanding the development of present-day floras of austral regions, and have verified that the austral flora includes fragments of one that formerly occupied a great Southern continent (Hooker, 1847). This great Southern Continent was the Gondwanan assembly of Early Cretaceous times. At that time South America, Africa, Madagascar, India and Australia were clustered around Antarctica which straddled high southern latitudes (Text-figure 1a). By the latest Cretaceous (Text-figure 1d) the Indian and South Atlantic oceans had opened and Africa and India were

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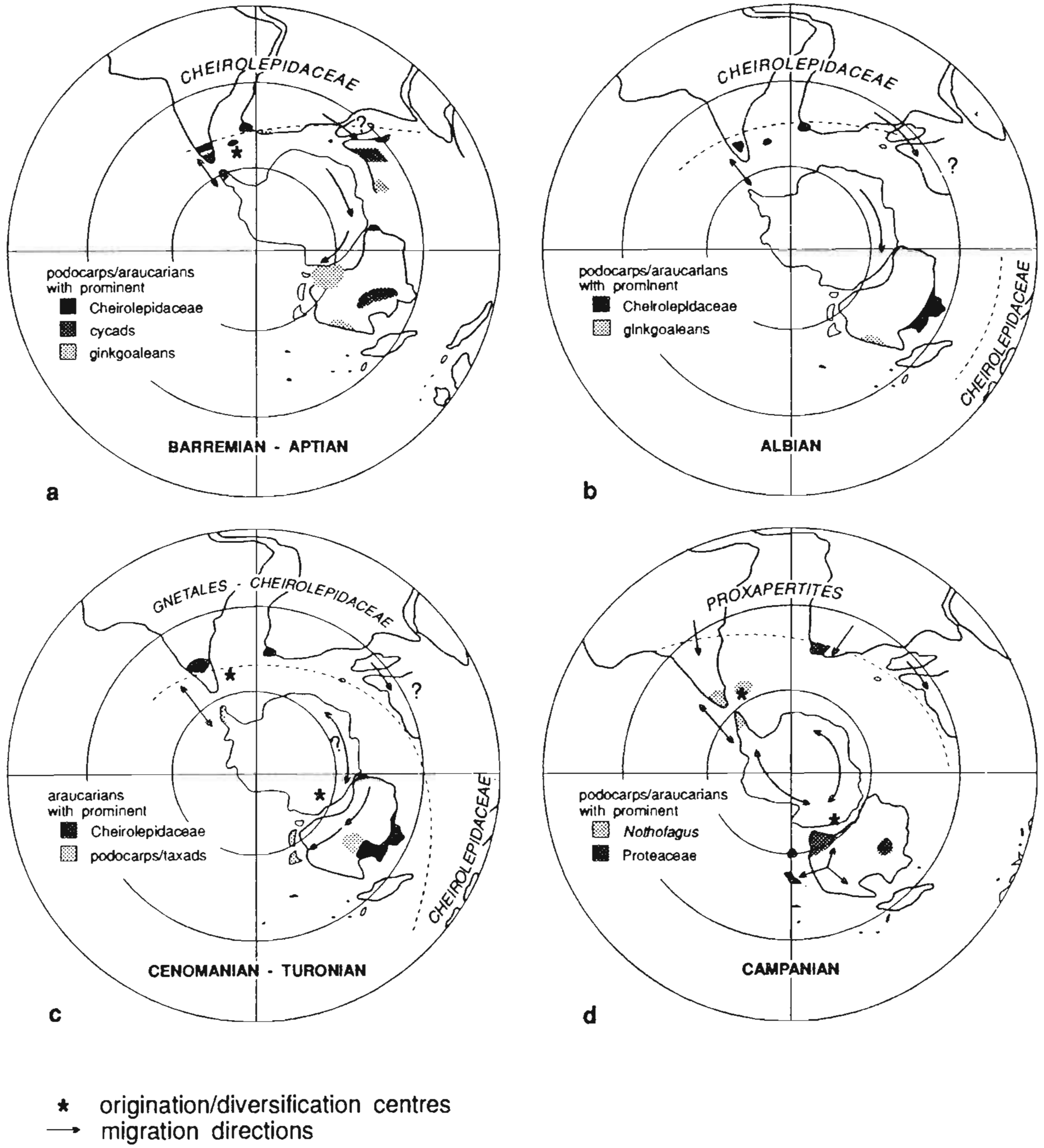


Text-figure 1—Maps of Southern Hemisphere for: **a**, Barremian-Aptian; **b**, Albian; **c**, Cenomanian-Turonian; and **d**, Campanian showing distribution of vegetational zones, origination/diversification centres, and migration directions delineated in southern Gondwana (after Dettmann, in press).

isolated from the partially united southern portion of the assembly that comprised southern South America, Antarctica, and Australasia. During the Early Cretaceous angiosperms evolved in the northern Gondwanan/southern Laurasian area and radiated world-wide; those lineages that were established in southern Gondwana by the close of the Cretaceous formed the foundation from which developed present-day austral floras.

This paper focuses on the significance of palaeobotanical/palynological data for elucidating Cretaceous plant evolution in the Southern Hemisphere and the biogeography of austral angiosperm groups. The mechanisms that motivated plant evolution and migration are also explored with particular reference to breakup events of the

Gondwanan assembly, to climates, and to environments.

CRETACEOUS VEGETATION OF SOUTHERN GONDWANA

In earliest Cretaceous times the Gondwanan assembly comprised two broad floristic regions. In northern areas (i.e., South America and Africa) cheirolepidacean conifers were important in the climax vegetation, whereas in southern Gondwana (Antarctica, Australasia, southernmost South America, and India) the vegetation was characterised by a series of podocarp/araucarian forests. In the Antarctic Peninsula/South American region, floral zonation across the latitudes was steep with an interfingering of austral podocarp/araucarian and northern Gondwanan cheirolepidacean communities (Text-figure 1a). The geographical limits of the podocarp/araucarian forests fluctuated during opening and enlargement of the South Atlantic, Indian, and Southern oceans (Text-figure 1b-d), and with progressive opening of these oceans austral planktonic dinocyst floras achieved circumpolar distribution (Dettmann & Thomson, 1987). Angiosperms were introduced into the region during latest Barremian-Aptian times from a source area centred in northern Gondwana or southern Laurasia (Dettmann, 1989).

Preangiospermous flora

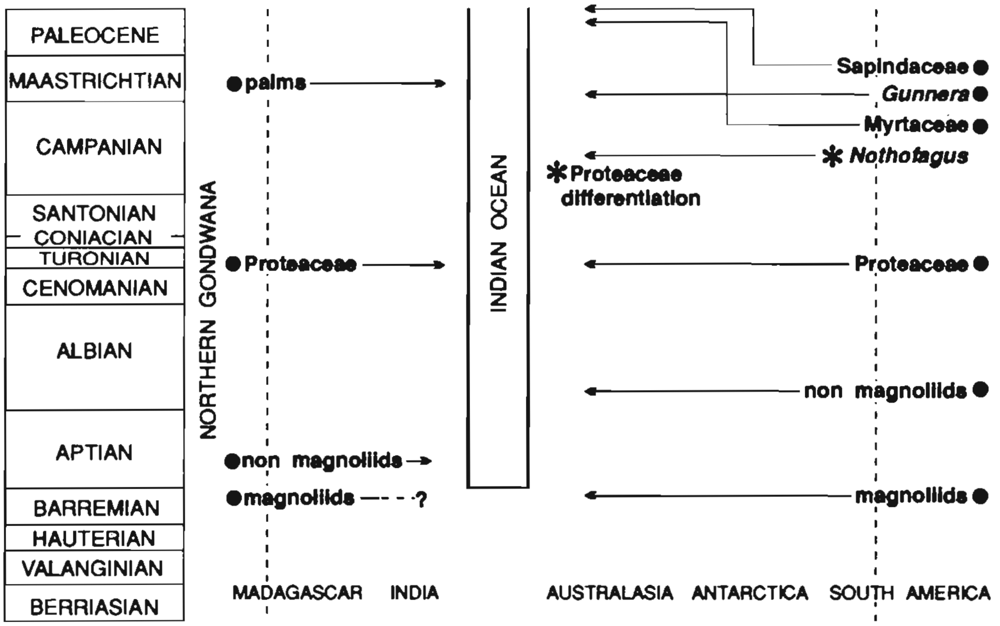
The Cretaceous preangiospermous vegetation of southern Gondwana was characterized by araucarian/podocarp forests. Other communities included woodlands of cheirolepidaceans, heathlands of ferns, and aquatic or semi-aquatic moss/hepatic/isoetalean/equisetalean associations. Regionalism was evident within both overstorey and understorey associations, and the regionalism is believed to have been influenced by climatic as well as topographic and edaphic factors. Associated with the forests and forest fringes of podocarps and araucarians were ginkgos, cycads, taeniopterids, pteridosperms, bennettitaleans, and osmundalean and dicksonialean "tree" ferns together with ground communities of terrestrial ferns, lycopods, and bryophytes. In northern areas of the assembly (India, Patagonia, the Antarctic Peninsula, northern Australia), araucarians were more important in the canopy than the podocarps, whereas in southern humid regions podocarps were dominant. Cycads were more plentiful in interior and northern coastal areas than ginkgos which appear to have preferred more humid habitats (Text-figure 1a). Woodlands of cheirolepidacean conifers intermingled with the forests in coastal regions of northern and Western Australia as the Indian Ocean opened, and formed a substantive part of the vegetation in the southernmost South America/Falkland Plateau/southernmost South Africa region during early opening of the southern South Atlantic Ocean (Text-figure 1a). Cryptogam associations also varied across southern Gondwana; fern spores are more plentiful and diverse in what were coastal regions, whereas lycopods (mainly *Lycopodium*) thrived about river/lake systems of inland areas (Dettmann, in press). Spores of sphagnalean mosses and hepatics are more abundant in depositional basins that were set in low relief terranes than elsewhere.

The structure of the forests also varied. In high latitudinal regions the forests had open canopies and productivity was high under cool-temperate climatic regimes. Jefferson's forest on the Antarctic Peninsula exemplifies the widely spaced, conical-crowned trees of the forests at latitudes of 70°S (Jefferson, 1983). At lower latitudes within the southern Gondwanan assembly climates were warmer, and light regimes were sufficient to support an understorey in closed-forests in humid areas (Specht *et al.*, in press), or in open woodlands of drier regions.

As the oceans opened, disturbances to adjacent land areas appear to have been the driving force for floral evolution and exchange (Dettmann, 1989). Many bryophytic, fern ally, and fern taxa migrated into southern Gondwana after origination in northern Gondwana (Dettmann, 1989; Dettmann & Clifford, in press). Migration across southern Gondwana was mostly in an easterly direction and dispersal to eastern Australasia was later than to southern South America, India, and Antarctica (Text-figure 1a). Several taxa evolved in areas fringing the opening South Atlantic Ocean, and evolution was concurrent with environmental disturbance (Dettmann, 1989). Coincidentally southernmost South America was an "overlap area" of the northern and southern Gondwana phytogeographic regions (Text-figure 1a). Rift valley systems between Antarctica, Australasia, and India are believed to have served as migrational pathways (Dettmann, 1989).

Invasion of early angiosperms

Although inconclusive, the evidence for angiosperm introduction into southern Gondwana points to routes involving Africa and South America; radiation was contemporaneous with opening of the South Atlantic and Indian oceans. The first



Text-figure 2—Schematic outline of ages of introduction and migration of selected angiosperm components in southern Gondwana.

angiosperms to migrate were herbaceous or shrubby chloranthaceous taxa (Dettmann, in press), which would have competed with taxa in the ground or shrubby strata at forest fringes or those of the understorey within the open-forests. Introduction of angiosperms to southern South America was during the Barremian (Archangelsky, 1980), and their introduction was concurrent with opening of the South Atlantic Ocean. Barremian-Aptian taxa reported are of magnoliid affinity (Text-figure 2). The arrival of angiosperms in Australia is dated as latest Barremian-Aptian, and types represented are exclusively of magnoliid stock (Dettmann, 1986; Burger, 1990). Barremian-Aptian sediments of the southern rift valley contain the oldest known flower branchlet which indicates a plant of prostrate habit (Taylor & Hickey, 1990). Associated vegetation existed under cool-cold, humid climates, and the forests had open canopies, not closed canopies, as light regimes at the high southern latitudes were insufficient for growth of an understorey within closed-forests (Creber & Chaloner, 1987; Specht *et al.*, in press). Magnoliid angiosperms colonised areas adjacent to interior basins of northeastern Australia during the Barremian, but appear to have retreated when the area was inundated by shallow seas in the Aptian (Burger, 1990; Dettmann, in press). Their reappearance in the Early Albian was coincident with partial regression of the sea; habitats were adjacent to the shallow seas and lake systems. Burger (1990) argues that angiosperms migrated to Australia via India and/or Southeast Asia but whilst an Indian route is feasible, a southerly route involving Antarctica (Text-figures 1a, 2) for the magnoliid types is favoured by the pollen evidence.

The introduction of angiosperms into the Indian vegetation was concurrent with volcanic activity (Tripathi & Tiwari, 1991). Precise dates have yet to be determined for flows associated with earliest recorded pollen, but dates of 115 ± 10 Ma (i.e., Barremian-Aptian) have been resolved for volcanics elsewhere in India. Although several of the forms interpreted as representing mono- and trichotomosulcate pollen are only doubtfully of angiospermous affinity, tricolpate grains confirm the presence of non-magnoliid taxa (Tripathi & Tiwari, 1991).

A second wave of angiosperms migrated to southern Gondwana during Middle Albian-Cenomanian times and involved non-magnoliid dicotyledonous taxa whose lineages evolved in northern Gondwana near the Barremian/Aptian boundary (Brenner, 1976; Doyle *et al.*, 1982). Once again, migration across southern Gondwana appears to have been in an easterly direction (Text-figure 1b). Although non-magnoliid dicotyledons were represented in India by the Aptian, migration from India to either Australia or Antarctica seems unlikely as India had been isolated from the southern Gondwanan assembly since the Early Aptian (Text-figures 1b, 2). The meagre information on Indian Mid-Cretaceous vegetation (Venkatachala, 1977; Nandi, 1990) suggests that floral links with the Antarctic-Australasia region had been severed. Precise affinities of many of the immigrant angiosperms are unknown, but in Australia Platanaceae and winteraceous lineages are indicated in the pollen record (Dettmann, in press). The Australian introduction of the non-magnoliid dicots coincided with partial sea retreat in intracratonic basins, and with widening of the floodplain in the southern rift valley. Temperatures were warmer than for the Aptian, but precipitation may have been less or seasonal in interior regions. Environmental disturbances involving volcanism and tectonic displacement on the Antarctic Peninsula were also coincident with mid-Late Albian invasion of non-magnoliid angiosperms; this region was possibly the principle exchange corridor between South America and Australia.

By the Cenomanian Australia had commenced its slow drift north (Veevers & Eittreim, 1988), but remained in high southern latitudes, and in southern areas the forests would have had an open structure. Niches occupied by the non-magnoliid dicots included shorelines and floodplains, but distribution patterns of the two separate pollen associations delineated by Burger (1990) seem to imply that some of the angiosperms were established in the open-forests of hinterland regions of the Eromanga Basin. Near the Cenomanian/Turonian boundary angiosperms with pollen similar to that of *Callitriche* (Callitrichaceae) were introduced into the vegetation of the southern rift valley. *Callitriche*, which today occupies aquatic and semi-aquatic habitats, may well have had origins in northern Gondwana as the *Callitriche*-like pollen taxon, *Cretaceiporites scabratus* Jardiné & Magloire, has been recorded from older sediments (Albian-Cenomanian) in Brazil (Herngreen, 1973).

During the Albian-Cenomanian Australasia, Antarctica, southern South America, and the Falkland Plateau retained connections and formed the southern Gondwana assembly (Text-figure 1b, c). Most regions of this assembly were situated in high southern latitudes and the podocarp/araucarian forests would have had an open structure. As the South Atlantic Ocean opened and the climatic gradient moderated, podocarp/araucarian forests advanced over the Falkland Plateau and partially replaced the cheirolepidacean communities (Text-figure 1b). Here and on the Antarctic Peninsula, the forests were associated with ginkgos/cycadophytes, pteridosperms, and diverse terrestrial ferns, several of which are unknown from Australasia (Dettmann & Thomson, 1987). Other taxa had restricted geographic ranges within the southern Gondwana region. For instance, the brachyphyll that shed *Hoegisporis* was restricted to northern and western areas of Australia where the flora was richer in angiosperm, fern, and hepatic taxa than the vegetation of southeastern Australia. Cheirolepidacean conifers were well represented in northern coastal areas, but were only of local development about the estuary in the southeast rift valley (Text-figure 1b, c).

Differentiation and evolution of austral angiosperms

Angiosperm immigrants continued to migrate via southern South America to the Austro-Antarctic region from northern Gondwana during the remainder of the Cretaceous (Turonian-Maastrichtian), but many newly introduced taxa differentiated from northern Gondwanan lineages in southern high latitudes. Northern Gondwanan origins have been demonstrated for *Gunnera* (Jarzen & Dettmann, 1989), and *Belliolium/Bubbia* of the Winteraceae may have evolved in the same region (Dettmann & Jarzen, 1990). Pollen that may represent earliest Proteaceae occur in the Cenomanian-Turonian of northern Gondwana (Muller, 1981), but subsequent Late Cretaceous diversification of the family was centred in southern high latitudes (Dettmann & Jarzen, 1991). Four of the five subfamilies of extant Proteaceae are represented in the Campanian-Maastrichtian pollen record of the Austro-Antarctic rift valley. Amongst diverse assemblages of proteaceous pollen recorded from the Otway Basin, southeastern Australia are pollen indicating *Adenanthos, Beauprea*, and *Stirlingia* (Proteoideae), *Persoonia* (Persoonioideae), *Carnarvonia* (Carnarvonioideae), and *Grevillea, Telopea, Macadamia, Gevuina/Hicksbeachia*, and *Knightia* (Grevilleoideae). Diversification of the family coincided with habitat changes associated with early opening of the Southern Ocean (Text-figures 1d, 2). This region may also have been the origination centre of *Ilex* (Aquifoliaceae) in the Turonian (Martin, 1977) and of lineages of the Trimeniaceae and Epacridaceae in the Campanian (Dettmann & Jarzen, 1990).

Lagarostrobus, Dacrydium and *Dacrycarpus* (Podocarpaceae), and *Nothofagus*, which are important elements of temperate rainforests of the Southern Hemisphere, evolved in southern high latitudes during the Late Cretaceous (Dettmann *et al.*, 1990, 1992). The podocarps had successive introductions during Turonian-Santonian times, and ancestral *Nothofagus* appeared in the Campanian. Differentiation of *Nothofagus*, and appearance of its four extant subgenera has been shown to have occurred during the Late Campanian-Maastrichtian in the southern South America-Antarctic Peninsula region (Text-figure 2; Dettmann *et al.*, 1990). Diversification was concurrent with volcanic and tectonic activity under climates that were cooler than those of southern Australasia, the Late Cretaceous diversification centre of the Proteaceae. Migration of extant lineages of *Nothofagus* to Australia occurred during latest Cretaceous-Early Tertiary times and routes must have involved Antarctica (Dettmann *et al.*, 1990). The same route may have been utilised by the Myrtaceae, Olacaceae, Loranthaceae, and Sapindaceae. Members of these families were established on the Antarctic Peninsula during Campanian-Maastrichtian times, but are unknown from Australia prior to the Tertiary (Dettmann & Thomson, 1987; Askin, 1989; Dettmann, 1989). Antarctica probably served as dispersal route for several other taxa, with migration in the opposite direction. Present records indicate that several Proteaceae and Epacridaceae were introduced into Australia prior to their latest Cretaceous-Tertiary arrival in western Antarctica (Dettmann, 1989; Askin, 1989).

It has been postulated (Truswell *et al.*, 1987) that several of these elements (Olacaceae, Sapindaceae, Myrtaceae) may have been introduced to northern Australia using "stepping stones" from southeast Asia. Whilst this route is not supported by the pollen record for the Olacaceae and Sapindaceae, it should not be dismissed for the Myrtaceae. In addition to Campanian-Maastrichtian records from the Antarctic Peninsula, pollen of the Myrtaceae occur in the Santonian of Gabon, Maastrichtian of Colombia, and the Senonian of Borneo (Muller, 1981). Migration from the north does not conflict with the pollen record, but there is only meagre evidence for "stepping stones" between Borneo and northern Australia in latest Cretaceous times (Audley-Charles, 1990). Knowledge of Upper Cretaceous palynofloras from northern depositional basins of Australia will be important in elucidating whether floral exchange occurred between Southeast Asia and northern Australia during the Late Cretaceous, and may resolve whether or not "Sundaland" was offshore from Australia as suggested by Tarling (1990).

The pollen record firmly establishes that several important elements of present-day austral floras were established in southern areas by the close of the Cretaceous (Text-figure 2). Most were derived from Gondwanic stock; some evolved in northern Gondwana, and others in the Austro-Antarctic region. Many of the taxa are now associated in rainforests, but several (*Adenanthos, Stirlingia*, and some epacrids) are restricted to nutrient-deficient soils in the Mediterranean climatic region of southern Australia. Thus, the pollen record implies that sclerophylly in the Australian vegetation dates to the latest Cretaceous.

The Australasian-Antarctic-southern South American Late Cretaceous vegetation was strongly regionalised within the same latitudinal belt and across the latitudes (Text-figure 1c, d). The Proteaceae appears to have been important in the central Australian vegetation, but at higher southern latitudes (60-65°S) in southern Australia both podocarps and Proteaceae were well represented in the canopy of the open-forests (Text-figure 1d; Specht *et al.*, in press). Understorey to the forests included shrubby Proteaceae, Winteraceae, Trimeniaceae, and *Ilex*, as well as a ground stratum of diverse ferns. Temperature regimes in southeastern Australia were warmer (mean annual temperature 16.5-22°C) than at similar high latitudes in New Zealand (15-18°C) where canopy taxa of the open-forests were mostly podocarps, and the proteaceous understorey taxa less diverse. The Antarctic Peninsula was also situated at 60-65°S, but temperatures were even cooler (11-13°C) than those of southern Australia and New Zealand. Podocarps and *Nothofagus* were the major canopy taxa of the western Antarctic tall open-forests (Text-figure 1d), and the Proteaceae was less diverse than in Australasia (Specht *et al.*, in press). Moreover, the Antarctic forests contained myrtaceous taxa and were associated with wetland communities of sphagnalean mosses and salviniaceous ferns (Askin, 1990); these wetland communities were poorly represented in southern Australasia. *Nothofagus* and podocarps also occurred in southern South America and on the Falkland Plateau (Dettmann & Thomson, 1987). Palynofloras from these areas are incompletely documented, but available evidence suggests substantial representation of an angiosperm element that was rare or absent in other southern Gondwanan regions (Dettmann & Thomson, 1987).

Although southern South Africa was separated from adjacent land masses of southern Gondwana by the South Atlantic Ocean after the mid-Cretaceous, latest Cretaceous-Palaeocene palynofloras contain pollen of podocarps (*Podocarpus-, Microcachrys-* and *Dacrydium*-types), *Gunnera*, and several proteaceous taxa, including possible *Telopea/Embrothium* (McLachlan & Pieterse, 1978; Scholtz, 1985). Podocarps were established in the flora during Jurassic-Early Cretaceous times, and *Gunnera* probably migrated to the region from the north contemporaneous with radiation to other high southern latitudinal regions (Jarzen & Dettmann, 1990). The presence of *Telopea/Embrothium*, pollen of which is also known from the Late Cretaceous of southern South America and Australia (Dettmann & Jarzen, 1991), also implies evolution of one or both taxa in northern latitudes of Gondwana.

Indian latest Cretaceous palynofloras also contain podocarp and araucarian pollen, but the angiosperm component contains diverse palm pollen characteristic of coeval palynofloras of the northern Gondwanan region (Text-figure 2). Also represented are occasional Normapolles-type pollen (Nandi, 1990), which imply links with southern Laurasia near the end of the Cretaceous.

CONCLUSIONS

It is evident that the southern Gondwanan vegetation was floristically heterogeneous throughout the Cretaceous. Much of the area was forested, but woodlands, heathlands, and aquatic communities were also represented. The high latitude forests had an open structure and podocarps and araucarians were important canopy components. Understorey communities fringing and associated with the earliest Cretaceous forests were invaded by herbaceous and shrubby angiosperms during the latest Barremian-Aptian, and by the Santonian angiosperms had entered the canopy. Australia occupied a peripheral position in the southern Gondwanan assembly, and routes traversed by the earliest angiosperm invaders from northern Gondwana probably involved other landmasses in the assembly rather than Southeast Asia. The first migratory wave of magnoliid angiosperms into southern Gondwana occurred no later than the latest Barremian, and was coincident with lowered world sea levels, and early opening of the South Atlantic and Indian oceans.

Invasion of non-magnoliid angiosperms to the Austro-Antarctic assembly occurred during Middle Albian-Cenomanian times, well after India had severed its connections and drifted north (Text-figure 1b). Migration to Antarctica and Australia was via southern South America, whereas the non-magnoliid dicotyledons appear to have migrated to India during the Aptian, and routes may have involved Madagascar (Text-figures 1b, 2). Angiosperm migration along these separate routes continued during Turonian-Maastrichtian times. In high latitudinal areas there was *in situ* evolution and differentiation of austral groups in the Australian-Antarctic region. Two loci of evolution and diversification have been identified (Text-figures 1, 2). Areas surrounding the embryonic Southern Ocean was a diversification centre of the Proteaceae and may have been the cradle of *Ilex*. The diametrically opposite region embracing southern South America and the Antarctic Peninsula was a diversification centre of early *Nothofagus* during phases of volcanic and tectonic activity.

The pollen evidence counters Takhtajan's (1969, 1987) arguments that Australia was an origination centre for early angiosperms, and supports thesis of Webb *et al.* (1986) that Australian rainforests are remnants of a heterogeneous Gondwanan flora (Pl. 1, figs 1-20). Several of the proteaceous rainforest elements with a Cretaceous history are today concentrated in northeastern Australasia under

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PLATE 1

All photomicrographs × 1000. Locality and repository details are provided in references cited in explanations.

1. *Ascarina*-type; *Clavatipollenites* sp. of Dettmann 1973 (Dettmann, 1973).
2. cf. *Hedyosum*-type; *Asteropollis asteroides* Hedlund & Norris 1968 (Dettmann, 1973).
3. *Belliolium/Bubbia*-type; *Pseudowinterapollis wahooensis* (Stover) Mildenhall 1979 (Dettmann & Jarzen, 1990).
4. *Trimenia*-type; *"Polyporina" fragilis* Harris 1965 (Dettmann & Jarzen, 1990).
5. *Gunnera*-type; *Tricolpites reticulatus* Cookson ex Couper 1953 (Jarzen & Dettmann, 1989).
6. cf. Platanaceae-type; *Tricolpites minutus* (Brenner) Dettmann 1973 (Dettmann, 1973).
7. *Nothofagus* (ancestral)-type; *Nothofagidites senectus* Dettman & Playford 1968 (Dettman & Playford, 1968).
8. *Nothofagus* (*Menziesospora*)-type; *Nothofagidites asperus* (Cookson) Romero 1973 (Dettmann & Thomson, 1987).
9. *Clematis*-type; *Tubulifloridites lilliei* (Couper) Farabee & Canright 1986 (Dettmann & Thomson, 1987).
10. *Ilex*-type; *Ilexpollenites* sp. cf. *I. anguloclavatus* McIntyre 1968 (Dettmann & Jarzen, 1990).
11. Epacridaceae-type; *Ericipites scabratus* Harris 1965 (Dettmann & Jarzen, 1990).
12. Myrtaceae-type; *Myrtaceidites eugeniioides* Cookson & Pike 1953 (Dettmann & Thomson, 1987).
13. *Callitriche*-type; *Australopollis obscurus* (Harris) Krutzsch 1966 (Dettmann & Jarzen, 1990).
14. cf. Proteaceae-type; *Triorites punctulatus* Dettmann 1973 (Dettmann, 1973).
15. *Persoonia*-type; *Proteacidites* cf. sp. A of Hill & Macphail 1983 (Dettmann & Jarzen, 1991).
16. *Beauprea*-type; *Beaupreaidites elegansiformis* Cookson 1953 (Dettmann & Jarzen, 1988).
17. *Macadamia*-type; *Propylipollis* sp. cf. *P. crassimarginus* Dudgeon 1983 (Dettmann & Jarzen, 1990).
18. *Knightia*-type; *"Proteacidites" amolosexinus* Dettmann & Playford 1968 (Dettmann & Playford, 1968).
19. *Grevillea*-type; *Proteacidites* sp. 2 of Dettmann & Jarzen 1991 (Dettmann & Jarzen, 1991).
20. *Telopea*-type; *Triporopollenites ambiguus* Stover 1982 (Dettmann & Jarzen, 1991).

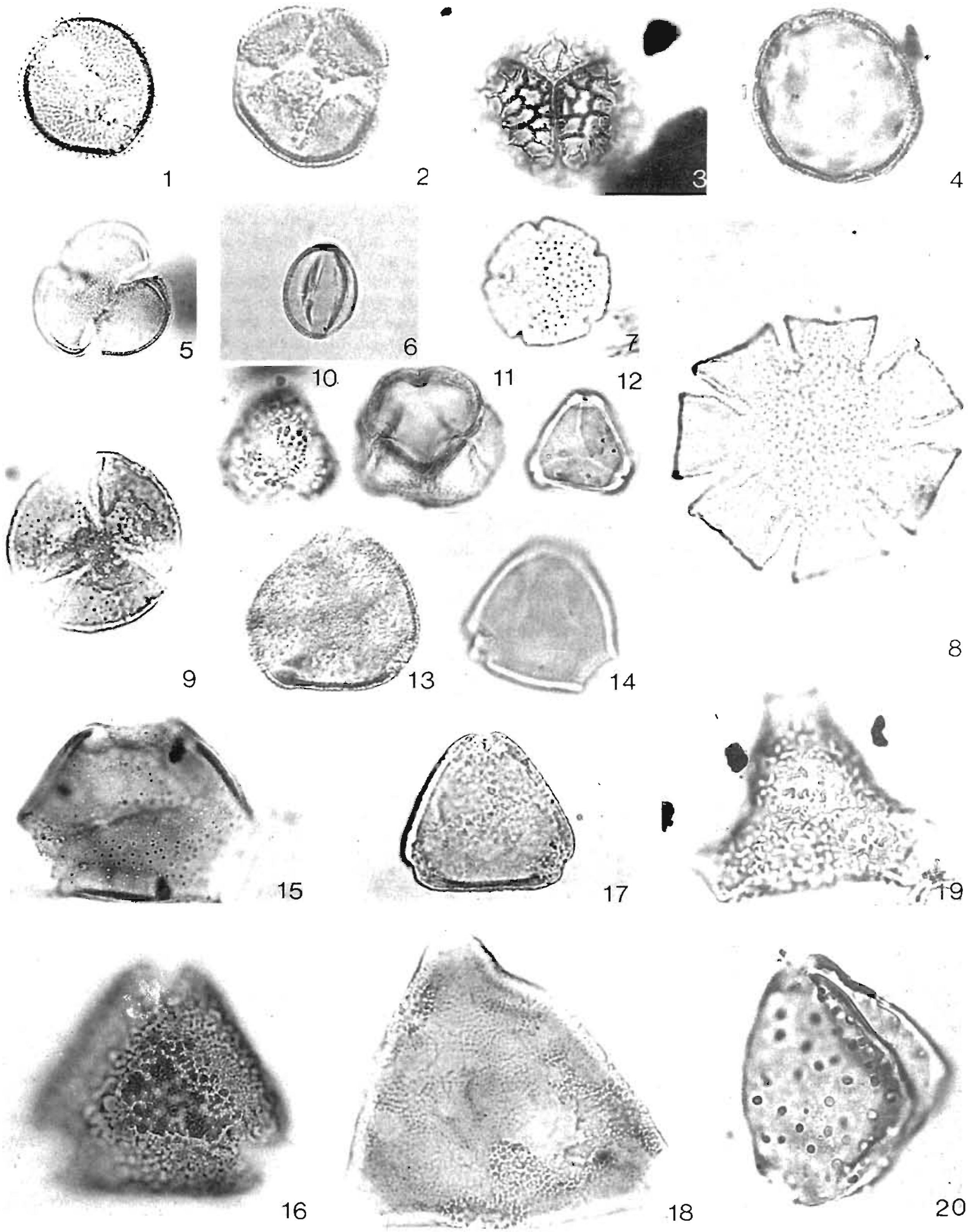

PLATE 1

temperate climates similar to those adduced for the Late Cretaceous in their likely cradle region in southern Australia. *Nothofagus* and possibly some of the podocarps differentiated in cooler climates which is to some extent reflected by their present distribution at higher latitudes and/or altitudes. Evidence for evolution of sclerophylly is also expressed in the Late Cretaceous pollen record of Australia. The sclerophyllous taxa probably formed communities on low nutrient or waterlogged soils on forest fringes (Specht *et al.*, in Press).

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