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Section 3: The Flora

Evolution of the Australian Flora:
Fossil Evidence

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EVOLUTION OF THE AUSTRALIAN FLORA: FOSSIL EVIDENCE

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Evolution of life in the Precambrian

The Precambrian accounts for a large proportion of the history of the Earth and incorporates most, if not all, of the major evolutionary events in the history of life (Fig. 56). It was the time of the origin of life itself, photosynthesis (and later oxygenic photosynthesis), eukaryotic organisation, and multicellular (including megascopic) life. By the close of the Precambrian, algal life was relatively well developed, and may even have made the transition to a terrestrial existence between 2200 and 1800 million years ago, as soon as the ozone shield was well-established (Beeunas & Knauth, 1985).

The origin of life

Australia is an ancient continent, and has an excellent Precambrian record. Some of the events mentioned above are recorded in Australian Precambrian sedimentary rocks. The time of the origin of life is still very uncertain, but it seems reasonable to assume that the only early constraint (excluding an extraterrestrial source for life) is the Earth's attainment of a solid crust and liquid water. That the Earth had a solid crust by 4275 million years ago is shown by the discovery of detrital zircon crystals of that age from the Jack Hills Metasedimentary Belt of Western Australia (Compston & Pidgeon, 1986). It has long been argued that catastrophic meteorite bombardment probably prevented the long term establishment of life until about 3900 to 3850 million years ago. This argument claims that before this time the formation of 1000 km diameter craters released so much energy that the oceans would have been repeatedly vaporised and the planet sterilised (Chyba, 1993). Therefore, although life could have existed from the time of a solid crust, about 4275 million years ago, extant life, which is almost certainly the result of a single origin, might represent a more recent event, postdating 3900 to 3850 million years ago.

The young age constraint on the origin of life is also in dispute. Living organisms differentially assimilate stable carbon isotopes, hence $^{12}C/^{13}C$ ratios differ between carbonaceous material of biological and non-biological origin. There is some carbon isotopic evidence for the existence of autotrophic life at 3800 million years, but these data come from strongly metamorphosed rocks in Greenland and are widely considered to be unreliable, since carbon isotopes are reset during high-grade metamorphism and the correction factors necessary to readjust data to original values are poorly established (Schopf, 1983; Schopf & Klein, 1992). Thus in order to be certain about a young age constraint on the origin of life it is necessary to look for the oldest mildly metamorphosed rocks. Low grade greenstones in the Pilbara Craton in Western Australia, approximately 3500 million years old, seem to have accumulated on crust that was already rigid, cool and buoyant (Buick *et al*., 1995). These rocks have only ever been heated to approximately 350–400°C, a temperature at which carbon isotopic data are still reliable. These rocks may prove critical to constraining the origins of life on Earth, since they can be tested for evidence of the characteristic fractionation imparted by autotrophic carbon fixation (R.Buick, *pers. comm*.).

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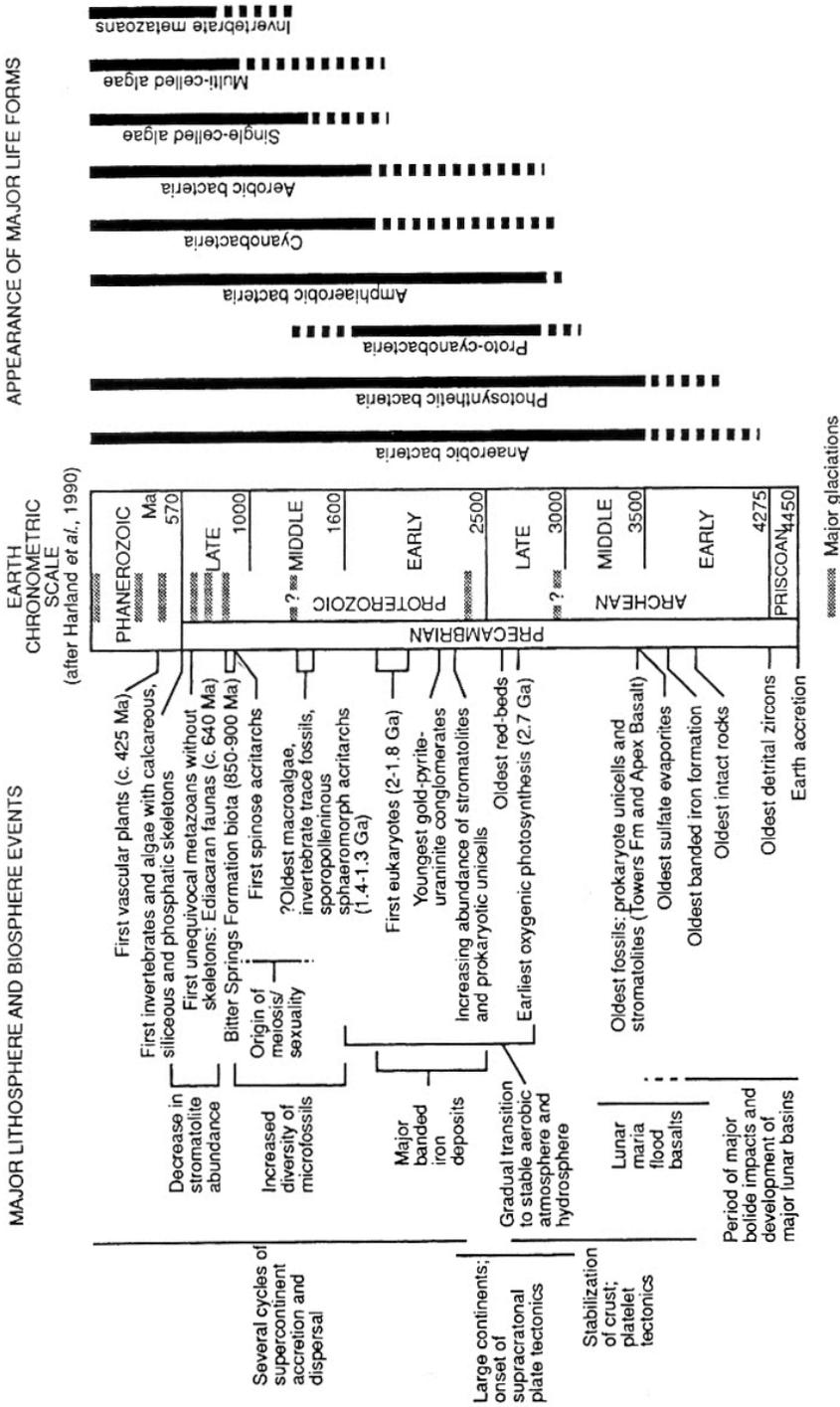[4] Botany Department, University of Queensland, St Lucia, Queensland 4067.

Figure 56. Major biological and geological events in early Earth history (modified from Schopf *et al.* 1983).

Photosynthesis

The earliest evidence for photosynthetic life is found in Australia and is dated at 3460 million years ago. Filamentous microfossils have been found in the Pilbara region (within the Towers Formation and Apex Basalt of the Warrawoona Group) that resemble cyanobacteria, although they also resemble non-photosynthetic gliding bacteria, so their morphology is not definitive (Schopf, 1992). Nevertheless, Schopf considered that these microfossils meet the three tests required to confirm the presence of early life: they are not contaminants, the geologic source of the rocks is known with certainty, and they are definitely the remains of ancient organisms rather than being, for example, 'biologic-shaped' mineral grains. Numerous different types of fossil filaments have been discovered in the Pilbara cherts, and their morphology matches that of living prokaryotic organisms very closely.

Stronger evidence for photosynthesis comes from stromatolites, dome-shaped sedimentary structures built up by phototropic micro-organisms. Stromatolites are the least controversial evidence of early life, since they are still extant today, with perhaps the best known examples occurring not far from the earliest fossils at Shark Bay in north-western Australia. Walter *et al*. (1980) described stromatolites from North Pole in north-western Australia (Warrawoona Group) that are between 3460 and 3520 million years old. These represent the oldest substantial evidence for life in the fossil record to date, although Schopf (1992) noted that the absence of micro-organisms with cellular preservation, while not surprising, leaves open the possibility of a non-biological origin. Although Walter *et al*. (1980) stressed that the presence of these stromatolites did not confirm the presence of oxygen-producing photosynthesis, they are associated with sedimentary sulphate minerals, which, given the reduced or neutral composition of the early atmosphere, can only have been produced as by-products of photosynthesis, either oxygenic or sulphur-oxidising (R.Buick, *pers. comm.*). The composition of the atmosphere during this time is still uncertain, since many recent attempts at modelling it suggest that it contained low levels of oxygen (Schopf, 1983).

In extremely ancient rocks it is impossible to tell what kind of photosynthesis was operating, and it is not until approximately 2715 million years ago that there is clear evidence of oxygenic photosynthesis of the type now employed by plants. This evidence also comes from the Pilbara region of Western Australia. There, in stromatolites that clearly grew within saline lakes, there is an odd succession of evaporite minerals that indicate sedimentary sulphate was not one of the by-products of photosynthesis. This leaves only oxygenic photosynthesis as the primary source of carbon fixation for the local biota (Hayes *et al*., 1983; Buick, 1992).

Eukaryotic organisation

All fossilised life forms from the early part of the Precambrian (Archean) are accepted as being prokaryotic, i.e. non-nucleated bacteria and cyanobacteria or their extinct relatives. A major step in the evolution of life was that from the prokaryotic to the eukaryotic condition, in which cells have a membrane-bound nucleus and organelles. This was a profound evolutionary event, allowing for the later appearance of all multicellular organisms. It is now generally accepted that the origin of eukaryotes involved the ingestion but not digestion of one set of prokaryotes by another, leading to such elegant symbioses that the process has only recently been widely recognised (Margulis & Sagan, 1986) after first being suggested early this century (Wallin, 1927).

The time of origin of eukaryotic organisation is difficult to determine, since the earliest eukaryotes were presumably simple unicells, similar in size and shape to co-occurring prokaryotes. The profound difference was the presence of membrane-bound organelles in the former, but recognition of this feature in fossils is problematic at best. Early eukaryotes can therefore only be determined with confidence in the fossil record if they had evolved substantially away from their prokaryotic ancestors. There is some indirect evidence to constrain the earliest appearance of eukaryotes. Most of them are strict aerobes, and thus it seems unlikely that they would have been widespread prior to the appearance of a global aerobic environment, somewhere between 1850 and 2200 million years ago (Holland & Beukes, 1990). The evidence for a transition from anaerobic to aerobic conditions during the

Palaeoproterozoic, about 2000 million years ago, derives chiefly from sedimentological features. Uraninite (UO_2) and pyrite (FeS_2) are common detrital components of Archean sedimentary rocks, but under oxidising conditions these minerals rapidly break down and are rare after the early part of the Proterozoic and in younger sediments. Conversely, terrestrial red-beds rich in haematite (Fe_2O_3) develop under oxidising conditions and are widespread only in post-Palaeoproterozoic sedimentary sequences. Banded iron formations contain a large proportion of haematite and formed predominantly around 2500–1800 million years ago, the period that probably corresponded to the transition to a consistently oxidising atmosphere (Fig. 56). Significantly, the abundance of stromatolites in the fossil record increases markedly in the Early Proterozoic (around 2300 million years ago).

Living spheroidal cyanobacteria, the largest coccoid prokaryotes, are generally less than 10 μm in diameter, although a few species are as large as 60 μm (Schopf, 1992). In contrast, living eukaryotic microalgae tend to have much larger cells, and thus there is a clear cell size differential apparent today which can be used to infer the cell type of fossils. According to Schopf (1992), the size range of fossil coccoid cells detected thus far in the early Proterozoic shallow-water stromatolitic units are within the prokaryotic size range, and thus probably do not include eukaryotes. However, offshore (deeper water) shales contain much larger cells, including possible eukaryotes, by 2000 million years ago, and assured eukaryotes by 1800 million years ago. According to Knoll (1992), these simple, spheroidal microalgae constitute the oldest evidence yet detected of the eukaryotic cell type.

Diverse types of planktonic, eukaryotic microalgae are now known from the later Proterozoic, but their exact biological relationships are unknown. For this reason, they are known as acritarchs, from the Greek *akritos* = doubtful, and *arche* = origin (Traverse, 1988). Relatively small sphaeromorph acritarchs (between 60 and 200 μm in diameter) are abundant from the Mesoproterozoic onwards, but truly large sphaeromorphs, more than a millimetre in diameter, are typical only of the Neoproterozoic, from about 1000 to about 675 million years ago (Zang & Walter, 1989, 1992; Schopf, 1992). The reason for the rise to prominence and subsequent decline of acritarchs is not yet fully understood. However, environmental fluctuations associated with extensive Late Proterozoic glaciations, competition from other newly emerging algal groups, and predation resulting from marked diversification of heterotrophic organisms towards the close of the Proterozoic were probably all significant factors influencing acritarch abundance (Fig. 56).

Precambrian rocks that are critical to our understanding of the evolution of eukaryotic life occur in the approximately 800 million year old Bitter Springs Formation of central Australia (Schopf, 1968; Schopf & Blacic, 1971; Oehler, 1976; Taylor & Taylor, 1993). Thirty taxa of microfossils have been described from these extraordinary cherts, including cyanobacteria, fungus-like filaments which are probably cyanobacterial sheaths, and possible Pyrrophyta and spheroidal green algae in which nuclear residues, pyrenoid-like bodies and other cellular structures were considered to have been cytologically preserved (Schopf, 1968). However, the identification of preserved organelles in these microfossils continues to generate controversy (Taylor & Taylor, 1993), with most workers now regarding these intracellular structures as remnants of degraded cytoplasm (Knoll & Barghoorn, 1975).

Multicellular life

The transition from unicellular to multicellular life clearly represents a critical phase in the evolution of both plant and animal life, although multicellularity is not restricted to those organisms. However, the fossil record is, at present, unhelpful in interpreting this transformation, and we are left to rely on several well-presented, but largely untested, hypotheses for this very significant transition. The fossil record contains quite a number of Precambrian multicellular fossils, the oldest certain example being of a bangiophyte red alga from Canada, about 1260 to 950 million years old (Butterfield *et al*., 1990). However, impressions of a possible multicellular brown alga like *Hormosira* have been found in Mesoproterozoic rocks of the Bangemall Group of Western Australia (Grey & Williams, 1990) and compressions of megascopic, possibly multicellular algae have recently been found in 2100 million year old rocks from Minnesota (Han & Runnegar, 1992). At timescales

of 750 to 700 million years ago a wide range of multicellular organisms are found in the Svanbergfjellet Formation of Spitsbergen, including simple coenocytic and coenobial forms, and truly multicellular forms showing significant cellular differentiation (Butterfield *et al*., 1994).

Relevant to the evolution of multicellularity in plants is the recent reinterpretation of the Ediacaran 'fauna' by Retallack (1994). The Ediacaran fossils, originally described from Ediacara in central South Australia, but now known from several localities around the world, have usually been interpreted as multicellular animals of varying affinities, and no doubt many of them are. However, Retallack (1994) has hypothesised that some of the organisms may in fact have been lichens, and as such had at least some eukaryotic algal component. This interpretation is controversial (Waggoner, 1995), and it is too early to determine whether it will have a lasting impact. However, it offers an interesting alternative to our current view of Precambrian life, since some of the Ediacaran organisms were up to one metre in diameter and were clearly multicellular. The proposition of a Precambrian landscape dominated by lichens of this type offers a foreign view to even the most creative of earlier hypotheses regarding the Precambrian landscape. It is certainly probable that some of the Ediacaran organisms were photosynthetic and Margulis & Sagan (1995) concluded that some of the later Ediacaran organisms were probably protoctists that photosynthesised in shallow seas.

It is certain that life diversified rapidly in aquatic environments beyond the end of the Precambrian. Multicellular algae, including some calcium carbonate-secreting (now known to occur in the latest Proterozoic; Horodyski & Mankiewicz, 1990; Grant *et al*., 1991) and reef-building forms, became common components of the marine realm. The next part of the evolutionary picture of major relevance to the terrestrial flora of Australia was the development of a land flora. It is probable that mosses and liverworts were an important part of the early land flora (Taylor & Taylor, 1993), but their fossil record in Australia is poor. The discussion here concentrates on the vascular land plants.

Australian early terrestrial floras (Silurian to Jurassic)

The pre-angiosperm floras of Australia are intimately linked to those of other Southern Hemisphere continents to which Australia was connected throughout most of the Palaeozoic and Mesozoic. Both changing continental positions and fluctuating global and regional climates are reflected in varying degrees of endemism or the cosmopolitan aspect of the floras through time. On several occasions through the late Palaeozoic and Mesozoic, gradual environmental change was punctuated by episodes of very rapid change, reflected in the plant fossil record by major extinction and radiation events.

Our knowledge of the succession of Australian floras is based on studies of plant macrofossils, palynomorphs (principally spores, pollen and algal cysts) and, to a lesser extent, the diversity and morphological characteristics of animals which fed on these plants (e.g. the increase in the proportion of grazing marsupials in the Late Tertiary and Quaternary suggests a response to a shift from closed to open forest and grassland vegetation in many areas). The plant macrofossil record is heavily biased towards plants growing in lowland environments, especially those areas experiencing rapid subsidence. This appears to be especially the case for pre-Tertiary floras. Wind and aqueous transport of spores and pollen from plants growing in non-depositional settings has ensured that in most cases a more complete picture of regional plant diversity can be gained from palynological studies. Palynomorphs also generally have the advantage of being preserved in a greater range of depositional environments, including marine settings. Nevertheless, problems remain with interpretations of the palynological record including the uncertain affinities of many spore-pollen groups in pre-Tertiary strata, the problem of excessive taxonomic splitting, and uncertainties surrounding the infraspecific morphological variation of spores and pollen produced by ancient plants.

Invasion of the land: the Late Silurian – Early Devonian Baragwanathia flora

The earliest vascular plants probably appeared during the late Early Silurian (Edwards & Fanning, 1985) based on records of fossilised dispersed spores and sporangia and small dichotomous axes with strengthening tissues. Reports of vascular plants from earlier periods based on dispersed spores, cuticles, or tracheid-like tubes (Richardson, 1985; Taylor, 1988) are less convincing, as these remains may be derived from algae or bryophytes. The earliest land plants preserved in Australia occur in Upper Silurian to Lower Devonian shallow marine sediments of Victoria. This flora contains a range of simple vascular plants assignable to the Rhyniophyta, Zosterophyllophyta, Trimerophyta, and Lycophyta. The flora is named after its most prominent element: the lycopod *Baragwanathia* (Fig. 57). Australia occupied equatorial latitudes during the mid-Palaeozoic (Smith *et al.*, 1981) and records of early vascular plants outside Australia are also mostly recorded from low palaeolatitudes (Edwards & Fanning, 1985; Scotese & McKerrow, 1990), suggesting a tropical origin for land plants.

The age of the Baragwanathia flora has attracted some controversy, due firstly to the relatively 'advanced' morphology of *Baragwanathia* contrasting with its occurrence in sediments of such apparent antiquity, and secondly due to uncertainties over the age of the associated marine fauna (Garratt, 1978, 1981; Edwards *et al.*, 1979; Hueber, 1983; Garratt *et al.*, 1984). A Late Silurian (Ludlovian) age for the oldest Victorian fossil floras now appears most probable, based on reassessment of the biostratigraphic range of the associated graptolite species (Garratt *et al.*, 1984).

Baragwanathia is the most robust plant in the Victorian assemblages and probably attained heights of up to 1 m, with axes up to 5 cm wide. Most of the preserved axes were probably transported subaerial portions of the plant (some bearing clusters of sporangia), but a few may represent prostrate or subterranean rhizomes.

Rhyniophytes like *Yarravia*, *Hedeia* and *Salopella* represent the simplest plants in the assemblage and are characterised by short unbranched or dichotomising leafless axes bearing simple terminal or subterminal sporangia (Tims, 1980; Tims & Chambers, 1984). Rhyniophytes now have uncertain phylogenetic status and may include many taxa with bryophytic affinities (Taylor, 1988). Zosterophyllophytes (represented by *Zosterophyllum*) show mainly simple dichotomous, or sometimes pseudomonopodially-branched axes, often with terminally aggregated reniform sporangia. Some zosterophyllophytes had simple spine-like enations on the axes and shared several other features in common with the lycophytes to which they are generally regarded as closely related (Taylor & Taylor, 1993).

Trimerophytes were generally more robust than rhyniophytes and zosterophyllophytes, and displayed more complex pseudomonopodial or monopodial branching patterns, circinnate vernation, and recurved sporangia clustered on the terminal axes. Spindle-shaped sporangia, sometimes attached to fragmentary, dichotomously branched axes assigned to *Dawsonites* (of presumed trimerophyte affinities) are common within the Victorian Upper Silurian to Lower Devonian deposits (Tims & Chambers, 1984).

All plants in the Baragwanathia flora were herbaceous and probably occupied moist habitats because they undoubtedly required the presence of an aqueous environment for gamete exchange. The relatively complete preservation of many of the plant macrofossils and their frequent association with marine graptolites in the Victorian strata suggest that these plants were growing in coastal areas, perhaps in low herbfield communities along river flats and delta swamps (Tims, 1980). Various thalloid fossils are co-preserved with vascular plants of the Baragwanathia flora, but a lack of diagnostic features generally inhibits their assignation to particular algal groups.

The first trees: the Middle Devonian to Early Carboniferous lycophyte flora

Late Emsian or early Eifelian to Frasnian (late Early to early Late Devonian) plant assemblages record the first appearance of shrub- to tree-sized lycophyte floras in Australia and Antarctica which at that time were contiguous landmasses (Walkom, 1928; Gould, 1975; Truswell, 1991; McLoughlin & Long, 1994). The late Early and Middle Devonian floras were mostly dominated by herbaceous to shrub-sized lycophytes attributed to *Haplostigma*,

Leclercqia, *Archaeosigillaria* and *Protolepidodendron*. Trimerophytes, early sphenophytes, and some plants of uncertain affinities (e.g. *Praeranunculus*) were probably also significant components of these floras. By the end of the Devonian (Famennian) some lycophytes (e.g. *Leptophloeum*) had attained the structure of tall trees (perhaps up to 20 m) and were colonists of lowland floodplains and coastal environments (Gould, 1975). As almost all elements in the Late Devonian floras probably relied on free water for transfer of their motile gametes, it is likely that large tracts of upland and drier habitats remained poorly- or un-vegetated.

Leptophloeum, the dominant element of the Late Devonian floras (Fig. 57), persisted into the Early Carboniferous and may have at least partly occupied strandline environments, based on the presence of log impressions often found associated with marine invertebrate fossils (Wyatt & Jell, 1967). Riverine transport to the marine environment and deposition as driftwood may also account for the co-preservation of these terrestrial and marine biotas. Apart from *Leptophloeum*, the Australian Late Devonian to Early Carboniferous floras contained a number of herbaceous, shrub-sized and arborescent lycophytes generally assigned to *Protolepidodendron*, *Ulodendron* and *Lepidodendron*. Species and genera of Devonian lycophytes are principally distinguished by differences in leaf morphology, shape and arrangement of leaf scars, and the arrangement of the vascular trace and parichnos scars on the plant axes. Relatively few detailed studies have been carried out on Australian floras of this age and most of the recognised genera were initially described from the Northern Hemisphere. Although Devonian floras do show a cosmopolitan aspect at higher taxonomic levels (Meyen, 1987), it is anticipated that future detailed studies of the Australian floras will show a greater degree of endemism at species level than is currently recognised.

The arborescent habit was mostly attained in lycophytes by the production of thick-walled periderm cells via secondary growth in the outer cortex. Some secondary growth was also achieved in the vascular tissue of arborescent lycophytes, but the thick cortical tissues appear to have been the chief means of physical support. This contrasts with arborescent progymnosperms and seed plants, which appeared at about the same time (progymnosperms in the Middle Devonian, 'seed-ferns' in the Late Devonian), and relied largely on secondary xylem tissue production for physical support. Ultimately, the use of secondary vascular tissue for support, together with improved vascular transport pathways, more elaborate leaf and branch modifications, and more sophisticated reproductive strategies, probably gave gymnosperms a competitive advantage in most terrestrial environments. Following Permian aridification in the Northern Hemisphere and glaciation in the Southern Hemisphere, the lycophytes appear never to have regained the stature of tall trees, although some pleuromeian lycophytes may have reached a few metres in height during the Triassic (Retallack, 1975).

A few zosterophyllophytes (*Barinophyton*) and rhyniophytes (*Taeniocrada*) appear to have persisted into the Australian Late Devonian floras but became increasingly overshadowed by new elements including sphenophytes (*Archaeocalamites*), ferns (*Adiantites*), and progymnosperms (?*Archaeopteris*) (Dun, 1897; White, 1986). Relatively diverse assemblages of cavate and acavate trilete spores preserved in Australian Devonian sequences also indicate the establishment of substantial lycophyte, fern, and sphenophyte communities during this period (Balme, 1962; Balme & Hassell, 1962; Playford, 1976; Grey, 1992).

Australian Middle and Late Devonian floras are generally considered to reflect warm conditions. Lycophyte axes from these floras typically do not show seasonal fluctuations in the size and arrangements of leaf scars, suggesting fairly uniform conditions throughout the year. Palaeomagnetic data indicate that Australia occupied low to middle southern latitudes in the Late Devonian (Embleton, 1984). Development of stromatoporoid- and coral-dominated reefs in north-western and eastern Australia, high marine invertebrate diversities, and development of red-beds and evaporites in central and north-eastern Australia are also evidence for the prevalence of warm climates (Wyatt & Jell, 1967, 1980; Quilty, 1984). Although terrestrial plant life was well-established by Late Devonian times, the only coals of this period are thin coaly laminae preserved in the Amadeus Basin of central Australia (Playford *et al.*, 1976).

While reefal limestones continued to accumulate in the north-west of the continent during the Early Carboniferous, Australia shifted towards higher latitudes and marine faunas from the south-east of the continent show a reduction in diversity probably corresponding to the onset of cool-water conditions. Terrestrial floras of the Early Carboniferous continued to be dominated by lycophytes, but evidence of more seasonal conditions is reflected in pronounced regular growth increments on the axes of these plants (Morris, 1980). Typical Late Devonian species were progressively replaced through the Early Carboniferous by a range of new lycophyte taxa, of which *Bumbudendron queenslandii* is one of the most prominent. Other Early Carboniferous plants included sphenophytes (*Archaeocalamites*), zygopterid ferns (*Austroclepsis*), and the first Australian seed-producing plants (*Nothorhacopteris*) of probable calamopityalean or callistophytalean affinities.

Carboniferous sedimentary sequences of North America and Europe incorporate thick coal deposits derived largely from lycophytes, sphenophytes, cordaitaleans, and medullosan seed-ferns. Extensive development of mire forests and the resulting large quantities of organic matter locked up in coal deposits probably induced marked changes in the proportions of O_2 and CO_2 in the atmosphere (Fig. 57) which in turn may have strongly influenced global climates. While some thin Carboniferous coals exist in eastern Australia (Rattigan, 1964), coal measure development was not nearly as pronounced as in the Northern Hemisphere. The dearth of Gondwanan coals probably relates to both unfavourable climates for development of persistent swamp communities (especially in the Late Carboniferous) and unfavourable geological settings for the accumulation of thick terrestrial sequences.

The first crisis: the Late Carboniferous to Early Permian Gondwanan glaciation

Between the Silurian and Permian periods Australia shifted from equatorial to near-polar latitudes (Embleton, 1984) (Fig. 57). This latitudinal shift was marked by dramatic climatic transformations and corresponding changes in the terrestrial flora. While Early Carboniferous floras contain lycophytes similar to those of the preceding Devonian period, Mid- to Late Carboniferous times saw a waning of the lycophyte floras and their replacement by low-diversity floras dominated by seed-ferns. Seed-ferns (also known as pteridosperms) were a polyphyletic group of plants which produced fern-like foliage but retained the megagametophyte stage upon the dominant sporophytic plant and encased their ovules in seeds. Seed-ferns also typically displayed some degree of secondary growth in their vascular tissues. Some seed-ferns (e.g. Calamopityales, Callistophytales) were probably derived from progymnosperm groups, some (e.g. Medullosales) shared affinities with cycadophytes, others (e.g. Glossopteridales) were probably related to conifers, cordaitaleans and ginkgophytes, while some Mesozoic representatives (e.g. Corystospermales, Bennettitales, Caytoniales) were possibly sister groups to the anthophytes (Crane, 1985; Meyen, 1987).

By the later part of the Early Carboniferous (late Visean or Namurian times), plants bearing pinnate *Nothorhacopteris* foliage dominated the Australian floras (Fig. 57). During the Late Carboniferous (Westphalian–Stephanian) *Nothorhacopteris* was replaced successively by *Fedekurtzia* and *Botrychiopsis* (Morris, 1980; Retallack, 1980) (Fig. 57). *Nothorhacopteris*, *Fedekurtzia*, *Botrychiopsis* and some less-common elements in the Late Carboniferous floras (e.g. *Cyclopteris* of Rigby, 1973) all share a basic pinnate or bipinnate frond morphology with gently divergent dichotomous venation in their pinnules, and are probably closely related. The botanical affinities of these plants are not yet clear, as convincing associated fructifications are yet to be found. Nevertheless, the Australian forms show strong similarities in their sterile foliage to Northern Hemisphere taxa attributed to both progymnosperms like the Archaeopteridales and seed-ferns like the Calamopityales and Callistophytales (Meyen, 1987). The *Nothorhacopteris-Fedekurtzia-Botrychiopsis* complex appears to have developed with the onset of cool climatic conditions in the mid-Carboniferous, reached its greatest abundance and diversity during the Late Carboniferous immediately prior to extensive Gondwanan glaciations, and persisted as minor elements (*Botrychiopsis* and *Bergiopteris*) within the succeeding *Glossopteris* flora until at least mid-Permian times.
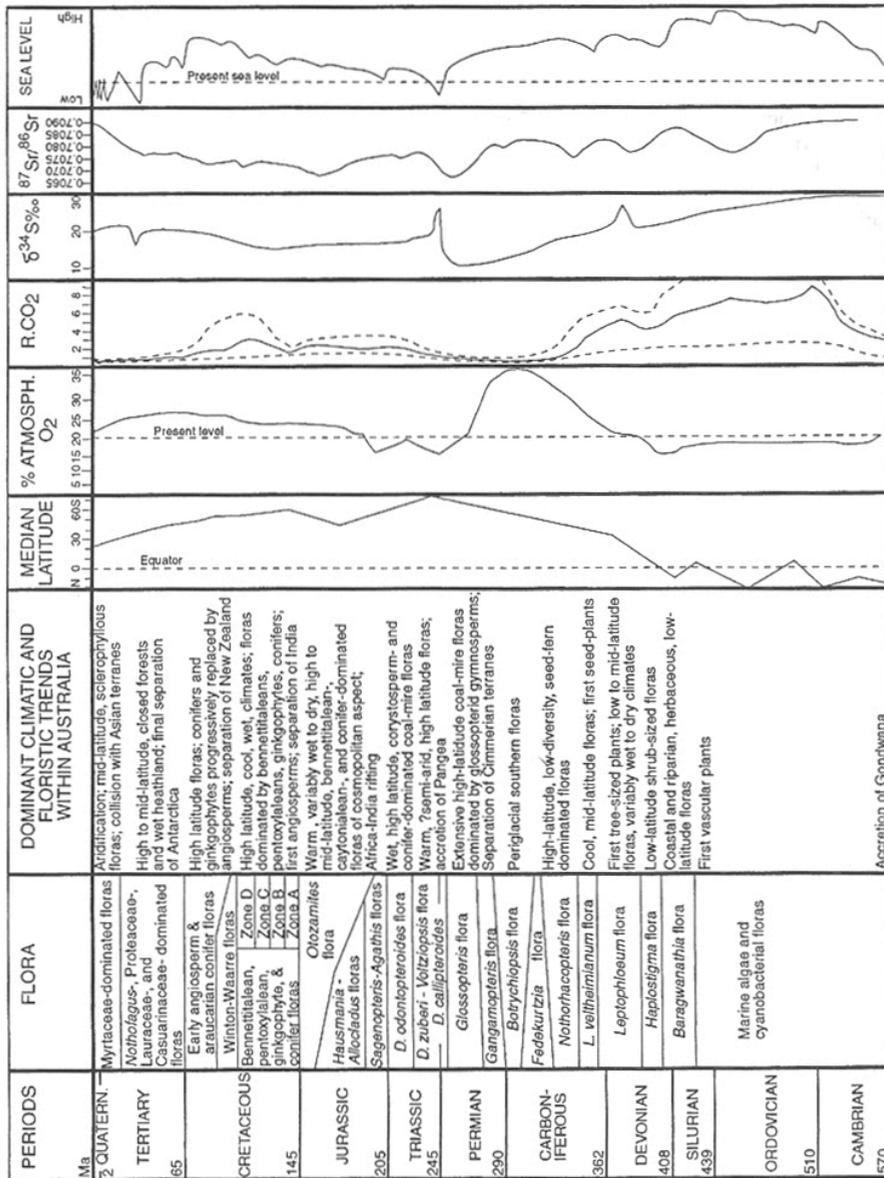
Figure 57. The succession of Australian terrestrial floras plotted against various geochemical, sea-level and latitudinal trends for the Phanerozoic. Time scales after Harland *et al*. (1990); Australia's median latitudinal position through time after Embleton (1984); best estimate of the percentage of O_2 in the atmosphere through time after Berner & Canfield (1989); best estimate of atmospheric CO_2 measured as a ratio of the mass of CO_2 at time *t* to that in the present atmosphere (dashed lines represent range of uncertainty) after Berner (1990); plot of mean $\delta^{34}S$ in sulphates through time after Odin *et al*. (1982); plot of strontium $^{87}Sr/^{86}Sr$ variation from marine carbonate, evaporite, and phosphate samples through time after Burke *et al*. (1982); broad-scale (mostly first- and second-order magnitude) phanerozoic sea-level fluctuation after Vail *et al*. (1977) and Hallam (1984).

Other plants occurring in the Late Carboniferous floras include calamitalean sphenophytes, lycophytes and rare ferns, but overall diversity within these floras was low. While low diversity may have been partly due to an unfavourable climatic setting, it may also be attributable to a dearth of systematic studies on these floras.

Lower Carboniferous palynofloras, like those of Upper Devonian sequences, comprise a diverse array of lycophyte, fern, sphenophyte and bryophyte spores (Playford, 1976, 1978; Powis, 1984; Playford & Satterthwait, 1985, 1986, 1988; Satterthwait & Playford, 1986). Although some spore-pollen taxa are long-ranging, the Upper Devonian to Lower Carboniferous palynofloras show progressive replacement of older taxa by new forms, potentially allowing detailed biostratigraphic zonation of the host strata (Playford, 1985). Mid-Carboniferous palynofloras continued to be dominated by trilete spores presumably derived from a range of lycophytes, sphenophytes, ferns and bryophytes, but monosaccate gymnosperm pollen also appears in the fossil record in low quantities around this time (Kemp *et al*., 1977; Powis, 1984). Late Carboniferous (Stage 1) palynofloras contain a wealth of bilaterally and radially symmetrical monosaccate pollen, significant proportions of cryptogam spores, and very small amounts of bisaccate pollen (Balme, 1980). The rise in monosaccate abundance probably corresponds to global diversification of cordaitaleans and early conifers at this time. Although the macrofossil record for these groups in the Late Carboniferous and Early Permian of Australia is scanty, Argentinian sequences indicate that cordaites and conifers were well-established in Gondwana by this time (Archangelsky & Cúneo, 1987, 1991).

Post-glacial recovery: the Permian Glossopteris flora

The late Palaeozoic glaciation may have been diachronous across Gondwana (Crowell, 1995), but Australia appears to have been chiefly affected during the very late Carboniferous and Early Permian. During peak glacial times substantial ice caps probably covered many upland areas leaving evidence of glacial striae (Bourman & Alley, 1988), tillites (Crowell, 1971), and dropstones in marine sediments (Draper, 1983). Intervening lowland areas may have remained ice-free, and distinctive Gondwanan floristic elements (e.g. *Botrychiopsis*) persist from the Late Carboniferous through to the Early Permian. Major ice caps probably disappeared by mid-Permian times, and the post-glacial floras of Australia (and other major Gondwanan landmasses) were soon dominated by a newly evolved group of seed plants, the glossopterids (Fig. 57). Glossopterids produced distinctive, spatulate, reticulate-veined leaves and taeniate, bisaccate pollen, and both macrofossil and pollen remains of this group are first recorded at about the Carboniferous-Permian boundary (Rösler, 1978; Powis, 1984; Archangelsky *et al*., 1987). Many Early Permian glossopterids possessed loosely meshed veins along the midline of their leaves; these forms are generally assigned to *Gangamopteris*. Leaves with medial veins strongly aggregated to form a prominent midrib are assigned to *Glossopteris* and occurred throughout the Permian but were dominant in the latter half of the Period. The differentiation of *Gangamopteris* and *Glossopteris* is arbitrary as both forms have been found attached to the same axes (Rigby, 1967).

Glossopterids hold a crucial place in both the economic development of Southern Hemisphere nations and in the understanding of past continental configurations. Permian coal deposits, composed predominantly of the remains of *Glossopteris* and allied plants, represent by far the dominant coal resources of the Southern Hemisphere. Measured and inferred Permian coal resources within Australia alone amount to well in excess of 120×10^9 tonnes (Maher *et al*., 1995). The distribution of *Glossopteris* across the now widely separated landmasses was one of the key pieces of evidence used to support early propositions of continental drift and the former existence of a single Southern Hemisphere supercontinent, Gondwana (du Toit, 1937).

Glossopterids were primarily trees of lowland mire environments. Their distinctive root remains (*Vertebraria*) possess schizogenous cavities which were probably an adaptation for gas exchange in anoxic substrates (Neish *et al*., 1993). Glossopterid leaves are often found in densely matted horizons suggesting a deciduous habit (Plumstead, 1969; Retallack, 1980). By the Late Permian the *Glossopteris* flora occupied a broad tract of the high southern

latitudes (c. 40°–90°S, Fig. 58) and the deciduous habit may have been a response to strong seasonal photoperiod variation, and in some cases, several months of darkness. Fossil woods from the Permian of Australia and other Gondwanan continents invariably show prominent growth rings which probably also represented a response to a strongly seasonal climate.

The phylogenetic affinities of glossopterids have provoked more debate than perhaps any other group of plants. Much of the debate revolves around interpretation of the morphology and structural homologies of glossopterid ovulate fructifications. Two principal arguments currently prevail. The first suggests that the reproductive organs of glossopterids are homologous with the cupules of Mesozoic seed-ferns such as the Corystospermales and Caytoniales (Crane, 1985; Doyle & Donoghue, 1986). However, others have suggested that Mesozoic seed-fern cupules developed independently (Taylor *et al.*, 1994), and that glossopterid fructifications may represent modified leaf and axillary shoot complexes more akin to cordaitaleans and early conifers (Schopf, 1976; McLoughlin, 1993a; McLoughlin & Drinnan, 1996).

Other plants represented in the Permian floras of Australia include cordaitaleans (*Noeggerathiopsis*), conifers (*Walkomiella*), osmundaceous ferns (*Neomariopteris*, *Dichotomopteris*, *Palaeosmunda*), numerous herbaceous sphenophytes (*Sphenophyllum*, *Trizygia*, *Phyllotheca*, *Lelstotheca*, *Raniganjia*, *Austroannularia*, *Gondwanophyton*), herbaceous lycophytes (*Cyclodendron*, *Selaginella*), cycadophytes (*Pseudoctenis*, *Pterophyllum*, *Dunedoonia*), rare ginkgophytes, and residual Palaeozoic seed-ferns (*Bergiopteris*). Despite the abundance of Permian plant fossils in Australia, the macroflora as a whole is of relatively low generic diversity. Greater diversity is apparent in the palynofloras, especially among pteridophytes (Foster, 1979; Gilby & Foster, 1988; Backhouse, 1993). It is possible that many pteridophytes occupied environments or had growth habits that did not favour preservation of their foliage in the fossil record, and distributional evidence of other plant groups (e.g. *Noeggerathiopsis* and *Walkomiella*) suggests that plant remains from upland areas were only rarely preserved along the cratonic flanks of the major sedimentary basins (for map of sedimentary basins see Fig. 32) or in small intracratonic basins (Retallack, 1980; McLoughlin, 1993b). Algal palynomorphs (presumably of freshwater origin) are also well-represented in Australian fluvial and paludal deposits (Balme & Segroves, 1966; Segroves, 1970; Foster, 1979; Backhouse, 1993) and occasionally formed thick accumulations of oil shale (Guy-Ohlsen, 1992).

Although by Permian times, most of the world's continental areas were united into a continuous landmass (Pangea), the strong equator-pole climatic gradients imposed by Gondwanan glaciation at the beginning of the period led to pronounced provincialism in the world's floras (Fig. 58). The *Glossopteris* flora represents the first expression of a truly unique Southern Hemisphere vegetation. Upper Carboniferous and Permian floras were also significant in that they saw the evolution of the conifers, ginkgophytes, peltasperms, cycads, and corystosperms, groups that were to become major components of the Mesozoic floras.

A second crisis: The Permian-Triassic extinction event

Close to the end of the Permian, coal measure sedimentation gave way to non-coaly fluvial deposits and red-beds in many parts of Australia and other Gondwanan landmasses. This sedimentological change closely corresponds to a sharp transition from glossopterid-dominated to moderate-diversity, corystosperm-, conifer-, and lycophyte-dominated floras. Palynological data suggest that the Permian-Triassic boundary (initially defined in European sedimentary sequences) is slightly higher in the succession than the major macrofloral and sedimentological transition in Australia (Foster, 1982).

The demise of glossopterids, and the disappearance or decline of medullosan seed-ferns, cordaitaleans, and gigantopterid gymnosperms in the Northern Hemisphere, together with the disappearance of numerous marine invertebrate taxa at or around the Permian-Triassic boundary, represent one of the major floristic extinction events in Earth history. Most recent studies dealing with the causes of extinction invoke broad-scale environmental changes (often prolonged marine regression at the end of the Permian followed by sharp
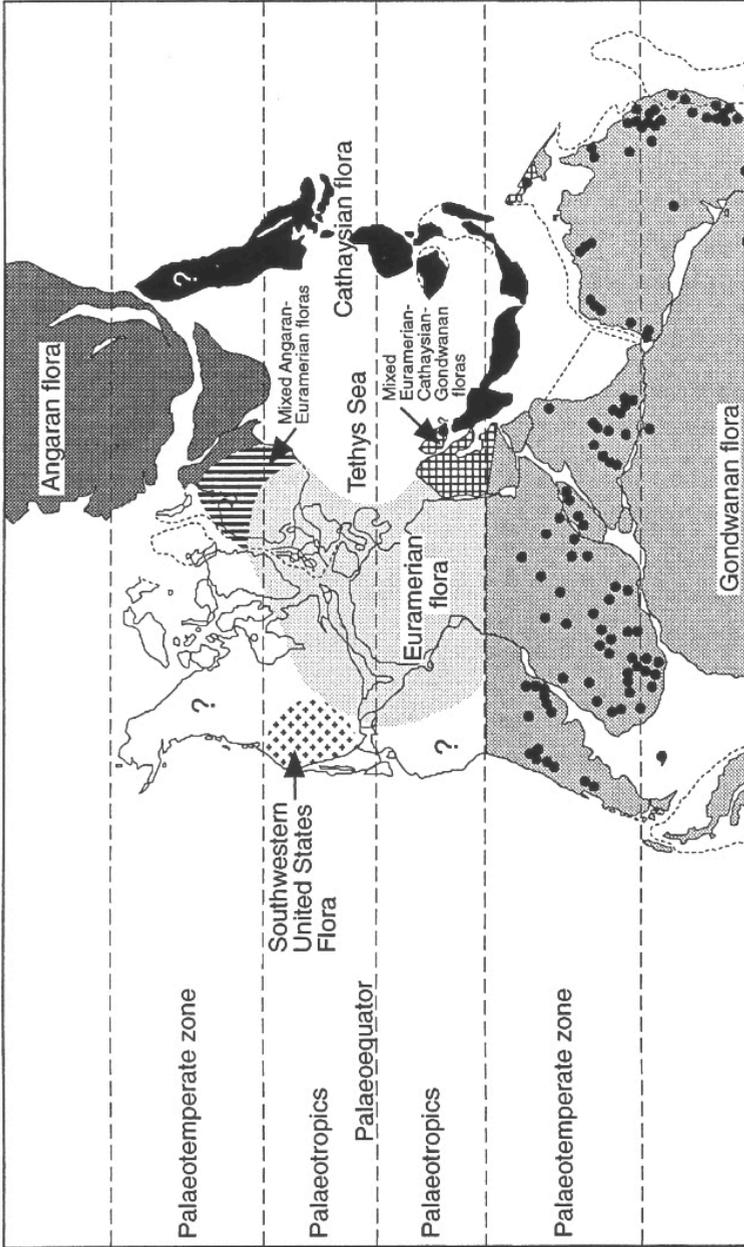
Figure 58. Reconstruction of Late Permian plate positions showing the distribution of the five major floristic provinces (modified from Chaloner & Creber, 1988). Gondwanan and Angaran floras are strongly correlated to southern and northern temperate to polar latitudes respectively, whereas the south-west United States, Euramerian, and Cathaysian floras are confined to the palaeotropics and occupied different humidity/aridity regimes or geographically isolated landmasses. Solid dots indicate the major sites of macrofossil assemblages of the *Glossopteris* flora.

transgression, and/or a shift towards more widespread arid conditions; Erwin, 1995). Clearly the end of the Permian was marked by major excursions from average sea-levels and ratios of stable isotopes in marine sediments (Erwin, 1994) (Fig. 57) reflecting rapid and pronounced environmental change. There is some evidence to suggest that the transition from floras of Palaeozoic to Mesozoic aspect was not globally synchronous, and that the transition in equatorial areas may have been more gradual than at higher latitudes (Meyen, 1987). Regardless of causes, the end-Permian extinctions probably provided opportunities for diversification of newly evolved groups like the Corystospermales, Caytoniales, cycadophytes, ginkgophytes and groups which had previously been more ecologically or geographically restricted (e.g. conifers and peltaspermalean seed-ferns).

The best Australian Early Triassic floras derive from the Sydney and Lorne Basins and the Nymboida Coal Measures. These floras are dominated by small-leafed voltzialean conifers (*Voltziopsis*), various *Dicroidium* (corystosperm) species, pleuromeian lycophytes (*Pleuromeia*, *Cyclostrobus*, *Cyclomeia*, *Cidarophyton*), osmundaceous (*Cladophlebis*), gleicheniacean (*Gleichenites*), dicksoniacean (*Todites*) and possibly marattiacean (*Rienitsia*) ferns, ginkgophytes (*Rhipidopsis*/*Sphenobaiera*), and possible pentoxylaleans or cycadophytes (*Taeniopteris*) (Walkom, 1925; Burges, 1935; Retallack, 1975, 1977; White, 1981; Chaloner & Turner, 1987; Holmes & Ash, 1979). Remains of these plant groups occur in varying assemblages through space and time and in association with differing palaeosol profiles and sedimentary deposits, leading Retallack (1977) to define three 'ecostratigraphic' assemblages for the Early Triassic. His 'Voltziopsetum' assemblage was dominated by conifer remains in association with humic and grey-brown podzolic soils and was interpreted as representing mainly coniferous forests developed on immature volcanic soils. The 'Dicroidietum zuberi' assemblage represented *Dicroidium*-dominated delta-top heaths and lagoon-margin, mire woodlands. The 'Pleuromeietum' assemblage, comprising an almost monospecific association of herbaceous to shrub-sized lycophytes, was interpreted to represent a coastal or saline, lagoon-margin flora. A marked increase in trilete, cavate spores (e.g. *Aratrisporites*, *Krauselisporites*, *Indotriradites*, *Densoisporites*, *Lundbladispora*) in Australian Early Triassic palynofloras is probably a result of rapid migration and diversification of opportunistic lycophyte species along the coasts of Pangea during Early Triassic transgression-regression cycles. Palynofloras from Early Triassic marine sequences in Australia are marked by low diversities but high abundances of simple spinose acritarchs which probably represent encystment stages of various unicellular algae (Balme, 1963; Balme & Helby, 1973).

Recovery and diversification in the Middle to Late Triassic: the *Dicroidium* flora

During the Middle and Late Triassic, climatic amelioration and local tectonism combined to favour a return to coal measure deposition in several isolated sedimentary basins of eastern and southern Australia. Generic diversity within Late Triassic coal measure floras (especially among the gymnosperm groups) is substantially greater than that in the glossopterid-dominated Permian coal floras. Late Triassic coal-mire floras were dominated by several species of corystosperm (*Dicroidium*) together with ginkgophytes (*Sphenobaiera*, *Ginkgoites*), cycadaleans (*Pseudoctenis*, *Nilssonia*), bennettitaleans (*Zamites*, *Anomozamites*), voltzialean and podocarp conifers (*Heidiphyllum*, *Rissikia*), peltasperms (*Lepidopteris*), dipteridacean (*Dictyophyllum*), marattiacean (*Ogmos*, *Marantoidea*), and osmundaceous (*Cladophlebis*, *Australosmunda*) ferns, sphenophytes (*Neocalamites*), bryophytes (see Webb & Holmes, 1982), and various seed-ferns of uncertain affinities (*Linguifolium*, *Yabiella*, *Pachydermophyllum*, *Dejerseya*, *Taeniopteris*).

As Middle and Late Triassic floras of eastern Australia become better understood, some compositional changes are now evident between floras of the various basins (Balme *et al*., 1995) and between Australia and other Gondwanan regions (Anderson & Anderson, 1989). Triassic macrofloras of western and northern Australia are poorly known (White, 1961) but appear to contain at least some elements in common with eastern Australia. However, Late Triassic palynofloras from Western Australia include Tethyan (equatorial) elements that are absent in eastern Australia (Dolby & Balme, 1976). Tethyan-influenced palynofloras similar

to the Western Australian (Onslow-type) assemblages are recorded from lower latitude portions of Gondwana flanking the Tethys Embayment, whereas eastern Australian (Ipswich-type) assemblages characterise higher Gondwanan palaeolatitudes (Foster *et al*., 1994).

Apart from regional variation, macrofloral assemblages also show compositional differences according to local habitats and depositional environments. In the Middle Triassic of the Sydney basin, plants bearing *Taeniopteris* foliage appear to have preferentially colonised levee banks of sluggish lowland rivers whereas *Dicroidium elongatum* occupied low-fertility, broad, sandy, floodplains. *Dicroidium odontopteroides*- and *Linguifolium*-dominated assemblages in the Late Triassic (Fig. 57) probably represent broad-leafed forests of coastal plain floodbasins. Assemblages dominated by *Heidiphyllum*, *Dicroidium stelznerianum*, *D. coriacea* and ginkgophytes, often occurring in coarse-grained sediments, probably represent accumulations of material derived from plants growing on well-drained sites (elevated levee banks and alluvial fans flanking upland regions). *Pachydermophyllum* associations from New Zealand (then a contiguous landmass with eastern Australia) are possibly derived from mangrove-like coastal communities (Retallack, 1977).

Many of the gymnospermous plants in the *Dicroidium* flora were probably deciduous, based on occurrences of their foliage in densely matted horizons, abscission of whole leaves, and the expanded bases and well-defined abscission zones on some leaves (Anderson & Anderson, 1989). The transition, in many areas, from red-beds in the Early and Middle Triassic to coal measures in the Late Triassic, probably reflects a shift towards generally wetter conditions. Thick cuticles and strong stomatal protection on some plants of the *Dicroidium* flora may represent adaptations to combat water stress (Cantrill *et al*., 1995). On the other hand, wet and relatively warm conditions are suggested by the presence of dipteridacean and marattiacean ferns, although it is difficult to judge whether Triassic representatives of these groups favoured the same climatic conditions as their extant relatives. Thick cuticles and stomatal protection on some of these plants may have been a response to growth on infertile or relatively arid substrates (Retallack, 1977).

Dinoflagellates (Division Pyrrophyta) underwent a major phase of diversification in marine environments during the Late Triassic and retained high diversities throughout the remainder of the Mesozoic and Cainozoic. It is likely that many of the Palaeozoic and Triassic acritarchs from marine sediments represent encystment stages of dinoflagellates or their close relatives. Coccolithophores (Division Chrysophyta; Class Coccolithophyceae) also first appeared in the Late Triassic and underwent a major radiation in the Early Jurassic. Like the dinoflagellates, they appear to have reached peak diversity in the extensive shallow seas of the Late Cretaceous, and remain important components of the modern oceanic phytoplankton.

Masters of the Jurassic: bennettitaleans, pentoxylaleans, and conifers

Early Jurassic floras are not well-represented in Australia; assemblages are known only from Queensland and New South Wales. Several notable Late Triassic genera (e.g. *Dicroidium*, *Linguifolium*, *Dejerseya*, *Yabiella* and *Heidiphyllum*) are absent from the Early Jurassic floras, indicating a major extinction event coinciding with that experienced globally by terrestrial vertebrate and marine invertebrate faunas (Stanley, 1987). Dinosaurs, which had first appeared during the Triassic, came to dominate the large terrestrial herbivore and carnivore niches following the end-Triassic extinctions and remained the dominant terrestrial vertebrates for the remainder of the Mesozoic. Accompanying the faunal turnovers, new plant taxa including representatives of the Bennettitales (*Otozamites*), Caytoniales (*Sagenopteris*), and cheirolepidacean conifers (known only from their abundant, dispersed, *Classopollis* pollen) take the place of some of the Late Triassic gymnosperms, although total diversity appears to have fallen (Balme *et al*., 1995). Other elements in the Early Jurassic floras include marattiacean (*Phlebopteris*), osmundacean (*Cladophlebis*), dicksoniacean (*Todites*) and dipteridacean (*Dictyophyllum*) ferns, equisetaleans (*Equisetum*), lycophytes (*Selaginella*, *Isoetites*), cycadaleans (*Nilssonia*), podocarp and araucariacean conifers (*Rissikia*/ *Elatocladus*, *Allocladus*, *Agathis*), pentoxylaleans (*Taeniopteris*), and some seed-ferns of uncertain alliance (*Pachypteris*, *Thinnfeldia*).

Australia occupied middle to high (c. 35°–65°) southern latitudes in the Jurassic, probably resulting in a considerable north-west to south-east climatic gradient across the continent. The palaeoclimatic signatures of many of the Jurassic plant groups are unclear as they were either widely dispersed in the Jurassic and/or have few or no close extant relatives. Although some endemic or strongly Gondwanan elements are evident in the Early Jurassic floras (pentoxylaleans, araucariaceans), the floras have a more cosmopolitan aspect than those of the Permian and Triassic, and this may imply both easy migration pathways through a united Pangea and more equable climates globally. Although good palaeoclimatic indicators are often lacking, stable isotope studies, the absence of red-beds, presence of local coal deposits and the lack of evidence for glaciation suggests that conditions were generally warm and, on the whole, relatively humid during the Australian Jurassic. However, it must be emphasised that much of the macrofossil data for this period derives from eastern Australia and some palynological studies from Western Australia have suggested the possibility of arid conditions in that region, at least for the Early Jurassic (Filatoff, 1975).

Middle Jurassic floras are best known from the Walloon Coal Measures and their equivalents in the Clarence-Moreton and Surat Basins of southern Queensland and northern New South Wales. These floras share many taxa with Early Jurassic assemblages but lack caytonialeans (*Sagenopteris*). The Walloon floras show considerable compositional differences between assemblages derived from coal seams and carbonaceous floodbasin deposits underlying coals, and those derived from interseam channel, levee and crevasse deposits. The former are rich in equisetaleans (*Equisetum*), osmundaceous (*Cladophlebis*, *Osmundacaulis*, *Millerocaulis*, *Grammatocaulis*, *Ashicaulis*) and dipteridacean (*Hausmannia*) ferns, and pentoxylaleans (*Pentoxylon*, *Taeniopteris*), whereas the latter are generally dominated by bennettitaleans (*Otozamites*, *Ptilophyllum*) and podocarp and araucarian conifers (*Mataia*, *Pagiophyllum*, *Araucaria*, *Allocladus*, *Bellarinea*). Several studies of the Walloon floras have noted the conspicuous absence of ginkgophytes in contrast to their prominent representation in contemporaneous floras from other parts of the world (Gould, 1980; McLoughlin & Drinnan, 1995). Other elements in the Middle Jurassic floras include dicksoniacean ferns (*Coniopteris*), ferns of uncertain affinities (*Sphenopteris*) and gymnosperms of uncertain alliance (*Pachypteris*, *Palissya*). *Palissya* has occasionally been considered to have affinities with *Elatocladus*-type foliage and is therefore often regarded as coniferous, but no direct connection between cone and foliage has yet been found and the structure of *Palissya* is unlike that of other conifer reproductive organs (Parris *et al.*, 1995). Late Jurassic floras are very poorly known but appear to incorporate most of the same elements (at generic level) as Middle Jurassic floras and are especially well-represented by osmundaceous (*Cladophlebis*, *Osmundacaulis*, *Millerocaulis*, *Ashicaulis*), cyatheacean (*Oguracaulis*, *Cibotium*) and dicksoniacean (*Coniopteris*) ferns, bennettitaleans (*Otozamites*, *Ptilophyllum*) and conifers (Gould, 1975, 1978; Tidwell *et al.*, 1987, 1991).

Diatoms (Phylum Chrysophyta; Class Bacillariophyceae) first appear in Late Jurassic marine sediments and the group consistently diversified throughout the remainder of the Mesozoic and Cainozoic. They presently represent a major component of the marine phytoplankton and have successfully invaded freshwater and some terrestrial habitats. As diatom species commonly have distinct temperature, salinity, acidity, oxygen, and mineral nutrient requirements, their fossil distribution has been of great value for palaeoenvironmental and palaeoclimatic studies (Brasier, 1980).

The Middle and Late Jurassic floras of eastern Australia occurred at palaeolatitudes of around 55°–65°S (Embleton, 1984; Veevers *et al.*, 1991). These floras contain some apparently deciduous elements (*Taeniopteris*), and both floral diversity and oxygen isotope data suggest that humid mesothermal to microthermal climates prevailed (Gould, 1980). A Middle to Late Jurassic flora from Western Australia, which developed in palaeolatitudes of around 35°–40°S, appears to have a higher proportion of araucarian conifers and bennettitaleans (Arber, 1910; Walkom, 1921; McLoughlin & Hill, 1996) and may represent

(1) a flora botanically more akin to Early Cretaceous assemblages,

(2) an assemblage derived from a generally drier or warmer climate, or

(3) an assemblage derived from upland plant communities.

The cosmopolitan aspect of the Australian flora evident in the Early Jurassic appears to have persisted to some extent until the end of the Jurassic although some distinctive Gondwanan elements are represented throughout the period. The Late Jurassic saw the initiation of rifting and sea-floor spreading on the north-western margin of Australia (Veevers *et al*., 1991) and between Africa and India. Rifting continued along the western, southern, and eastern margins of Australia through the Cretaceous and early Tertiary and had profound implications for the geographic isolation of the continent and the development of a unique Australian biota.

The Cretaceous flora

Most of the modern Australia flora had its genesis in the long span of time called the Cretaceous Period. Recently, the three-element invasion hypothesis that was initially advocated by Hooker (1860) (but see Crisp *et al*., this volume) to explain the present-day Australian flora has been rejected (Barlow, 1981; Webb *et al*., 1986; Dettmann, 1994) and replaced by a more complex set of hypotheses indicating autochthonous differentiation from an ancient Gondwanan flora during the Late Cretaceous and Early Tertiary (Webb *et al*., 1986), and possibly a Late Cretaceous-Early Tertiary phase of floristic exchange between Australia and regions to the north, with dispersal occurring in both directions (Truswell *et al*., 1987; Hill, 1992; Hill & Dettmann, 1996). Evidence countering invasion from the north during the Late Cretaceous has accrued (Dettmann & Thomson, 1987; Dettmann & Jarzen, 1988, 1990; Dettmann, 1989; Jarzen & Dettmann, 1989; Dettmann *et al*., 1990) and further testing of this hypothesis requires detailed palynological records from the Late Cretaceous of northern Australasia. From patterns of pollen introductions in separate regions of the southern Gondwana assembly it is clear that many elements of the Australian Cretaceous flora either evolved within the Austro-Antarctic region or entered Australia using an Antarctic route (Dettmann, 1981, 1989; Dettmann & Jarzen, 1990). Clearly, the Cretaceous was a time of enormous significance to the evolution of the current Australian flora.

Throughout the Cretaceous, Australia remained connected to Antarctica and was situated at very high latitudes (especially the southernmost parts, Fig. 59). Given the lack of the extreme polar cold that is experienced today, this led to growth conditions that have no modern analogue, i.e. extreme fluctuations in annual photoperiod coupled with a relatively benign climate. There were probably also atmospheric CO_2 levels well above those within human experience (Barron & Washington, 1985), and disturbance patterns associated with the rifting of Gondwana that were well beyond any experienced in Australia in more recent times. Some of the direct and indirect consequences of these physical conditions are considered prior to an examination of the fossil record.

High latitude areas as regions of evolutionary novelty

High latitude areas have been suggested as important sources of evolutionary novelties, a hypothesis that has its origins in the work of Jablonski *et al*. (1983), who noted the preferential generation of evolutionary novelties in nearshore, as opposed to offshore, communities in the fossil record. They proposed two reasons for this:

- Evolutionary novelties are equally likely in all speciation events, but the greater extinction resistance in nearshore species permits novelties to persist long enough to diversify (i.e. nearshore innovations have a higher probability of persisting long enough to diversify, and there is also an increase in the total number of speciation events in a clade over its lifetime).

- The ecological constraints of certain types of environments enhance the likelihood of large evolutionary jumps during speciation events.
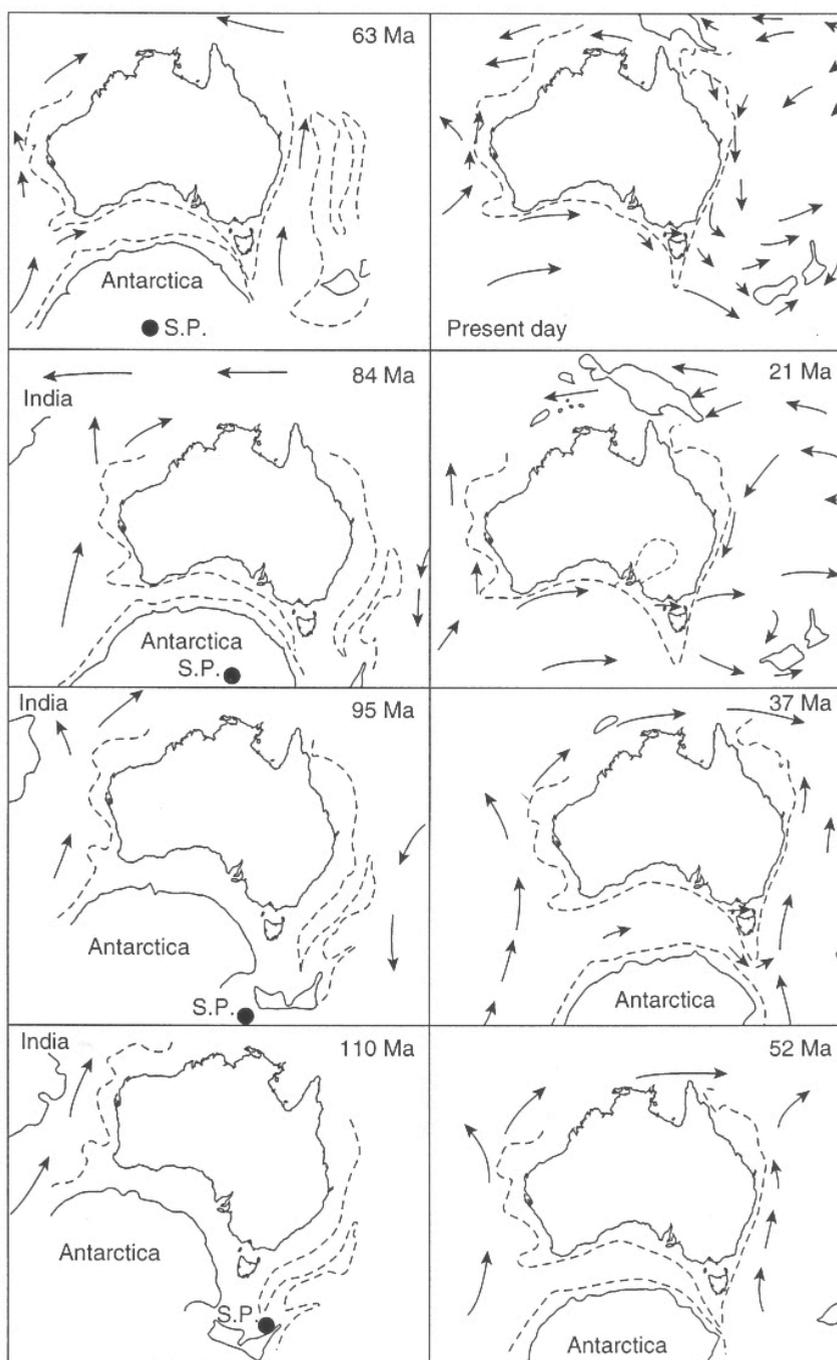
Figure 59. Variation in oceanic current patterns through the Cretaceous and Cenozoic of Australia. S.P. = South Pole. Arrows indicate positions of surface currents. Present continental outlines are shown as solid lines and bear little relation to positions of past coastlines. Broken lines represent the continent-ocean boundaries. Modified from Quilty (1994).

Lewin (1983) took the important step of equating the nearshore environment of Jablonski *et al.* (1983) with a high latitude terrestrial habitat. High latitude habitats are generally hazardous places to live compared with the relatively stable low latitude habitats. Consequently, low latitude species are able to thrive as small, geographically restricted populations, leading to characteristically high species diversity in the tropics, whereas high latitude regions are composed of large, widely distributed populations. Lewin (1983) proposed that peripherally isolated groups drawn from such a large, widespread population may undergo 'minigenetic revolutions', which could shift developmental patterns sufficiently to produce truly novel forms (a phenomenon called 'genetic transilience' by Templeton (in Lewin, 1983)). It is not yet clear whether either or both of these options operate.

Hickey *et al.* (1983) provided strong evidence to support the hypothesis that the terrestrial Arctic biota of the latest Cretaceous and Palaeogene was profoundly out of phase with that of more southerly latitudes, with many taxa appearing first at the higher latitudes. They concluded that during much of the Phanerozoic the currently inhospitable Arctic region may have served as the birthplace for important biotic innovations and for major groups that later radiated to lower latitudes.
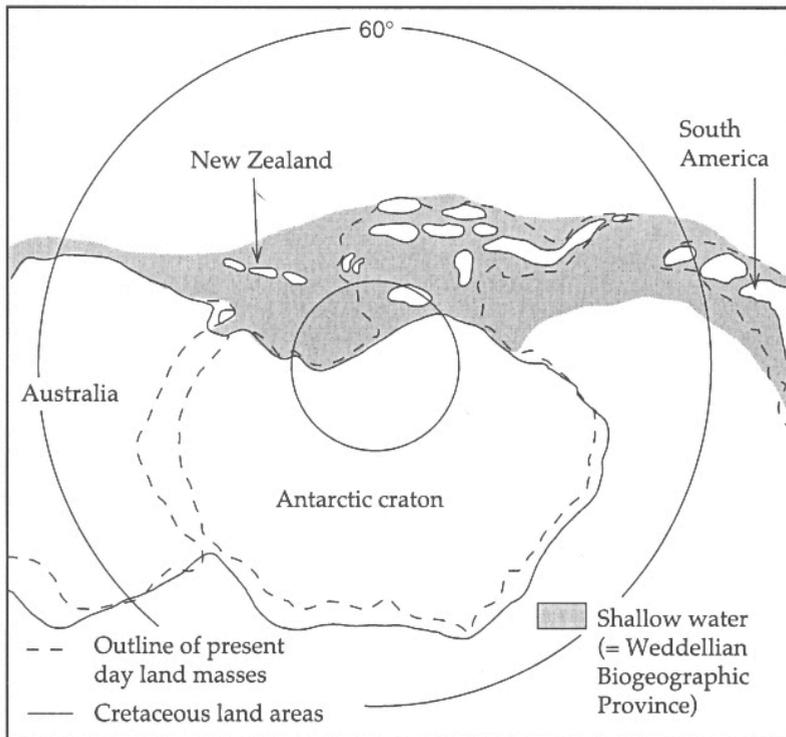

Figure 60. Reconstruction of the Weddellian Biogeographic Province (stippled area) during the Late Cretaceous and Paleogene. Modified from Case (1988) who considered that the stippled area should represent a continuous coastal environment bordered by shallow seas.

Zinmeister & Feldman (1984) provided data supporting a similar high latitude heterochroneity for Southern Hemisphere marine faunas during the Cretaceous, and Case (1988, 1989) extended the Weddellian Zoogeographic Province (Fig. 60) to a 'biogeographic province' to take account of this for the terrestrial biota. Case hypothesised that this province was a centre of origin and diversification for many taxa, particularly marsupials and species of *Nothofagus*, during the Late Cretaceous and Palaeogene. Askin (1989) concluded that although much of the Antarctic Cretaceous-Cainozoic endemic flora remained isolated because of geographical, climatic or biological barriers, many plants spread northwards, introducing dominant taxa to later mid-latitude floras, and other taxa to mid- to low-latitude floras. As will be seen in the following discussion of the fossil record, it is now clear that the Weddellian Biogeographic Province was the source of much of the Australian flora, and there is strong evidence for a Southern Hemisphere equivalent of the heterochroneity reported by Hickey *et al*. (1983) for high northern latitudes (Askin, 1989; Dettmann, 1989; Hill & Scriven, 1995).

The role of disturbance in Gondwana and early angiosperm migration

Angiosperms evolved in the northern Gondwana/southern Laurasia area during the Early Cretaceous and radiated world-wide (Drinnan & Crane, 1990; Dettmann, 1992). Retallack & Dilcher (1981) hypothesised that early angiosperms had generalised pollination and dispersal strategies. This made them ideal for long-range dispersal by pioneering the fresh sedimentary surfaces of coastal deltas, lagoons, and tidal flats. As the extent of marine transgression and regression increased in North America during the Early Cretaceous, these pioneering early angiosperms or angiosperm ancestors dispersed along coastlines out of the rift valley of West Gondwana (between Africa and South America). More recent research has confirmed an early successional role for early angiosperms (e.g. Wing & Tiffney, 1987), and this has been used in a novel but as yet untested way to account for the early radiation of angiosperms in a dinosaur-dominated world (Bakker, 1988).

Angiosperms spread generally into Gondwana during latest Barremian–Aptian times (Dettmann, 1989), and those lineages that were established in southern Gondwana by the close of the Cretaceous formed the foundation from which present-day austral floras developed (Dettmann, 1992). Dettmann (1989) noted that rift valley systems at high southern latitudes acted as migrational pathways for early angiosperms, perhaps because of the high disturbance level in these environments and the colonising nature of these angiosperms.

Some of the prominent taxa in the early high southern latitude flora still exist elsewhere today, and their ecology is well-understood. A good example is *Nothofagus*, which has been studied extensively across its range. For example, Veblen *et al*. (1977, 1980) noted that *Nothofagus* in South America does not usually regenerate continuously at low altitudes, especially at lower latitudes, where climatic conditions favour more complex forests and *Nothofagus* seedlings cannot establish. In these environments, *Nothofagus* relies on catastrophic disturbance, a relatively common phenomenon in the highly unstable Andes mountain chain, to provide a fresh, cleared substrate which is readily colonised by seedlings. This regeneration behaviour is probably very similar to that which occurred early in the history of the genus, when it occupied either dense forests on unstable sites, and was unable to regenerate in the absence of disturbance, or occurred in more sparse forest on less equable sites where its seedlings could survive in the understorey. Hill (1987, 1992) hypothesised that the large reduction in *Nothofagus* diversity at high latitudes today, especially away from the Andes, may be due to the relative stability of the modern landscape, which, coupled with the density of the forest cover, does not provide a suitable environment for the continued presence of many *Nothofagus* species.

Thus it is highly probable that unstable habitats at high southern latitudes during the Cretaceous-Palaeogene provided both a pathway for the migration of early angiosperms and the potential for peripheral isolation of populations of widespread species. This may have been a critical factor for evolution in the region (Hill & Scriven, 1995).

Plant growth at high southern latitudes

One obvious question about forest growth at high southern latitudes in the Cretaceous-Palaeogene is: how did plants grow and what form did the communities take in such an unusual photoperiod? It is a real limitation of the fossil record in general that behavioural traits such as dormancy rarely leave a clear imprint (Truswell, 1991). However, information on physiological adaptations to life at high latitudes can be obtained from an examination of fossil wood and leaf form. Cretaceous gymnospermous wood from palaeolatitudes probably higher than 70°S, shows a consistent pattern of growth, with increments, probably annual in origin, clearly delineated, and indicating a pronounced seasonal influence (Jefferson, 1982). The amount of wood added annually was usually large, even when compared with modern low-latitude trees, but there is considerable variation in ring widths from year to year, suggesting that the trees were highly sensitive to environmental fluctuations (Truswell, 1991). A fossil forest at one early Cretaceous site had trees spaced 3–5 m apart and the tallest preserved trunk height is 7 m (Jefferson, 1982). Hill (1994a) used these data to explain the reduction in wind pollination in understorey plants during the very early Palaeogene in southern Australia. With the sun at a low angle in the sky during summer and tracking an almost circular path around the horizon during the day, he concluded that it was likely that the forest structure was quite different to that observed in heavily forested regions of Australia today. As has been postulated for the Late Cretaceous (Specht *et al*., 1992), relatively widely spaced conical trees probably dominated, and thus wind pollination was a viable strategy for understorey plants below the open canopy. As Australia moved into lower latitudes and the sun angle increased, a closed forest structure developed as the most efficient way of utilising incoming solar radiation. This may have been critical for the loss of wind pollination as a viable strategy in the associated understorey plants.

Leaf physiognomy is a well-established palaeobotanical data source, but its application to high latitude macrofloras is controversial. The extremely unusual light conditions present in southern Australia and Antarctica probably had a profound effect on leaf structure in the forests of the Cretaceous-Palaeogene. For example, Wells & Hill (1993) proposed that leaves in Palaeogene forests of southern Australia may have hung vertically to increase light capture, because the sun was continually at a low angle. If this was so, then the same would have applied in the Cretaceous, and such a strategy may well have led to the evolution of unusual leaf sizes and shapes which are not amenable to comparison with data gathered from extant forests (Hill & Scriven, 1995).

Another approach to predicting palaeoclimate is to examine in detail the morphology of fossil leaves. This has been done for the podocarp genera *Acmopyle* and *Dacrycarpus* in the Palaeogene of south-eastern Australia (Hill & Carpenter, 1991; Hill, 1994a). Here leaf size and stomatal distribution were found to be related to climate (see below), but this approach has not yet been applied to Cretaceous fossils.

The presence of a relatively dense plant cover, including large and rapidly growing trees, in regions poleward of the Antarctic circle has long appeared enigmatic, given that today growth at high latitudes is viewed as being constrained by characteristic day-length patterns, and by the temperatures associated with a regime of long rigorous winters and short cool summers (Truswell, 1991). Truswell pointed out that the problems raised by the fossil record include:

- How plants coped with the conditions imposed by the polar night;

- How the growth of substantial forests could have been sustained at latitudes where no light, and as a consequence, little heat energy, was available for several months of the year, and where growing seasons were as short as two to three months.

Several explanations have been published to account for inconsistencies between the growth forms demonstrated by the fossil record, and the high latitude at which the past floras apparently grew.

Some of these explanations can be disregarded. Among these are the view that Antarctica only came to be in high latitudes relatively recently, a hypothesis which has been refuted by palaeomagnetic data on pole positions and the constraints imposed by seafloor spreading

data, which indicate that the Antarctic continent has occupied a near-polar position for much of the Phanerozoic (Smith *et al.*, 1981; Truswell, 1991). Similarly, changes in the angle of obliquity of the Earth's spin axis have occasionally been invoked (e.g. Wolfe, 1978, 1980; Douglas & Williams, 1982; Jefferson, 1982, 1983) to explain the presence of diverse vegetation at high latitudes. Creber & Chaloner (1985) examined and rejected all models proposed to account for changes in the angle of the Earth's axis.

It is far simpler to examine the most likely option, that plants can thrive in high latitudes provided the climate is not too hostile. The idea that light energy at high latitudes, at present values of axial obliquity, was sufficient to maintain forest growth in the past, provided that temperatures were higher, particularly in winter, was supported in arguments synthesised by Axelrod (1984), although these were not based on quantitative experimentation. More recently, physiological experiments on living plants have provided even more compelling support. Read & Francis (1992) examined the tolerance of some woody species to prolonged dark periods, particularly in warm and dark versus cold and dark conditions, and attempted to identify common characteristics among these species which may have influenced survival.

Their results indicated that at least some woody plant species native to the Southern Hemisphere can survive 10 weeks of continual darkness. Notably, survival across these species was higher under cold (at least to 4°C) dark conditions than under warm dark conditions. Species varied in their capacity to tolerate long dark periods, but the physiological determinants of this differential tolerance are as yet uncertain. However, from their limited data it appears that the deciduous habit may be advantageous, and in evergreen plants a low dark respiration rate, and perhaps other features of their light saturation curves, are potentially important. The latter characteristics may, however, decline in importance as the temperature during the dark period declines. It is apparent from the results of Read & Francis (1992) that some species experienced little stress under long dark periods, without critical loss of stored starch, and without any detectable irreversible effects on the leaf photosynthetic apparatus.

Lower winter temperatures of the more seasonal, inland continental climate at high southern latitudes in the Cretaceous-Palaeogene would have reduced respirational loss and would have been more suitable for many plant species than the milder climate at coastal margins. In addition, cloudiness, which is higher at the coastal margins than the interior of the current Antarctic landmass, has a considerable effect on sunshine hours. Interspecific differences in, for example, photosynthetic responses to light and temperature, may therefore have led to differential occurrence of species, habit (e.g. deciduous versus evergreen) and vegetation type, with respect to coastal versus inland regions of southern Australia and Antarctica.

These results also led Read & Francis (1992) to question the value of deciduousness in these high latitude floras. The apparent infrequency of deciduousness in Southern Hemisphere Cretaceous and Cainozoic fossil floras compared with those of the Northern Hemisphere may reflect differences in either winter or growing season conditions, but the recognition of deciduousness in the fossil record is often controversial, and data are required on the extent of this strategy as inferred from the fossil record (Hill & Scriven, 1995).

Creber & Chaloner (1984) reinforced the view that ambient temperature, rather than the available light, is the factor limiting tree growth in high latitudes today. They cited data which demonstrate that the amount of light energy available at latitudes within the Antarctic circle may not be significantly less than that at temperate latitudes. It is clearly adequate for tree growth, provided that the low-angle solar rays can be intercepted without excessive interference caused by mutual shading. The spacing and shape of trees are obviously crucial. Creber & Chaloner noted that the density of trees in Jefferson's (1982) Early Cretaceous forest, at one tree per 17 m^2, or 588 trees per hectare, is sparse enough for them to have intercepted sufficient illumination to produce the observed growth, provided the trees were tall and conical in shape, with a vertical canopy.

Creber & Chaloner (1985) also suggested that enhanced atmospheric CO_2 levels may have been influential in producing the high annual increments of growth observed in Cretaceous trees. The overall effect of the high predicted levels of CO_2 in the Cretaceous on plant growth is difficult to quantify, since experiments carried out on living plants are examining

the instantaneous effects of large changes in CO_2 concentration on plants which have evolved to a particular ambient level. When plants had evolved to accommodate higher levels (as in the Cretaceous) the result may have been even greater (Hill & Scriven, 1995).

The flora prior to angiosperm invasion (early Berriasian–Barremian)

In the earliest Cretaceous, Australia, Antarctica, New Zealand, the Lord Howe Rise, the Queensland Plateau, and greater India were conjoined as part of the Gondwana landmass, with Australia situated between latitudes of 50° and 80°S (Dettmann, 1994). Seafloor spreading at this time progressed southward and eastward around the Australian continent during the earliest Cretaceous (BMR Palaeogeographic Group, 1990; Veevers *et al.*, 1991).

The Early Cretaceous floras resembled those of the Middle and Late Jurassic, but by the end of the period many of the taxa had become extinct and the angiosperms had come into prominence (Douglas, 1994). Sediments preserved in over 20 major depositional basins in Australia contain a significant record of this vegetation, but the record is both spatially and temporally patchy.

The oldest macrofloras, assigned to Zone A by Douglas (1969) in the best researched area, the Otway Basin of south-eastern Australia, are little known because of the few known deposits and their poor preservation in the older subsurface part of the succession (Douglas, 1994). The best known element is the bennettitaleans, represented as three leaf compression taxa that are considered to have been understorey components, reminiscent of classical Jurassic (e.g. Yorkshire) floras (Douglas, 1994). Silcrete layers in the Algebuckina Sandstone (Eromanga Basin) of central Australia (Hopgood, 1987) suggest a canopy of conifers (*Brachyphyllum*) with an understorey of pteridosperms, cycads, bennettitaleans, and cryptogams. Terrestrial ferns, an *Isoetes*-like fossil, and two common leaves (*Rienitsia variabilis* and *Taeniopteris spatulata* (?Pentoxylales)) occur here, and they have more affinities with the later (Zone B of Douglas, 1969) floras of the south-east (Douglas, 1994). Preliminary work on collections from the Surat Basin in Queensland (Cantrill & Webb, 1987) indicates a conifer and *Ginkgo digitata* canopy over ferns, an *Equisetum*-like sphenopsid, and pteridosperms. Rozefelds (1988) reported the corystosperm *Pachypteris* and cryptogams from the Laura Basin in northern Queensland. Cretaceous macrofloras from a variety of localities in Western Australia incorporate a range of lycophytes, ferns, pteridosperms, bennettitaleans and conifers, and most closely resemble those from the Algebuckina Sandstone (McLoughlin, 1996) or possibly the Zone B floras of the Otway Basin.

The relationship of several orders of pteridosperms (e.g. Peltaspermales, Corystospermales, Caytoniales) is not clearly defined (Harland *et al.*, 1967) and thus it is difficult to reconstruct their ecological niches as well as their phylogenetic position (Douglas, 1994). Among the bennettitaleans *Ptilophyllum boolensis*, which has fine pinnate leaves, has been interpreted as a semi-prostrate ground cover, or climber (Douglas, 1994). Bennettitaleans are not preserved as the silicified trunks which occur in many overseas localities, and the only indication of a main axis is stem fragments bearing two or three pinnae (Douglas, 1994). Apart from a few rare occurrences in parts of the section of disputed age, bennettitalean macrofossils have not been found in younger Australian assemblages.

In the Zone B floras of the Otway Basin (Douglas, 1969), leaf fragments (*Ctenis? coronata*) provide one of the very few macrofossil records of the Cycadales in the Cretaceous of south-eastern Australia, where the order is not otherwise recorded until the Palaeogene (Hill, 1978, 1980; Douglas, 1994; Hill & Pole, 1994). *Ginkgo australis*, a key zone macrofossil in younger beds of the south-east of the continent, appears for the first time in the fossil record, with *Taeniopteris* and *Phyllopteroides*, in the Surat Basin. The Stanwell Coal Measures flora (Queensland) also contains these two latter genera (Cantrill & Webb, 1987).

The earliest Cretaceous palynological data indicate that araucarians and podocarps were important elements in the Australian vegetation (Dettmann, 1994). Abundant pollen of these austral conifers, including the *Araucaria*/*Agathis*-, *Podocarpus*-, and *Microcachrys*-types (Fig. 61), are associated with frequent pollen indicative of pteridosperms and/or bennettitaleans, and cycadophytes and/or ginkgophytes (Dettmann, 1994), and this is

Figure 61. Time ranges of selected taxa represented in the Cretaceous vegetation of Australia. Time ranges on a world basis are shown for each taxon. (After Dettmann, 1994). (con. = conifer).

mirrored by a macrofossil record of related taxa (see above). *Classopollis* and *Corollina*, indicators of cheirolepidacean conifers, occur in low frequencies in fluvial/lacustrine sediments, but are usually common in marginal marine sediments. Araucarian/podocarp forests probably surrounded river and lake systems, but in coastal regions the forests gave way to cheirolepidacean woodlands (Dettmann, 1994). Spores and/or macrofossils of ferns (including meagre evidence of the aquatic Marsileales), lycopods, isoetaleans, equisetaleans and bryophytes are both abundant and diverse in sediments that accumulated in coastal and inland regions (Dettmann, 1994; Douglas, 1994).

The floral evidence suggests some regionalism among overstorey and understorey communities in the earliest Cretaceous Australian vegetation. The broad riverine area of the Eromanga/Surat Basins supported a more diverse fern, lycopod and moss flora than the narrow depressions of the Otway/Gippsland Basins in the southern rift valleys, which appear to have been more uniformly forested (Dettmann, 1994). In the Perth Basin in Western Australia, diverse assemblages of ferns were represented, including several taxa that are unknown from the south-east prior to the Barremian (Dettmann, 1986a; Helby *et al.*, 1987; Dettmann *et al.*, 1992). Migration of these taxa from the west may have been triggered by tectonic/volcanic disturbances that heralded rifting of India from south-western Australia and widening of the southern rift valley (Dettmann, 1994).

A major rise in relative sea level during late Valanginian to early Barremian times led to marked changes in depositional patterns. India broke away from Australia accompanied by widespread faulting and extrusion of basalts, and the rift between Australia and Antarctica slowly widened, but drainage patterns changed little.

Fossil floras from this time indicate a response of the vegetation to these environmental disturbances. There was an increased representation of the Podocarpaceae, possibly in response to increased precipitation (Dettmann, 1994; Douglas, 1994). However, cheirolepidacean woodlands were well-developed in coastal regions of south-western Australia (Backhouse, 1988).

Earlier concepts of a uniform flora over Australia during earliest Cretaceous times have been revised. Distinct community associations recorded from the disparate depositional areas indicate a regionalised vegetation that reflects latitudinal control as well as habitat differences related to topographic and substrate variations (Dettmann 1986a, 1986b, 1994; Dettmann *et al.*, 1992; Douglas, 1994). Forests of conifers dominated by the Araucariaceae and Podocarpaceae associated with pteridosperms, bennettitaleans, *Ginkgo* and/or cycads occurred over much of the continent, but cheirolepidacean conifers appear to have been more important in the vegetation of coastal regions and *Ginkgo* and cycadophytes in northern areas (Dettmann, 1994; Douglas, 1994). Cryptogam communities also varied across Australia, with more diverse ferns in the south-west, and greater development of lycopod communities about the river systems in the south-east and north-east (Dettmann, 1994).

Early angiosperms in Australia (latest Barremian–Cenomanian)

Angiosperms are first recorded in Australia during latest Barremian or earliest Aptian times (Fig. 61), with magnoliid taxa being the first present (Dettmann, 1994). The earliest occurring pollen (Barremian) are known from the Eromanga and Gippsland Basins and are referable to *Clavatipollenites*, which includes pollen comparable to that of *Ascarina* of the Chloranthaceae (Dettmann, 1986a; Burger, 1990). In the Gippsland Basin the pollen is associated with the oldest known flower branchlet which has been interpreted as representing a plant of prostrate herbaceous habit (Taylor & Hickey, 1990). Seeds tentatively assigned to the angiosperms (Douglas, 1963) are also an important part of this flora. Habitats of these early angiosperms included lakeside and riverine areas in the southern rift valley as well as the broad coastal plains adjacent to the estuary of the Eromanga Basin (Dettmann, 1994). Important macrofossils at this time include *Ginkgo australis*, which was widespread, and the spathulate-leaved pentoxylalean, *Taeniopteris daintreei*, which thrived in a range of habitats had leaves up to 200 mm in length (Douglas, 1994). Sometimes *T. daintreei* is accompanied by masses of seeds, and the pollen-bearing organ ascribed to this plant (*Sahnia laxiphora*) has been recognised from the well-known Koonwarra Fish Beds.

The earliest angiosperms represented in the Australian region probably migrated from a source in northern Gondwana or southern Laurasia (Muller, 1981; Dettmann, 1986a; Burger, 1990). Migration was more rapid than initially postulated (e.g. Dettmann, 1973) since there is only a brief time lag between latest Barremian/Aptian introduction in Australia and Hauterivian first appearances in the northern Gondwanan/southern Laurasian region (Brenner, 1984; Hughes & McDougall, 1986; Hughes, 1994). This evidence argues against Australia as a cradle region of the angiosperms (Takhtajan, 1969) and, further, provides little support for inception and diversification of earliest angiosperms on fragments of the Australian plate which rafted northwards during the Late Jurassic (Takhatjan, 1987). Radiation from the source region coincided with early opening of the North and South Atlantic Oceans, and it has been argued that associated environmental disturbances provided the trigger for dispersal (Dettmann, 1986b). The route to Australia may well have been via Antarctica and thence into southern Australia with the southern rift valley forming the
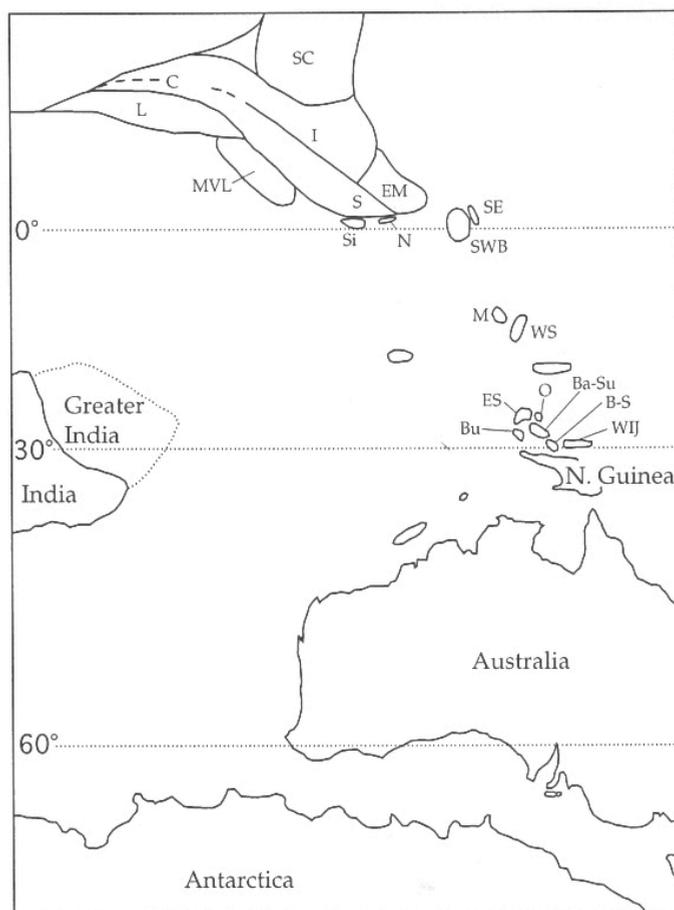

Figure 62. Speculative reconstruction of SE Asian terranes in relation to Australia for the Late Cretaceous (after Metcalfe, 1990). SC = South China; C = Changtang; L = Lhasa; I = Indochina; MVL = Mount Victoria Land; S = Sibumasu; Si = Sikuleh; EM = East Malaya; N = Natal; SE = Semitau; SWB = South West Borneo; M = Mangkalihat; WS = West Sulawesi; O = Obi-Bacan; ES = East Sulawesi; BU = Buton; Ba-Su = Bangai-Sula; B-S = Buru-Seram; WIJ = West Irian Jaya.

vehicle for floral channelling (Dettmann, 1986a, 1989). As noted earlier, migration from East Asia to northern Australia using a series of postulated microcontinents (Burger, 1981, 1990; Truswell *et al.*, 1987) (Fig. 62) awaits substantiation, but theoretically provides a route for the ancestors of some important taxa (e.g. *Nothofagus* (Hill 1992; Hill & Dettmann, 1996; Hill, 1996). Modification of the vegetation associated with angiosperm invasion in Australia seems to have been more important in understorey communities than in canopy associations, with sporadic increases in hepatic and fern diversity occurring in the understorey (Dettmann, 1994).

With a major rise in sea levels during the early Aptian, shallow seas flooded the intracratonic basins, and the Australian landmass was reduced to several large islands, the eastern ones of which retained connections with Antarctica, the Lord Howe Rise, and the Queensland Plateau (Dettmann, 1994). In the forest vegetation of the interior basins podocarps were important canopy components, and the understorey included pteridosperms/bennettitaleans together with osmundalean and dicksonialean tree ferns, and communities of diverse terrestrial ferns (Dettmann, 1994). Angiospermous pollen is thus far unrecorded from the palynofloras, and flooding of the formerly broad coastal and lakeside plains may signify denudation of habitats of the early angiosperm invaders within the Eromanga Basin during the Aptian (Dettmann, 1994).

Podocarp forests and cheirolepidacean woodlands also occurred on the western island (comprising south-western areas of Western Australia), but knowledge of the vegetation is poor, except for the Perth Basin (Backhouse, 1988). Angiospermous pollen again has not been reported.

By contrast, coeval sediments in the Gippsland and Otway Basins contain *Clavatipollenites*, which confirms the presence of shrubby or herbaceous angiosperms in the south-east during the Aptian. The forests of the rift valley were floristically simpler than those surrounding the Eromanga, Surat and Perth Basins, where terrestrial ferns were more diverse and the Gleicheniales were abundantly represented (Dettmann, 1994). Moreover, the coastal vegetation of the Perth Basin included communities of Cheirolepidaceae, which were poorly developed about the inland seas and in the southern rift valley.

Near the Aptian/Albian boundary the inland sea retreated from the Surat and Maryborough Basins, and in the Eromanga Basin the eastern exit was closed and the southern limit advanced southwards. The south-western seaway extended east of the Officer/Eucla embayment to the Otway Basin where brackish conditions occurred in low lying areas. Volcanics were extruded in the Otway Basin, and non-marine deposition occurred in the Bass and Gippsland Basins (Dettmann, 1994).

A major vegetational change and the disappearance of several plant groups are recorded in the macrofossil record in the Otway Basin. Fossil assemblages are dominated by the osmundaceous fern *Phyllopteroides dentata* (often fossilised in company with its spore bearing organ *Cacumen*) and a new suite of araucarian and podocarp conifers (Douglas, 1994). Cantrill (1989, 1991) described several Araucariaceae taxa (seven foliage, one wood, and nine fertile organ taxa), three Podocarpaceae (one foliage and two wood taxa), and three Taxodiaceae (one foliage, one root and one wood taxon). *Geinitzia tetragona* (Taxodiaceae), associated with mycorrhizal rootlets in a palaeosol, is considered to indicate nutrient deficiency (Cantrill & Douglas, 1988). This vegetation prevailed over a much more subdued relief with flood plains prominent. *Ginkgo australis* was replaced by less digitate, smaller-leaved forms which may represent a distinct species. Terrestrial and aquatic ferns and hepatics prevailed in damp environments, and two small ferns with very long, narrow pinnae, *Alamatus bifarius* and *Amanda floribunda*, formed part of the community around the mud banks (Douglas, 1994). *Alamatus* bore oval sori in rows on each side of a main vein, while *Amanda* had unusual fertile spikes with sori in elongate clusters on modified pinnae. The angiosperms, although still rare at most outcrop localities, are represented by crenate leaved species, including the probably aquatic *Hydrocotylophyllum lusitanicum*, the first lanceolate leaf (Medwell, 1954) and cuticular debris in bore cores (Douglas, 1994).

Palynological evidence also indicates increasing regionalism of the Australian vegetation, and more widely distributed angiosperms (Dettmann, 1994). Angiosperms persisted in the

south-east and, after retreat of the inland sea, were re-established in the Eromanga Basin and spread to the Surat Basin (Burger, 1990). Only chloranthaceous types are known, but the diversity had increased slightly within this group. The angiosperms probably colonised newly exposed areas, which were also invaded by aquatic, riparian and dry-zone communities of sphagnalean mosses and marsilealean, gleichenialean and schizaealean ferns (Dettmann, 1994). In the south-east portion of the Australian-Antarctic rift valley podocarp/araucarian forests persisted, but the floodplain flora expanded in response to widening of the river/lake systems. Even so, terrestrial and aquatic ferns were considerably less diverse than those of northern regions, and the vegetation retained a substantial lycopod component (Dettmann, 1994).

During the middle Albian the sea in the Eromanga/Surat Basins contracted further and was fringed by brackish lagoons and estuaries. Inundation of the Eromanga Basin by the sea occurred in the early late Albian, but the sea retreated again in the latest Albian with re-establishment of broad lagoonal and estuarine areas (Dettmann, 1994). To the east, coal-forming swamps occurred in depressions of the Maryborough and Styx Basins. The Eucla embayment was of lesser extent, but the easterly-extending estuary was flanked by rivers and lakes. River and lake systems also occurred in the Bass and Gippsland Basins (Dettmann, 1994).

Walkom (1919) described angiosperm leaves (*?Celastrophyllum* and *Phyllites* sp.) from the Styx Coal Measures in Queensland, but *Taeniopteris*, an indicator of Aptian or earlier deposits in the south-east, survives in this assemblage (and in the Cenomanian Winton flora, see below), which has caused some confusion about the age of these sediments. The Burrum Coal Measures assemblage of the Maryborough Basin in Queensland, which is the same age as the Styx assemblage (Day *et al.*, 1983), contains equisetaleans, *Ginkgo australis*, cycads and Araucariaceae similar to those of the Otway Basin (Douglas, 1994).

Palynological evidence confirms that non-magnoliid angiosperms were present in the Australian vegetation by the middle Albian and diversified rapidly during the late Albian (Burger, 1990; Dettmann *et al.*, 1992), and Burger (1993) recognised about 40 angiosperm species from pollen retrieved from the early to middle Cretaceous of the Eromanga Basin. Diversification was coincident with regression of the sea in the Eromanga/Surat Basins, and with widening of the floodplain in the southern rift valley (Dettmann, 1994). Precise affinities of the majority of non-magnoliid angiosperms are unknown, but *Tricolpites minutus* has an *in situ* association with fossil flowers of the Platanaceae in North America (Friis *et al.*, 1988). Several of the angiosperm pollen taxa have restricted distribution, and assemblages from northern areas of Australia are more diverse than those from the south-east (Dettmann, 1973; Burger, 1990). There are few data from Western Australia, but tricolpate angiosperm pollen occur in Albian sediments (Balme, 1964).

Cryptogams and gymnosperms also express regionalism at this time, particularly with respect to understorey communities (Dettmann, 1981; Dettmann & Thomson, 1987; Dettmann *et al.*, 1992). Community associations were also regionalised. Palynofloras of the intracratonic basins imply heathland and aquatic associations of diverse ferns, mosses and hepatics, whereas in the Styx and Burrum coal swamps the moss/hepatic element was poorly represented (Barnbaum, 1976). Understorey of the Otway Basin forests included dry-zone and aquatic ferns, hepatics and lycopods, but the ferns were less diverse and the gleicheniaceous types less prolific than in northern regions (Dettmann, 1994).

Early in the Cenomanian there was a major change in drainage systems and environmental patterns as Australia began to assume its present shape. Lakes and swamps developed in the Eromanga Basin after retreat of the sea. This was coincident with a major change in the tectonic regime when uplift was initiated along the eastern margin and subsidence occurred along the western margin. Seafloor spreading commenced along the southern margin, where marine conditions were established as far east as the Otway Basin. A lake system persisted in the Bass Basin, and to the east of the Gippsland Basin, the proto-Tasman Sea was initiated (Veevers *et al.*, 1991; Dettmann, 1994).

Palynofloras indicate that profound vegetational changes were associated with the dramatic changes in environment. In the south-east, riparian and aquatic communities appear to have

been largely replaced by dry-zone associations. Notable is the increased diversity and representation of *Anemia* and *Selaginella*-type spores. Araucarian pollen is common and canopy associates of the araucarians included podocarps of the *Microcachrys*- and *Podocarpus*-type. *Classopollis* is occasionally frequent, implying the presence of cheirolepidacean woodlands. Magnoliid and non-magnoliid dicotyledonous angiosperms are represented by sulcate, tricolpate, tricolporoidate, and tricolporate pollen. Sulcate types similar to liliaceous monocotyledonous pollen are also present and there are rare grains of *Australopollis obscurus*, a form reminiscent of pollen of *Callitriche* (Macphail & Partridge, 1991).

There are notable differences between latest Albian–Cenomanian palynofloras from the south-east and those from the Eromanga Basin. The gymnospermous component of the Eromanga palynofloras includes a high proportion of podocarp pollen, and the cryptogam spore assemblages are more diverse and contain greater proportions of *Gleichenia*- and *Anemia*-type spores than those from the south-east (Dettmann, 1994). Abundant marsilealean, hepatic, and equisetalean and/or isoetalean spores are also present. Angiosperm pollen assemblages are similar to those of coeval sediments from the south-east but are more diverse with respect to the tricolpates, tricolporoidates and tricolporates, and contain *?Afropollis*, which includes pollen of winteraceous affinity (Doyle *et al*., 1990). However, *Callitriche*-type pollen has not been reported from the latest Albian–Cenomanian of the Eromanga Basin. Palynofloras similar to those of the Eromanga Basin are known from Bathurst and Melville Islands, north of Darwin, but they contain higher frequencies of *Classopollis*, *Balmeiopsis* and *Hoegisporis* (Burger, 1976). Brachyphyll pollen and common gleicheniaceous spores have been reported from the latest Albian–Cenomanian of the Perth and Eucla Basins (Balme, 1964; Ingram, 1968).

The palynological record confirms regional differences in the Australian vegetation during latest Albian–Cenomanian times (Dettmann, 1994). The Eromanga lakes and swamps were surrounded by conifer/cycad woodlands and heathlands of ferns. Lakes and swamps supported aquatic and littoral communities of ferns, fern allies, and hepatics. Angiosperms were probably distributed throughout these habitats. The Cheirolepidaceae appears to have been more strongly represented in coastal vegetation than in inland areas. Compared to the Eromanga Basin, the Otway and Gippsland Basins had less diverse fern communities and only slight development of aquatic communities. Cheirolepidacean conifers probably occurred in coastal sites, but the brachyphylls that shed *Hoegisporis* were poorly represented in the south-east.

A particularly important Cenomanian macrofossil flora occurs in the Winton Formation of central Queensland. Bose (1955) described equisetalean nodal diaphragms (*Equisetites* sp.), araucarian foliage-bearing shoots (*Araucaria* spp.), bark impressions, and detached taxodiaceous foliage-bearing twigs and cones (*Athrotaxis* sp.). In the next significant study of the flora, Peters & Christophel (1978) described permineralised taxodiaceous cones (*Austrosequoia wintonensis*) from a locality that also yields remains of various ferns, conifers and angiosperms. McLoughlin *et al*. (1995) described a diverse impression flora containing ferns (?Osmundaceae, Gleicheniaceae, *Cladophlebis*, *Sphenopteris*), *Ginkgo*, diverse conifers (including *Araucaria*, ?Podocarpaceae (*?Elatocladus*), Taxodiaceae (cf. *Austrosequoia wintonensis*) and one unknown form), *Taeniopteris*, and abundant leaves of eight species of angiosperms, all assignable to the Hamamelidae and possibly all with betulaceous and fagaceous affinities. This flora provides the first direct macrofossil evidence of the transition from gymnosperm- to angiosperm-dominated floras in Australia during the Cretaceous.

The forests and heathlands of the Aptian-Cenomanian grew at high latitudes, and the palynological evidence suggests that the forests mostly had a well-developed understorey and that the canopy would have had an open structure. Aptian palaeotemperatures of 12°C for the Eromanga sea (Stevens & Clayton, 1971) and 0–5°C for the Otway Basin (Gregory *et al*., 1989) confirm cool to cold climates, possibly with strong seasonality (Dettmann *et al*., 1992). Middle to late Albian palaeotemperatures signify warmer seas than for the Aptian. The highest value (16°C) is from the south-western Eromanga Basin where circulation was restricted. In the northern part of the basin, recorded temperatures (12°C) are similar to those reported from the Carnarvon Basin, Western Australia (Dettmann *et al*., 1992), although

palaeotemperatures of Albian seawater from the Carnarvon Basin are approximately 7–11°C (Pirrie *et al.*, 1995). Cool to warm temperate climates with moderate to high precipitation occurred in the forested areas of the south-east and north-east, whereas in the Eromanga/Surat Basins, where there was extensive development of heathlands, rainfall may have been lower or seasonal (Douglas, 1986; Dettmann *et al.*, 1992).

Differentiation of Gondwanan elements and evolution of Australian elements (Turonian–Maastrichtian)

By the Turonian most of the continent was emergent. A river system developed in the former Eromanga Basin and drained south into the embryonic Southern Ocean, transporting sediment derived from the eastern highlands. Australia and Antarctica were linked through Tasmania, which separated the developing Southern Ocean on the west from the advancing Tasman Sea to the east. Lacustrine deposition continued in the Bass Basin and basalts were extruded in the Gippsland Basin (Veevers *et al.*, 1991; Dettmann, 1994).

Profound vegetational changes in both understorey and overstorey communities occurred in the south-east at about the Cenomanian/Turonian boundary. Some important components of extant austral floras appeared, such as *Lagarostrobos* and *Dacrydium* (Podocarpaceae). Early Proteaceae first occurred in the Turonian, followed by *Dacrycarpus* (Podocarpaceae) in the Santonian (Dettmann, 1994, Fig. 61). *Ilex*, which is now cosmopolitan, may have originated in the region (Martin, 1977). The podocarp/araucarian forest canopies probably included angiosperms, such as *Macadamia* and *Gevuina*/*Hicksbeachia* (Proteaceae; Dettmann & Jarzen, 1990)) by at least Santonian times (Dettmann, 1994). Angiosperm pollen assemblages increase steadily in diversity and there was considerable turnover of taxa among the cryptogams. *Ascarina*-type and liliaceous-like sulcate pollen occur infrequently, but *Callitriche*-type pollen is well-represented; aquatic and terrestrial herbs and shrubs were probably also present (Dettmann, 1994). Spores of hepatics and *Lycopodium* declined abruptly in diversity, whereas those of *Selaginella* increased. The fern component included *Lophosoria*, Gleicheniaceae, Osmundaceae and Marsileaceae, but Pteridaceae and Schizaeaceae were poorly represented. Several of these taxa migrated into the region during Turonian–Santonian times after earlier appearances elsewhere in Australia or southern Gondwana (Dettmann, 1994).

There are few published data from other areas. Sediments on Melville Island, off the Northern Territory coast, contain more diverse angiosperm pollen assemblages, but with several taxa in common with those from the south-east (Dettmann, 1973). Proteaceous-like pollen and abundant gleicheniaceous spores occur in Santonian spore-pollen assemblages from the Eucla Basin (Ingram, 1968).

During the Campanian and Maastrichtian, seafloor spreading continued along the southern margin, but Australia remained linked to Antarctica. Lakes occurred in the Bass Basin, and drained into the estuaries of the Gippsland and Otway Basins. The river system emptying into the Southern Ocean persisted, and a northward flowing river is believed to have developed in the Officer and Canning Basins. Igneous activity occurred along the eastern margin and may have been associated with the onset of seafloor spreading in the south-east and of rifting in the north-east. Emergent areas existed in the north-east linking Australia to eastern Papua New Guinea and New Caledonia (Dettmann, 1994).

Knowledge of the Australian Campanian-Maastrichtian vegetation comes mainly from the Gippsland, Otway and Bass Basins. Palynological data confirm that the area was forested, with components of the older (Turonian–Santonian) vegetation and newly introduced taxa. There were araucarians, diverse podocarps, *Nothofagus* (Nothofagaceae) for the first time, and increasingly diverse Proteaceae (Dettmann 1994).

Among the Proteaceae, several taxa (*Knightia*, *Macadamia*, *Bleasdalea*(=*Turrillia*), *Grevillea*) were probably in the canopy; others (*Carnarvonia*, *Telopea*, *Persoonia*) in the forest understorey; and yet others (*Stirlingia*, *Adenanthos*, *Beauprea*, *Beaupreopsis*) in sclerophyllous communities on forest fringes and/or nutrient deficient soils (Dettmann & Jarzen, 1991, 1996). Other rainforest associates included Winteraceae, *Ascarina*, *Ilex*

(Aquifoliaceae) and *Gunnera* (Gunneraceae). Pollen that may represent *Clematis* (Ranunculaceae), Trimeniaceae, *Callitriche* (Callitrichaceae), and Epacridaceae also occur (Dettmann & Jarzen, 1990; Dettmann, 1994). The cryptogam flora included mosses, hepatics and diverse selaginellids. Gleicheniaceae, Osmundaceae, *Culcita* (Culcitaceae), *Blechnum/Doodia* (Blechnaceae), *Pteris* (Pteridaceae), *Actinostachys* (Schizaeaceae), and possibly *Azolla* (Azollaceae) were represented in fern communities (Dettmann, 1994).

A site near the Olgas in central Australia has palynofloras rich in Proteaceae associated with less frequent podocarps and very rare *Nothofagus* (Twidale & Harris, 1977; Harris & Twidale, 1991). *Gunnera* pollen and microsporangia of ?*Azolla* are also present. Another site, in the Capricorn Basin off the central Queensland coast, contains common Casuarinaceae pollen and fern spores associated with rare *Clematis*-type pollen in assemblages that are questionably of latest Cretaceous age (Hekel, 1972). The vegetation of these northern sites was distinct from that in the south-east, but it is uncertain whether these dissimilarities represent geographic or age differences.

During the Turonian–Maastrichtian, Australia slowly drifted northwards and by the close of the Cretaceous the south-east was at latitudes of 65°S. Evidence for climates of the Turonian is conflicting; a single ammonite from the Otway Basin provided a palaeotemperature of 28°C (Dorman, 1966), but associated foraminiferal faunas indicate cold waters (Taylor, 1964). Palynological evidence confirms forests dominated by Podocarpaceae, which probably had an open canopy structure. During the Santonian-Maastrichtian, proteaceous trees (*Knightia*, *Macadamia*, *Bleasdalea*) were represented in the canopy. The cool temperate conditions implied by palaeotemperature determinations (16.5–19°C) and foraminiferal faunas (Dorman, 1966; Taylor, 1964) indicate tall open-forests (up to 30 m in height) with canopy taxa (mainly podocarps and Proteaceae, but also rare *Nothofagus* subg. *Brassospora* having conical-shaped crowns and coriaceous, notophyll-sized leaves (Specht *et al*., 1992). An open-forest structure at the high latitudes would allow some light to penetrate to a shrubby understorey of Proteaceae (*Carnarvonia*, *Telopea*), Winteraceae, Trimeniaceae and *Ilex*, and a ground stratum of diverse cryptogams. Many of the taxa represented in the Late Cretaceous open-forests survive today in closed-forests (rainforests) in the Australasian flora and some (e.g. *Dacrydium*, *Dacrycarpus* (Podocarpaceae), and *Knightia*, *Bleasdalea*, *Macadamia* and *Carnarvonia* (Proteaceae)) are restricted to north-eastern Australasia (Dettmann, 1994). She noted that although rarely dominant in present-day perhumid forests, canopy taxa with a Cretaceous history have slender, conical crowns that are sometimes emergent above the dominants which have spreading, dome-shaped crowns. Dettman speculated that, as Australia drifted into lower latitudes during the Tertiary, the gaps between the canopy taxa of the Cretaceous forests were filled by invasive or newly evolved autochthonous taxa with growth habits that maximised solar absorption in mid to low latitudes.

Cretaceous–Tertiary (K–T) boundary event

There are no well exposed Cretaceous–Tertiary boundary sections in Australia, and hence no evidence in the form of the iridium layer or otherwise of a catastrophic event at this time. There is also scant palaeobotanical evidence for the effect of the K–T boundary event in Australia. Wolfe (1991) concluded that the impact event which caused mass extinction at the K–T boundary occurred in June, based on the reproductive stage reached by fossil aquatic plants in the Northern Hemisphere. He noted that the 'impact winter' had little effect on the land biota at high southern latitudes, which were, by his argument, in mid-winter. Many deciduous plants were present at high southern latitudes at this time, and they would have been in a leafless, dormant state, while evergreen plants at these high latitudes would have been in a dormant phase. Wolfe (1987) predicted that if mesothermal vegetation had been devastated in the Southern Hemisphere by an 'impact winter', a rise to dominance of *Nothofagus* might be expected. However, he noted that in inferred mesothermal regions, Paleocene palynofloras represent a diverse forest containing taxa that are now exclusively evergreen. This, along with evidence on the vulnerability of modern wood tissues to freezing, led Wolfe to conclude that no effect of an 'impact winter' can be detected in Southern Hemisphere vegetation. Wolfe's scenario explains the lack of evidence to date for the effect

of the K–T impact on high southern latitude vegetation. However, some of the assumptions made by Wolfe (1987) in reaching his conclusion have now been questioned. It is important to recognise that there are fundamental differences between the floras of the Northern and Southern Hemispheres and these differences have a complex history, which cannot be attributed to a single cause, no matter how catastrophic it may have been (Hill & Scriven, 1995).

Bore core macerations and microfloras indicate that many of the angiosperm families that achieved prominence as the Tertiary proceeded were present in the latest Cretaceous. Although available evidence indicates that the vegetation was modified considerably at or near the Cretaceous/Tertiary boundary (Helby *et al.*, 1987), Dettmann (1994) concluded that a mass extinction event is not evident. She noted that many of the Cretaceous taxa range into the Tertiary, but some have broken stratigraphic ranges involving the Paleocene. This phenomenon has been interpreted as indicating short distance retreat of the plants during the earliest Tertiary, followed by advance during latest Paleocene-Eocene times (Dettmann & Jarzen, 1991). Causative mechanisms may have involved alterations to drainage patterns near the close of the Cretaceous. However, Macphail *et al.*, (1994) noted an apparently massive impoverishment of the angiosperm flora at the K–T boundary and a possibly related major expansion of gymnosperms, which they believed was best interpreted in terms of mass extinction.

Macrofossil data are almost non-existent. Although there has been no systematic examination of cores from the 40 or so bores that may provide information on Cretaceous–Tertiary boundary events in the Otway Basin, preliminary observations reveal no macrofossil changes anywhere near as marked as those between zonations within the Cretaceous recognised by Douglas (1969).

Southern mid–high latitudinal phytogeographic region; source and dispersal corridor of austral plants

Close floral relationships existed between Australia and associated high latitudinal areas of southern Gondwana throughout the Cretaceous (Dettmann, 1981, 1986b; Dettmann & Thomson, 1987; Dettmann *et al.*, 1992) in the Southern Gondwana Floristic Province (Brenner, 1976) (also known as the Weddellian Biogeographic Province (Case, 1989)). This region was characterised by a series of podocarp/araucarian forests, and was invaded by early angiosperms during latest Barremian–Aptian times from a source in northern Gondwana. 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 (Dettmann, 1986b, 1994), the geographical limits of which fluctuated during opening and enlargement of the South Atlantic, Indian, and Southern Oceans (Dettmann & Thomson, 1987).

The Cretaceous pre-angiospermous vegetation of southern Gondwana was characterised by regionalism within both overstorey and understorey associations, which is believed to have been influenced by climatic as well as topographic and edaphic factors (Dettmann, 1986b, 1994; Askin, 1989). Associated with the canopy of podocarps and araucarians were ginkgos, cycads, taeniopterids, pteridosperms and bennettitaleans together with ground communities of ferns, lycopods and bryophytes. In northern areas (India, Patagonia, northern Australia), araucarians were more important in the canopy than the podocarps, and cycads were more plentiful in interior and northern coastal areas than ginkgos which appear to have preferred more humid habitats (Dettmann, 1994). Cryptogam associations also varied across southern Gondwana; fern spores are more plentiful and diverse in what were coastal regions, whereas lycopods (mainly *Lycopodium*) thrived in inland areas. Spores of sphagnalean mosses and hepatics have greater abundance in depositional basins in low-relief compared with high-relief terrains (Dettmann, 1986b, 1994).

As the oceans opened, disturbances to adjacent land areas appear to have been the driving force for floral evolution and exchange (Dettmann, 1989; see earlier discussion). Many taxa migrated to Australia after originating elsewhere, and migration was predominantly in an easterly direction in the southern Gondwanan assembly, with South America, India, and

Antarctica being crucial migrational pathways during the earliest Cretaceous (Dettmann, 1994).

Evidence for angiosperm introduction into Australia suggests routes involving southern Gondwana, and radiation was contemporaneous with opening of the South Atlantic and Indian Oceans. As was typical of southern Gondwana, the first angiosperms to arrive in Australia were herbaceous or shrubby chloranthaceous taxa, which would have competed with taxa in the shrubby strata at forest fringes, or those of the understorey within the forests (Dettmann, 1994). The latest Barremian–Aptian vegetation existed under cool to cold, humid climates, and the forests had open canopies (Creber & Chaloner, 1987; Specht *et al*., 1992).

A second wave of angiosperms migrated to Australia 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 was in an easterly direction, involving southern South America and Antarctica. India became isolated from the southern Gondwanan assembly, and the meagre information on its mid-Cretaceous vegetation suggests that its floral links with Australia had diminished (Dettmann, 1992). Temperatures were warmer at this time in Australia than for the Aptian, but precipitation may have been less or seasonal in interior regions. By the Cenomanian Australia had commenced its slow drift north (Veevers & Eittreim, 1988), but remained in high southern latitudes where the forests would have had an open structure. Niches occupied by the non-magnoliid dicotyledons included shoreline and floodplain situations, but distribution patterns of the two separate pollen associations delineated by Burger (1990) 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 *Callitriche* were introduced into the vegetation of the southern rift valley. *Callitriche*, which today occupies aquatic and semi-aquatic habitats, may well have had its origins in northern Gondwana (Herngreen, 1973; Dettmann, 1994).

During the Albian–Cenomanian Australasia, Antarctica, southern South America and the Falkland Plateau retained connections and formed the southern Gondwana assembly at high southern latitudes. As the South Atlantic Ocean opened, forests advanced over the Falkland Plateau and partially replaced the cheirolepidacean communities. 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. Thus, for example, 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 south-eastern Australia (Dettmann, 1994). Cheirolepidacean conifers were well represented in northern coastal areas, but were only locally developed about the estuary in the south-east rift valley.

During the remainder of the Cretaceous (Turonian–Maastrichtian), angiosperms continued to migrate into Australia from northern Gondwana, but many newly introduced taxa differentiated from northern Gondwanan lineages in the Australasian-Antarctic region. Northern Gondwanan origins have been demonstrated for *Gunnera* (Jarzen & Dettmann, 1989) (Fig. 63), and *Belliolium*/*Bubbia* (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 Proteaceae was centred in southern high latitudes (Dettmann & Jarzen, 1991). Four of the seven subfamilies of extant Proteaceae are represented in the Campanian-Maastrichtian pollen record of the Austro-Antarctic rift valley (Dettmann, 1994). Diverse assemblages of proteaceous pollen recorded from the Otway Basin, south-eastern Australia includes taxa aligned to *Adenanthos*, *Beauprea* and *Beaupreopsis* (Proteoideae), *Persoonia* (Persoonioideae), *Carnarvonia* (Carnarvonioideae), and *Grevillea*, *Telopea*, *Macadamia*, *Bleasdalea* and *Knightia* (Grevilleoideae) (Dettmann, 1994; Dettmann & Jarzen, 1996). Diversification of the family coincided with habitat changes associated with early opening of the Southern Ocean (Fig. 64). This region may also have been the centre of origin of *Ilex* in the Turonian (Martin, 1977) and of lineages of the Trimeniaceae and Epacridaceae in the Campanian (Dettmann & Jarzen, 1990).

Lagarostrobos, *Dacrydium* and *Dacrycarpus* (Podocarpaceae) and *Nothofagus* (Nothofagaceae), which are important elements of austral temperate rainforests, first appeared in the Austro-Antarctic region 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. Over the years there has been considerable debate concerning the centre of origin of *Nothofagus* or its immediate ancestor in particular, and this was recently summarised by Hill (1992, 1994a) and Hill & Dettmann (1996). The most probable options now seem to be southern South America/Antarctic Peninsula, or SE Asia. Although there is considerable doubt about these centres of origin, the fossil record is very clear on the evolution and diversification of *Nothofagus* (Fig. 65). Differentiation of *Nothofagus*, and appearance in the fossil record of its four extant subgenera occurred during the late Campanian-Maastrichtian in the southern South America/Antarctic Peninsula region. 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. Extant lineages of *Nothofagus* migrated to Australia during the latest Cretaceous–Palaeogene and routes must have involved Antarctica (Dettmann *et al.*, 1990). The same route may have been followed by the Myrtaceae, Olacaceae, Loranthaceae and Sapindaceae (Dettmann, 1994). Antarctica probably served as a dispersal route for several other taxa, with migration in the opposite direction, including several Proteaceae and Epacridaceae that were in Australia prior to their latest Cretaceous–Tertiary arrival in western Antarctica (Dettmann, 1989; Askin, 1989).
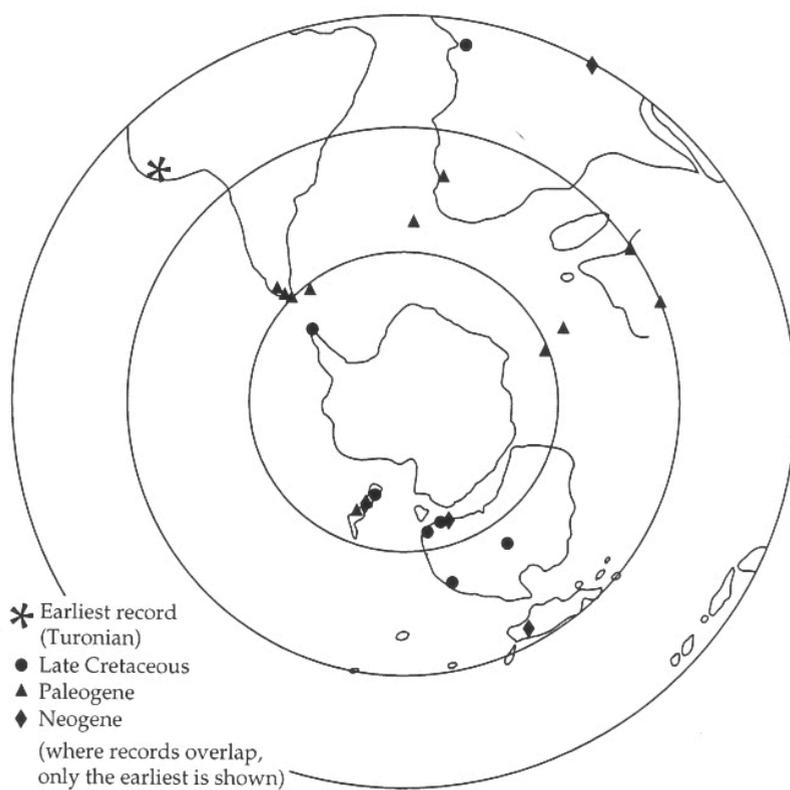

Figure 63. Palaeogeographic reconstruction of the Southern Hemisphere at about Late Cretaceous time, showing the fossil distribution of *Gunnera.* Modified from Hill & Scriven (1995), with data from Jarzen & Dettmann (1989) and Dettmann & Jarzen (1990).
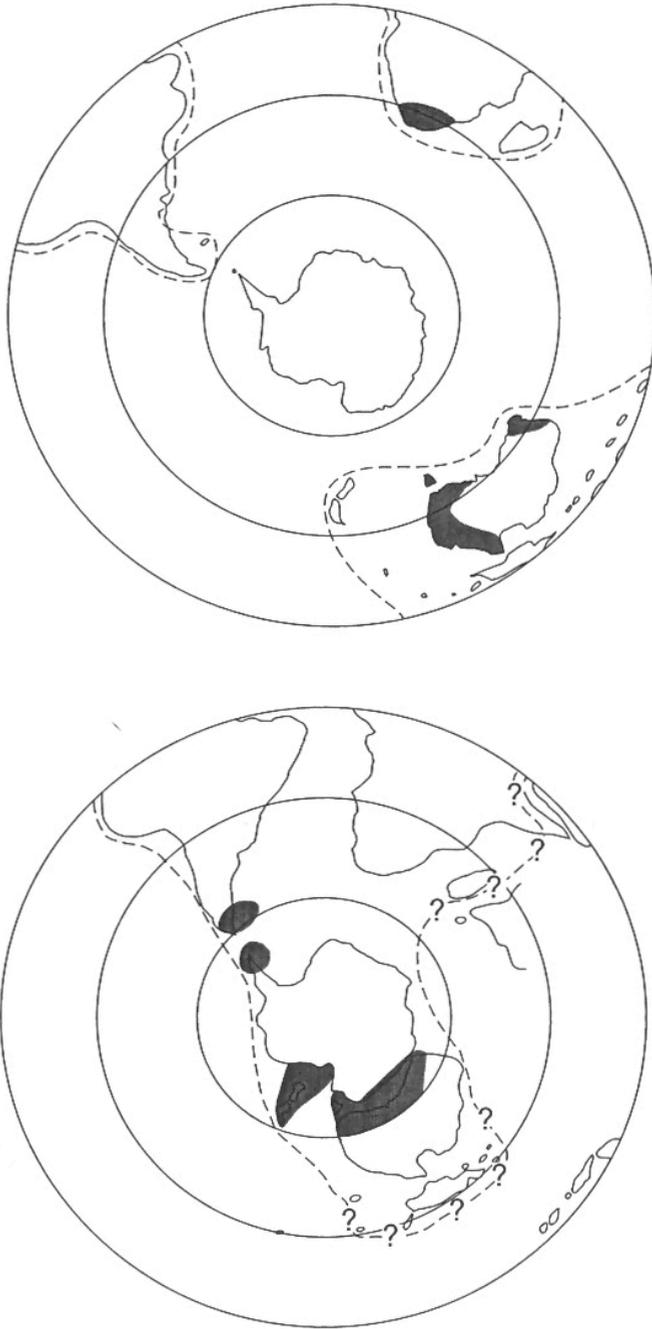
Figure 64. Present and Cretaceous distribution ranges of the Proteaceae plotted on south polar projections for the present (top) and Santonian (bottom). The known range is indicated by a broken line, and question marks indicate an inferred range. Shaded areas mark areas of greatest concentration. Modified from Dettmann & Jarzen (1991).
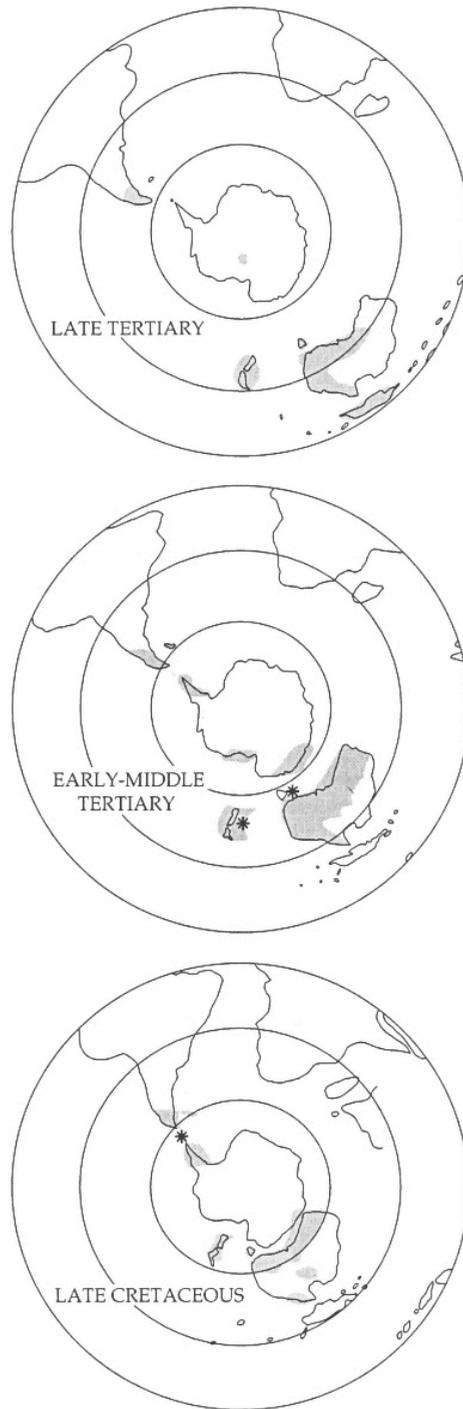
Figure 65. Distribution of *Nothofagidites* pollen plotted on south polar projections (* = diversification centre). After Hill & Dettmann (1996).

Truswell *et al*. (1987) postulated that several of these elements (Olacaceae, Sapindaceae, Myrtaceae) may have been introduced to northern Australia using 'stepping stones' from SE Asia (Fig. 62). Dettmann (1994) concluded that this route is not supported by the pollen record for the Olacaceae and Sapindaceae, but should not be dismissed for the Myrtaceae.

The pollen record demonstrates that several important elements of the modern vegetation were established by the close of the Cretaceous. Most were derived from Gondwanic stock; some evolved in northern Gondwana, and others in the Austro-Antarctic region (Dettmann, 1994). Many of these taxa are now associated in rainforests, but several (*Adenanthos*, *Stirlingia* and some Epacridaceae) are restricted to nutrient deficient soils in the Mediterranean climatic region of southern Australia, implying that sclerophylly in the Australian vegetation dates to the latest Cretaceous (Dettmann, 1994).

The southern Gondwanan Late Cretaceous vegetation was strongly regionalised within the same latitudinal belt and across the latitudes (Dettmann, 1994). The Proteaceae was important in central Australia, but at higher southern Australian latitudes (60–65°S) both Podocarpaceae and Proteaceae were well-represented in the canopy of open-forests (Specht *et al*., 1992). Forest understoreys included shrubby Proteaceae, Winteraceae, Trimeniaceae and *Ilex*, as well as a ground stratum of diverse ferns (Dettmann, 1994).

Summary of Cretaceous vegetation

It is clear that the southern Gondwana vegetation, including that of Australia, was floristically heterogeneous throughout the Cretaceous. Much of the area was forested, but woodlands, heathlands, and aquatic communities also occurred. The high latitude forests had an open structure, podocarps and araucarians were important canopy components, and these two families were established in Australia well before the Cretaceous. Herbaceous and shrubby angiosperms invaded understorey communities fringing and associated with the earliest Cretaceous forests during the latest Barremian–Aptian, and angiosperms had entered the canopy by the Santonian. This mid-Cretaceous interval saw the extinction or marked decline of a number of previously prominent gymnosperm and cryptogam groups, notably Bennettitales, Pentoxylales, *Pachypteris*, *Thinnfeldia*, *Rienitsia*, cheirolepidacean conifers, ginkgophytes and equisetaleans. It is not yet clear whether these extinctions were driven by changes in the physical environment or by competition from the newly arriving angiosperms, and this is an important problem for future research. Australia occupied a peripheral position in the southern Gondwana assembly, and routes traversed by the earliest angiosperm invaders from northern Gondwana predominantly involved other landmasses in the assembly with perhaps some input from SE Asia. The first migratory wave of magnoliid angiosperms occurred no later than the latest Barremian, and was coincident with lowered global sea levels, and early opening of the South Atlantic and Indian Oceans (Dettmann, 1994).

A subsequent angiosperm invasion during the middle Albian–Cenomanian included non-magnoliid lineages that evolved in northern Gondwana during the Aptian. Once again, angiosperms invaded shoreline communities after regression of the Aptian sea in intracratonic basins and widening of the flood plain of the Austro-Antarctic rift valley. Angiosperm migration from northern Gondwana continued during the Turonian–Maastrichtian and was concurrent with *in situ* evolution and differentiation of austral groups in the Australian-Antarctic region. Two loci of evolution and diversification have been identified. Areas surrounding the embryonic Southern Ocean were a diversification centre of the Proteaceae and may have been the place of genesis of *Ilex*. The region including 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) argument that Australia was a centre of origin for early angiosperms, and supports the hypothesis of Webb *et al*. (1986) that Australian rainforests are remnants of a heterogeneous Gondwanan flora, although perhaps with some Asian input. Evidence for the evolution of sclerophylly is also found in the Late Cretaceous pollen record. The sclerophyllous taxa probably formed communities on low nutrient or waterlogged soils on forest fringes (Specht *et al*., 1992).

The Australian Cainozoic

There have recently been major advances in our understanding of the environments of the Cainozoic in Australia. These can be identified in a number of different categories of research and include, from the geological side, a better understanding of the Tertiary timeframe, more data and fresh syntheses of sedimentary environments, and an enhanced understanding of the tectonic setting of Australia within the region. The quantity and the quality of palaeoclimatic and palaeontological information has also increased dramatically recently. Some of these developments are discussed in detail in other chapters, but a brief comment on some is informative here.

The Tertiary timescale

Refinement of the timescale for the Australian Cainozoic has been an ongoing problem since the first marine fossils were identified last century (Truswell, 1993). Standard reference sections for the global Tertiary were established in the Northern Hemisphere, at first with the standard sequences and stages of the Tertiary in Europe, and later, with the development of global timescales for marine planktonic faunas in the Neotropics. There has been considerable effort to relate Australian sequences to these standards, and this has been greatly assisted by using local faunal events in marine sections (e.g. the first and last appearances of planktonic foraminiferal species) and correlating these, with some hesitation, with scales such as the P and N zones (global reference zones based on evolution of taxa within tropical planktonic foraminifera and nanoplankton lineages).

Australian palynological zones, based both on pollen and dinoflagellates, have been erected in southern Australian coastal basins where it has been possible to link them to the local marine sequences. These in turn have been correlated, often tenuously, with international zonal standards. This correlation has been further complicated because Tertiary biostratigraphers have not yet reached agreement on a standard calibration for the timescale in terms of millions of years.

It is still difficult to date sequences of terrestrial origin in Australia. The standard zones have been established in southern coastal basins, and there is still uncertainty concerning just how far away from these basins the zones can be recognised with confidence. This is an issue in trying to establish the age of sediments in the Murray Basin and in central Australia.

There has been some calibration of palynological zones against isotopically dated volcanic rocks in the Eastern Highlands of mainland Australia and Tasmania, where fossil-bearing deposits are interbedded with, or underlie, basalts. Unfortunately, for large parts of the continent there are no basalts. Palaeomagnetic techniques have also been used to calibrate the age of fossil floras. In Lake George, in southern New South Wales, Pliocene pollen-bearing sediments have been dated by magnetic reversal stratigraphy, and in central Australia Tertiary sequences have been related to a Cainozoic polar-wander curve derived from successive positions of the palaeo-pole through the interval (Truswell, 1993). However, despite these efforts, the dating of many fossil-bearing sequences remains a major obstacle to resolving some of the key issues in Australian vegetation history.

Regional geologic framework

The sequence of separation of Australia from the rest of Gondwana is now understood in considerable detail, with current knowledge on the timing of the separations of Australia and Antarctica and Australia and New Zealand summarised by Veevers *et al*. (1991).

The pattern of major tectonic events to the north of Australia is also better understood. It is now believed probable that slivers of continental crust have repeatedly rifted away from Australia's northern margin between the late Palaeozoic and Cainozoic and have become embedded within SE Asia. However, in most cases the precise timing of these rifting and collision events remains problematic. Nevertheless, a clear understanding of the geological history of this region is of immense importance in understanding the phytogeographic relationships between Australia and SE Asia. Information crucial to biology, such as where

the areas of emergent land might have been at particular times in the past is difficult to find, but is likely to represent a major field of research in the near future.

Another facet of geological information which is significant for vegetation (and climatic) history concerns the elevation of Australia's eastern highlands. After decades of controversy, reliable geological information now suggests that this region showed considerable elevation by the beginning of the Tertiary (Truswell, 1993). In the south-eastern highlands, there may have been as much as 800 metres of relief by the Paleocene (Taylor *et al.*, 1990). Such information provides a framework for interpreting possible altitudinal stratification of vegetation during the Tertiary.

Palaeoclimatic data

In dealing with palaeoclimates, it is important that information drawn from outside the vegetation record is clearly separated from that drawn from the plant fossils themselves, in order to avoid a circularity of argument. Sea-surface temperature is one of the important parameters in climatic reconstruction. There is now available a detailed estimate for sea surface temperatures off north-eastern Australia (Fig. 66) that shows temperatures for the Tertiary in the vicinity of the Coral Sea and Queensland Plateau. It has been built by extrapolating oxygen isotopic data from sites in the western Pacific, using latitudinal temperature gradients estimated for 19 time intervals during the Cainozoic. These are thus deduced temperatures.

The curve shows the effects of global cooling during the Palaeogene, and it also records the effects of the northward passage of the Australian plate. The decreasing temperatures during the early Tertiary reflect a high-latitude cooling trend that was global in its impact. In this part of the curve, peak warming in the early Eocene is followed by cooling into the Oligocene. The remainder of the curve reflects the passage of north-eastern Australia first into subtropical water masses and then into the tropical zone. It is interesting to note that, for the central part of the Great Barrier Reef, coral reefs did not begin to develop until tropical water masses were encountered in the Pliocene.

The north-eastern Australian curve describes conditions in areas well offshore. Another curve, developed for Victorian coastal sequences (Fig. 67), shows more local expressions
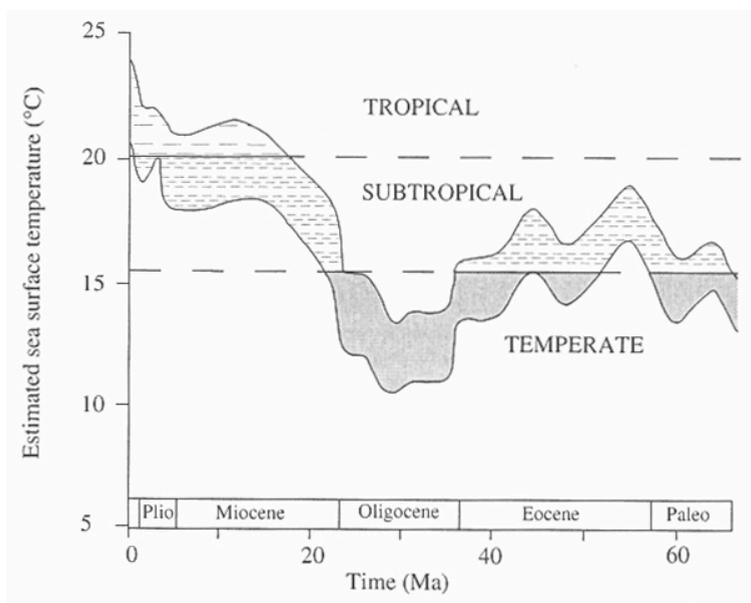

Figure 66. Sea-surface temperatures for north-eastern Australia during the Cenozoic. Simplified from Feary *et al.* (1991).

of global events. There are pronounced temperature drops across a short interval near the Eocene-Oligocene boundary; these are the culmination of declines in sea-surface temperatures that began earlier, probably about the middle Eocene. Locally, these temperature drops were followed by warming in the early Oligocene. Just how far afield these effects were felt is problematic, especially when recent evidence suggests that the first glaciations in Tasmania occurred in the early Oligocene (Macphail *et al.*, 1993).

It is more difficult to obtain quantitative palaeoclimatic data from terrestrial areas than it is from the marine realm. There have, however, been some attempts recently to quantify past climatic conditions on the basis of palynological assemblages, using the BIOCLIM database (see Kershaw & Nix, 1988). This methodology has been applied to pollen suites from the Paleocene and Eocene of the Eyre Formation in south-central Australia (Sluiter, 1991). On the assumption that climatic profiles have remained constant for key taxa, Sluiter estimated that the mean annual temperatures for the region were of the order of 18–19°C, with annual precipitation in excess of 1400 mm in the late Paleocene, and slightly higher in the Eocene.

Mean annual temperatures are only one facet of climatic controls on plant growth; the effects of variability are of equal, perhaps greater, importance. Ecophysiological studies of living genera, notably *Nothofagus*, have made a significant contribution to our understanding of the way in which climatic influences have acted to redistribute taxa that were mutually associated in the early Tertiary. The fossil record provides an empirical history – a series of snapshots – of what grew where at different intervals: the ecophysiological work, such as that undertaken by Read and others (e.g. Read & Hill, 1985, 1988, 1989; Hill *et al.*, 1988; Read & Hope, 1989; Read & Busby, 1990; Read *et al.*, 1990) provides possible reasons for the observed changes.

Other approaches to estimation of palaeoclimate include analysis of foliar physiognomy (leaf size, shape and margin type) and type and distribution of epiphyllous fungi. The former approach has been used extensively in Australia (e.g. Christophel & Greenwood, 1987a, 1989), but there is substantial doubt over the error incorporated in the results (Jordan, 1997). Epiphyllous fungi appear to offer great potential as a reliable method for determining rainfall (both amount and annual distribution), but so far only preliminary research has been carried out (e.g. Lange, 1976, 1978a; Wells & Hill, 1993).
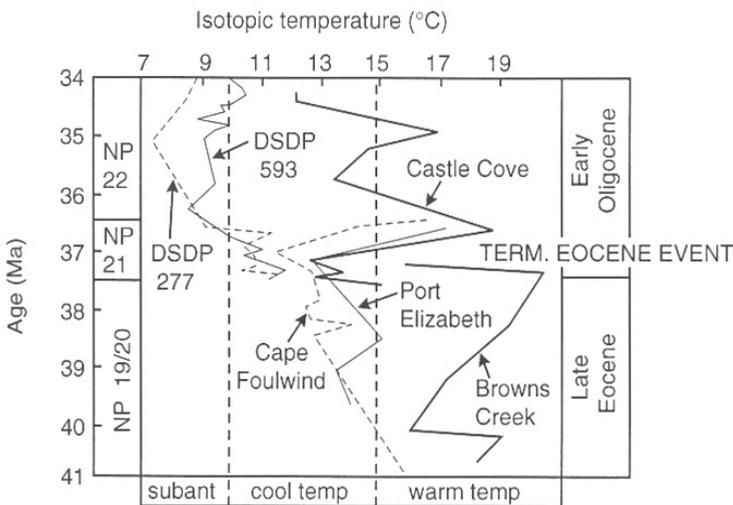

Figure 67. Late Eocene–early Oligocene sea-surface temperatures. The chronological scale on the left with NP zonal units is for nannofossils. The solid line on the right shows temperatures derived from coastal sequences at Browns Creek and Castle Cove in Victoria. Modified from Kamp *et al.* (1990) and Truswell (1993). (DSDP = Deep Sea Drilling Project, NP = Nannoplankton; Term. Eocene Event = Terminal Eocene Event, subant = subantarctic, cool temp = cool temperate, warm temp = warm temperate).

Major vegetation trends in the Tertiary

The main trends in the development of Australian vegetation types during the Tertiary can be identified by focussing on one or two key sites for different time intervals. These are only snapshots of vegetation events for particular intervals of time, and are of necessity selective, but provide at least an outline of important trends.

Palaeocene

At this time Australia was in the early phases of separation from Antarctica, and its southern margin lay at about 70°S, with new seafloor beginning to be generated in the older rift valley separating the two continents (Veevers *et al.*, 1991). Some union still lingered in the region of the South Tasman Rise. It was a phase of warming after the cooling of the Late Cretaceous, with temperatures higher than those of today. The relief of the continent was much as it is at present (BMR Palaeogeographic Group, 1990), but there were extensive river systems on the west Australian shield, carved probably during the Cretaceous, and there were thin sand sheets spread by braided rivers in the east (perhaps by sheet flooding) and continued volcanism in the eastern highlands.

There are palynological sites from northern Tasmania, through the Bass, Otway and Gippsland Basins up to the south-eastern highlands of New South Wales, extending possibly to the northern tablelands, through the Murray Basin and into the centre in the Lake Eyre Basin (Truswell, 1993). Paleocene spore-pollen assemblages have also been recovered from subsurface samples of the Kings Park Formation in the Perth area (Truswell, 1993). A single macrofossil site is known in the south-eastern tablelands (Taylor *et al.*, 1990).

An impression of the vegetation can be gained by reference to sites in the south-eastern highlands. A number of sites occur in this broad region, centred on Bombala, where lake sediments preserved between basalt flows have yielded pollen, a great deal of beautifully silicified wood and leaf floras. These were montane sites, with probably about 800 m of regional relief (Taylor *et al.*, 1990). In the pollen suite about 60 taxa have been identified. The suite is dominated by conifers, by Podocarpaceae in particular, including *Podocarpus*, *Dacrydium* and, very commonly, pollen of the *Lagarostrobos* type. The latter includes both the *L. franklinii* morphotype (now restricted to a monospecific genus on Tasmania's west coast) and a range of related species now extinct. Araucariaceae pollen is present in most samples, as *Araucariacites* and *Dilwynites*. It is interesting to note that *Dilwynites* pollen is being placed in the same lineage as the recently described Wollemi Pine (*Wollemia nobilis*, Jones *et al.*, 1995), due to an ornamentation consisting of scattered granules. The match, however, is not perfect since granules and tuberculae characterising the two described fossil species (*D. granulatus* and *D. tuberculatus*) are much more robustly developed than in *Wollemia nobilis* pollen (Macphail *et al.*, 1995; M.K.Macphail, *pers. comm.*). *Phyllocladus* and *Microstrobos* are also present. For the angiosperms, the ancestral form of *Nothofagus* (*Nothofagidites senectus*) is most common, but there are other *Nothofagus* species too. *Ilex* and Casuarinaceae are present and there are extinct taxa represented by pollen types with no modern affiliates.

At the generic level, the thermal responses of descendant taxa suggest vegetation in the mesotherm response group of Nix (1982), with mean annual temperatures in the 14–20°C range. No overview of the macrofossils is yet available to provide constraints on vegetation reconstruction, but there appear to be about 40 species of angiosperms and conifers including *Eucryphia* (Eucryphiaceae; Hill, 1991a), *Banksieaephyllum* (Proteaceae tribe Banksieae; Carpenter *et al.*, 1994b), *Gymnostoma* (Casuarinaceae; Scriven & Hill, 1995) and *Acmopyle* (Podocarpaceae; Hill & Carpenter, 1991). The evidence suggests that there was temperate rainforest here, more diverse than present Tasmanian rainforests, with gymnosperms forming the main canopy layer. The role of *Nothofagus* is unknown but it may have formed part of the canopy. There was a fairly diverse understorey of largely angiospermous shrubs (R.S.Hill, unpublished data; MacPhail *et al.*, 1994)).

The fossil woods are difficult to identify, except for some which are podocarpaceous, others related to Araucariaceae, and one possible *Nothofagus* (Taylor *et al.*, 1990). Structurally,

most specimens show a wide zone of thin-walled early wood cells, terminated abruptly by a few thick-walled late wood cells, in what are markedly seasonal growth patterns. The annual rings are very narrow, with an average increment of something less than a millimetre, and consistency in width from year to year, all characters which suggest cool, rather uniform climates. There is no sign of frost damage. An essentially mild climate is suggested, with short winter days.

Virtually nothing is known of the structure of the vegetation, although it is reasonable to assume that this might have been controlled by high-latitude factors such as sun angle. From Cretaceous floras on the Antarctic Peninsula (see above) it is evident that the wide spacing of conical trees is a stratagem to maximise available solar radiation at such latitudes. This kind of evidence cautions against interpreting these Paleocene forests as closed forest communities. It is also probable that leaf arrangement in these forests was different to that found today in lower latitude areas, since Wells & Hill (1993) speculated that leaves may have tended to hang vertically to make better use of incoming light from the sun which was low in the sky. This would probably affect leaf size and shape and add a major difficulty to the utilisation of these characters in predicting prevailing climate.

While this was a highland vegetation, the pollen record suggests that lowland forests in the Gippsland Basin differed only in minor detail (Macphail *et al*., 1994), so it seems there was little altitudinal zonation in Australia's south-east at this time.

Eocene

In the Eocene, in spite of its continued high-latitude position, Australia experienced considerable warmth (Feary *et al*., 1991), and the early Eocene was probably warmer than at any other time in the Cainozoic. Fully marine conditions were established along the southern margin and a succession of high sea-levels flooded the coastal basins in south-western and southern Australia (BMR Palaeogeographic Group, 1990), in the west flooding old palaeovalleys almost as far north as Kalgoorlie. Each of these incursions carried its own suite of marine dinoflagellates (Harris, 1985; McGowran, 1989), which have provided a reasonably precise chronology.

Early Eocene: The palynological data suggest that the early Eocene in southern Australia was a period of major development of rainforests, which displayed some megatherm response characteristics (Macphail *et al*., 1994). In extant terms, these are taxa which flourish under mean annual temperatures in excess of 24° Celsius and which are currently confined to the lowland tropics. It may be that the high moisture levels experienced at that time mitigated the seasonal effects that must have come with such high latitudes.

The megatherm character shows up in the diversity and dominance of angiosperms, which, in a most general way, contrasts with the Paleocene. *Nothofagus* species, however, were rare. In the coastal regions the megatherm character is seen in the most southerly expansion of mangroves, such as the palm *Nypa* and the fern *Acrostichum aureum*, which were associated in tidal wetlands as far south as Strahan in western Tasmania (Truswell, 1993).

Middle to Late Eocene: During the middle to late Eocene a cooling trend began that continued in a series of steps to the end of the Eocene. The general trend was interrupted with warmer phases, and these were related to the marine transgressions that crossed Australia's southern margins during the middle to late Eocene (see McGowran, 1989, for an overview).

Fossil floras are the most widespread of any phase of the Tertiary. The spread of sites ranges from oil shales in Queensland, through the south-east, into central Australia, across to the buried drainage channels in the western Australian shield. There are a number of key macrofossil floras, including those at Maslin Bay and Golden Grove, South Australia (Christophel & Blackburn, 1978; Christophel & Greenwood, 1987b; Scriven, 1993), Nerriga, New South Wales (Hill, 1978, 1980, 1982, 1986, 1989a) and Anglesea, Victoria.

Anglesea provides the best studied site, with both macrofossil and palynological data available together (Christophel *et al*., 1987). Here, leaves and other macrofossils, including

flowers and fruit, occur in a number of lenses in the sedimentary sequence. It is apparent that the local vegetation contributing to each lens was of a different character. The overall aspects of the assemblages suggested to Christophel *et al*. (1987) that the most instructive comparison was with living communities in lowland forest north of the Daintree River, Queensland, although the fruitlessness of trying to find precise analogues was acknowledged. The similarities rest on the abundant *Gymnostoma* remains in the assemblage, on fossil relatives of *Diospyros* and *Musgravea*, on numerous leaves of Lauraceae, Myrtaceae, *Brachychiton*, *Elaeocarpus*, Cunoniaceae, *Quintinia*, on *Podocarpus* and on the presence of rainforest cycads and ferns, including *Lygodium*. This kind of vegetation, with abundant broad-leaved, entire-margined angiosperms, occurs at all the known macrofossil sites except some in central and south-western Australia, but there are important floristic differences among the sites. In general, leaf physiognomy suggests mainly mesothermal vegetation, with perhaps some megathermal elements. There are probably numerous extinct species, and many leaves for which affinities remain unknown, but the links seem to be with low-latitude regions and not with present temperate vegetation.

The pollen record at Anglesea by and large mirrors the macrofossil, although there are some minor irregularities. The overall number of taxa is similar, and the major groups expected are all present in the pollen suites. But there are two major divergences: the pollen suites contain a much greater diversity of Proteaceae than the macrofossils do, and *Nothofagus* is well represented as pollen but unrecorded as macrofossils. *Nothofagus* pollen is present in frequencies up to 30%, and includes nine identifiable species in all subgenera, although subg. *Brassospora* species dominate. However, the difference in *Nothofagus* may be more apparent than real (see below), and a similar distinction in Proteaceae noted for Maslin Bay (Christophel & Blackburn, 1978), disappeared when the macroflora was examined in detail (Scriven, 1993).

This high representation of *Nothofagus* distinguishes all pollen floras of the interval. At about the early to middle Eocene boundary, across most of the sites in southern Australia, there is a marked increase in the representation of the genus. It applies to all subgenera, but particularly to subg. *Brassospora*, which may reach levels of 50–60% of the pollen spectra. Leaves of *Nothofagus* have not yet been generally reported from before the late Eocene (Hill, 1988; Pole, 1992), although Scriven *et al*. (1995) have reported a deciduous *Nothofagus* leaf from Maslin Bay and Carpenter & Pole (1995) have described dispersed cuticle of *Nothofagus* subg. *Lophozonia* from Lake Lefroy in Western Australia. It is not until the Oligocene that there are records of subg. *Brassospora* remains among the macrofossils (Hill, 1987, 1991b).

The conclusion to be drawn is that *Nothofagus* species may have been canopy dominants in areas away from the forest edges, and removed from the catchment areas for the macrofossils (Hill, 1990a) yet close enough to dominate the pollen suites. The ecophysiological studies provide a clue to this differentiation of habitat niches in that the living subg. *Brassospora* pollen producers appear to have a lower tolerance to temperature extremes and may have been less competitive in the exposed forest edges, whence most macrofossils come (Read *et al*., 1990). There may also have been other restricting factors such as soil character. However, no really satisfactory explanation has yet been suggested to account for the absence of *Nothofagus* subg. *Brassospora* parent plants among the macrofossil floras of the Early Tertiary, particularly as there was little topographic relief over much of the continent. It is worth noting some possible reasons why this absence may not be as significant as previously suggested. Firstly, the one *Nothofagus* leaf now reported from the extremely diverse Maslin Bay macroflora was deciduous, and thus not robust and unlikely to fossilise (Scriven *et al*., 1995). Maslin Bay is largely an impression flora, but where leaves are usually recovered as mummifications (e.g. Anglesea), deciduous leaves will not be found as they will not survive the chemical processing required. Secondly, Hill (1994a) noted that many leaves of *Nothofagus* subg. *Brassospora* are notophylls with entire or near entire margins. This is exactly the leaf type that dominates the mid-Eocene macrofloras and which have been targeted as being extremely difficult to identify. It is far too early to conclude that this subgenus is absent from these leaf floras. A single macrofossil site from the middle Eocene of central Australia (Christophel *et al*., 1992) suggests that provincialism was well-developed

at this time, since it contains a more sclerophyllous vegetation than in the major contemporaneous floras from south-eastern Australia.

The pollen suites show marked regional differences in the Eocene. For instance, in the floras of coastal Queensland, *Nothofagus* is subordinate to Casuarinaceae, Araucariaceae and often Myrtaceae, a situation which contrasts with that in south-eastern Australia. It is in the minor elements of the pollen suites that key differences occur. In Queensland, taxa such as *Alyxia* (Apocynaceae), Arecaceae (including dicolpate pollen forms), Caesalpiniaceae, *Canthium* (Rubiaceae), and, commonly, Convolvulaceae are present. Many of these taxa are also found in the Murray Basin during the same time interval. Clearly, the vegetation of this wide marshy lowland had much more in common with that of Queensland than with that of the Gippsland and Bass Basins.

There is another suggestion of increasing provincialism at this time, when the palynological record from south-western Australia is examined. While most of the taxa at these sites are shared with those of eastern Australia (see Hos, 1975; Stover & Partridge, 1982; Milne, 1988), there are features that hint at the present strong endemism in the flora having a very long history. For instance, there is an extraordinary diversity of Proteaceae in the Eocene there; in sites near Zanthus individual pollen spectra have produced some 46 species of the family (Milne, 1988). The same spectra have also produced *Acacia* pollen, which is among the earliest records in Australia. A single macroflora from the region, which is unfortunately poorly dated, shows a great diversity of sclerophyllous Proteaceae and Myrtaceae, and bears little resemblance to macrofloras from the eastern seaboard (Hill & Merrifield, 1993). It has been concluded that this site demonstrates a sclerophyllous flora which had evolved in response to low nutrients. Later it was to be influenced by declining rainfall, at which time many of the conifers, *Nothofagus*, and *Gymnostoma* among others, became regionally extinct (Hill & Merrifield, 1993). Sclerophylly continued to increase at this time as well, and this is especially evident in the Proteaceae (Hill & Christophel, 1988). Other macrofloras are present in Western Australia (Carpenter & Pole, 1995; McLoughlin & Hill, 1996) and while they already offer support to the conclusions reached from the West Dale macroflora, further research is required on all these macrofloras to test existing hypotheses.

Early Oligocene to Middle Miocene

Continued northward migration of the continent occurred during this interval, with its northern margin reaching around 20°S (Veevers *et al*., 1991). There was a major fall in sea level in the middle of the Oligocene, associated with the buildup of Antarctic ice. Later, in the early Miocene, there were extensive incursions of shallow seas. These flooded the Eucla Basin, depositing the Nullarbor limestones; there was also extensive deposition of limestones and mudstones in the Murray Basin. In the Gippsland Basin peat accumulated in large freshwater swamps. Inland, there were extensive lakes and slow-moving rivers (BMR Palaeogeographic Group, 1990). Climatically, global temperatures continued to decline after the dramatic drops at the end of the Eocene. Broadly summarised, this was a time of global cooling, with major ice build-up on Antarctica, but there were local intervals of warmer excursions that are marked by marine transgressions in southern Australia.

There is a wealth of vegetation data but poor biostratigraphic control obscures its real significance. This was an interval of about 18 million years, with only a very limited number of rather uncertain subdivisions within it (Truswell, 1993). However, the fossil record preserves a variety of habitats and it is possible to identify some distinctive communities from the available evidence. For example, there were the lowland peat swamps of the Gippsland Basin, the highland floras of New South Wales and Tasmania, lowland, alluvial-fan deposits in Tasmania, and the enormous and complex riverine plain of the Murray Basin.

In the Oligocene there is the first extensive evidence for taxa having affinities with species growing in present-day high-latitude, cool-temperate rainforests. The influences of cooling in southern Australia can be seen in Tasmanian fossil sites such as at Pioneer, Cethana, Lemonthyme Creek, Little Rapid River and Lea River (Hill, 1983, 1987, 1990a, 1990b; Hill & Macphail 1983; Hill & Bigwood, 1987; Wells & Hill, 1989; Hill & Carpenter, 1991; Carpenter *et al*., 1994a; Scriven & Hill, 1996; Hill & Scriven, 1997). However, there are

differences among these, so generalisations are difficult. The rich macrofossil floras contain a variety of *Nothofagus* remains including, at some sites, subg. *Brassospora* species, which were thus part of the nearby vegetation. One of the most interesting features of these floras is that they contain all four of the extant subgenera of *Nothofagus*, with three of them sometimes co-occurring in a single small catchment. These subgenera are currently separated by thousands of kilometres latitudinally (from the equator to about 40°S) and longitudinally from South America (where subg. *Nothofagus* is now endemic) to south-eastern Australia and New Zealand. This poses many important palaeoecological questions, the answers to which are still only partly understood. Another critical feature of the *Nothofagus* macrofossil record is that it provides insights into the evolution of the genus in response to climatic change. Leaf size changes, probably in response to cooling climates, have been recorded for the subg. *Lophozonia* (Hill, 1983, 1991b, 1994a) and subg. *Nothofagus* (Scriven & Hill, 1996), and interestingly the rate of response seems to have differed between the two. There is also important evidence of a much higher proportion of deciduous *Nothofagus* species in southern Australia than at present, where the only surviving deciduous species, *Nothofagus gunnii*, is now the only winter deciduous species in Australia. Finally, evidence from fossil cupules demonstrates that some of the extreme reduction common in subg. *Brassospora* in New Guinea (e.g. reduction of the number of fruits per cupule to one, and reduction of the two cupule valves to membranous flaps much smaller than the fruits) occurred in Tasmania in the Oligocene (Hill, 1994b), and thus cannot be considered as an adaptation to the extant New Guinea ecosystem.

There is also a range of conifers, including some taxa with descendants still in Tasmania (e.g. *Lagarostrobos*, *Athrotaxis* and *Phyllocladus* (Wells & Hill, 1989; Hill, 1989b; Hill *et al.*, 1993), and also taxa that are now extinct in Australia, but which have near relatives on other southern land areas. These include the cupressaceous *Libocedrus* now restricted to New Zealand and New Caledonia, *Austrocedrus* and *Fitzroya* (South America), *Papuacedrus* (New Guinea), the podocarpaceous *Acmopyle* (New Caledonia and Fiji), and the more widespread *Dacrycarpus* and *Dacrydium* (Hill & Carpenter, 1989; Wells & Hill, 1989; Hill & Whang, 1996). Extinct genera of podocarps have also been described (Hill & Pole, 1992). The presence of these taxa cautions against trying to find living analogues for these Tertiary communities.

Trends in leaf size and stomatal distribution thought to be linked to climate change have also been described in some conifer genera. In particular, *Dacrycarpus* decreased its leaf area by reducing the amount of bilaterally flattened foliage and reduced the stomata on the bifacially flattened foliage, eventually losing them altogether from the abaxial surface. *Acmopyle* appears to have been unable to modify its leaf area, but was able to reduce its stomatal distribution by producing hypoplastic stomata on the functional upper surface of the bilaterally flattened foliage (Hill & Carpenter, 1991).

The pollen floras of this period are dominated by *Nothofagus*, mainly subg. *Brassospora*, but they show a diversity of other species, and a varied angiosperm flora, as well as the conifers. In essence, there is a mix of plants with relatives that now are geographically widespread; they have a latitudinal and an altitudinal spread that ranges from low altitude forests at low latitudes, to high altitudes at high latitudes. Hill (1990a) has grouped the taxa into those with affinities to taxa growing today only at low latitudes, including a number of conifer species, *Gymnostoma*, Lauraceae and *Nothofagus* subg. *Brassospora*; those which have migrated north but left descendants in the south, such as *Nothofagus cunninghamii*; those which occur now at mid-latitudes on Australia's east coast, for example *Nothofagus moorei* and *Eucryphia moorei*; and those taxa which have remained in the south, of which *Nothofagus gunnii*, *Phyllocladus*, *Athrotaxis* and *Microstrobos* are examples. There are also a number of extinct taxa within the fossil floras with no extant descendants. The evolution of the living forest types can be viewed as a sifting of these Oligocene 'mixed' forests over very long periods of time, in response to climatic change, or to a complex of selection pressures. One of these sifting mechanisms may have involved the replacement of forest dominants by recruitment from the relatively unstable habitats at the forest margins.

Evidence for the presence of open heath-like communities comes from the lowland peat swamps of the Gippsland Basin. Regional pollen assemblages are typical for the time in

being dominated by *Nothofagus*, but there are particular pollen suites in which Epacridaceae and Gleicheniaceae are common, with high *Banksia* and Restionaceae counts (Luly *et al.*, 1980). In the Yallourn Seam, which is probably mid-Miocene in age, there is a high content of fusinite or fossil charcoal, and the macrofossil suite is dominated by Gleicheniaceae and Typhaceae. Blackburn & Sluiter (1994) have suggested that these were reedy swamps growing under seasonally dry conditions and controlled by a natural fire regime (Fig. 68). *Banksia* remains are widespread in sediments as old as perhaps middle Eocene (McNamara & Scott, 1983), and Hill (1990a, 1994a) has suggested that fossils of this genus may provide evidence of the pathway by which the sclerophyllous heath flora evolved. Most leaves of the early taxa show little evidence for the protection of stomata from drying out, and may thus indicate that sclerophylly arose initially not in response to climate change but as an adaptation to edaphic factors; they were thus pre-adapted to the pressures of aridity in the later Cainozoic. However, the recent description of leaves from the Late Paleocene Lake Bungarby flora (Carpenter *et al.*, 1994b), which look very much like some extant Western Australian *Banksia* species, may change that interpretation. An explanation of the early evolution of scleromorphic taxa remains one of the great challenges to macrofossil palaeobotany in Australia.

The development of another vegetation type can be seen in the Murray Basin. A great variety of habitats is preserved there but, as elsewhere, floras tend to be dominated by *Nothofagus*, or by Casuarinaceae and gymnosperms. There are common halophytes (Chenopodiaceae for instance) and there is the best record in Australia of *Acacia*, which has an essentially continuous presence since the early Oligocene (Truswell, 1993).

Two points of major importance arise from the Murray Basin record. The first is that the sheer richness of species is much greater than that of contemporary floras in the Gippsland Basin and Tasmania, and no doubt reflects the diversity of habitats. The second point is that in this basin there is a clear palynological shift away from dominance by *Nothofagus* to dominance by Myrtaceae and Casuarinaceae, through a phase in which Araucariaceae are prominent. This shift happened in the late Oligocene to early Miocene, and is evident in pollen counts from a number of boreholes in the basin (Macphail & Truswell, 1989). Locally at least, it appears to have been time transgressive. Little is known about the early history of this drier style of rainforest, which has a notable presence of *Araucaria* and high Myrtaceae and podocarp frequencies. It could have expanded from dry areas in the centre of the continent, or could be a new association that developed with mid-Tertiary seasonal dryness. Apart from moving coastwards in the south-east, it also moved north, and is known from the north-east where there are records from the Pliocene and Quaternary, particularly during glacial maxima. Kershaw *et al*. (1994) have shown this spread diagrammatically. Fig. 69 shows how the proportions of 'dry' and 'wet' rainforest types varied geographically from the Miocene to the Quaternary, from the earliest known occurrence in the Murray Basin.

One special feature of this time period is that it marks the first reasonably widespread occurrence of *Eucalyptus s. lat.* macrofossils in Australia. *Eucalyptus s. lat.* has justifiably been called the 'universal Australian' (Pryor & Johnson, 1981). The group currently contains more than 700 taxa, which are nearly all endemic to Australia. Lange (1980) noted that eucalypts have been estimated to contribute 75% of the extant Australian vegetation, and at the wetter margins of the continent they dominate nearly all vegetation except rainforest and allied mesic types. Only in the arid Australian interior are eucalypts not dominant. Thus it is especially instructive to examine the fossil record of the eucalypts in some detail. In this discussion *Eucalyptus* is treated for convenience in its broad sense, rather than as *Eucalyptus s. str.*, *Angophora* and *Corymbia* (Hill & Johnson, 1995).

Eucalyptus is both highly diversified (Johnson, 1972; Pryor & Johnson, 1981) and dominant in many communities, it would therefore be expected to yield a complex and challenging fossil record. While this is not the case (Lange, 1978b, 1980, 1982), *Eucalyptus* does have a macrofossil record that is more detailed than is usually acknowledged (Hill, 1994a). While Maiden (1922) gave descriptions of 19 macrofossil *Eucalyptus* species, as well as four records of subfossils which were assigned to extant species, some later authors apparently ignored this in commenting on the almost total absence of the genus from the macrofossil
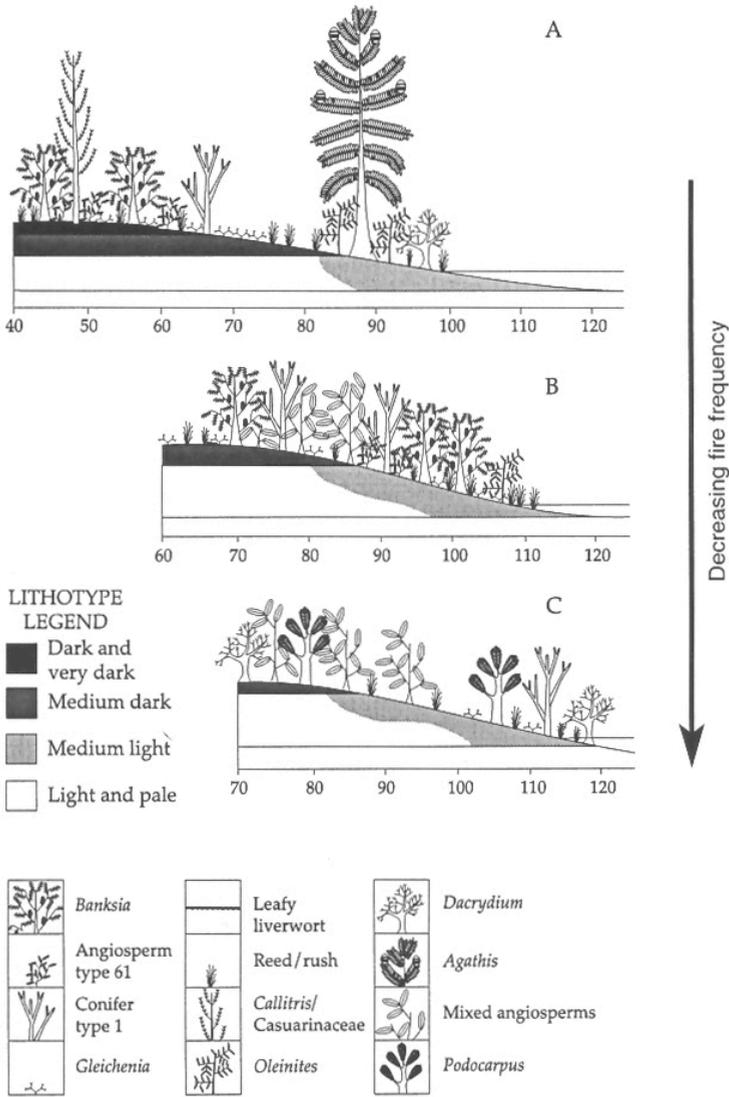
Figure 68. Hydroseral and pyric succession for three intervals from the Yallourn Open Cut. Water levels indicate probable permanent inundation. **A.** Succession under the influence of frequent fires. The margins of open water are essentially a *Dacrydium-Oleinites-Agathis*-reed/rush swamp. On drier areas above this is a reed/rush-*Gleichenia* moor. This grades into a *Banksia-Gleichenia*-conifer-reed/rush scrub. Rare *Callitris* and Casuarinaceae occur on the driest parts with leafy liverworts. **B.** Succession under the influence of infrequent fires. The margins of open water are occupied by an *Oleinites-Gleichenia*-reed/rush swamp. On the drier areas above this is a *Banksia-Gleichenia*-angiosperm-conifer scrub. Above this again is a region having a mixed angiosperm scrub. On the driest parts *Banksia-Gleichenia*-reed/rush scrub dominates. **C.** Succession under the influence of very infrequent fires. The margins of the open water are colonised by a *Dacrydium-Gleichenia*-conifer-reed/rush swamp. On the drier areas there is a mixed angiosperm-*Podocarpus-Dacrydium* scrub. Conifer type 1 and angiosperm type 61 represent currently unidentified macrofossil taxa. Modified from Blackburn & Sluiter (1994).

record (Lange, 1980; Christophel, 1989). Hill (1994a) comments on possible reasons for this change in attitude towards the macrofossil record.

The oldest reliably dated and described macrofossil associated with *Eucalyptus* currently reported is a tree stump which is probably *in situ*, and which is enclosed in a 21 Ma old basalt in the upper Lachlan Valley of New South Wales. The wood is reasonably well-preserved and has been identified by Bishop & Bamber (1985) as 'Myrtaceae with affinities to *Eucalyptus* B' (of Dadswell, 1972), although confirmation of this by identification of diffuse parenchyma cells was not possible. Holmes *et al.* (1982) described *Eucalyptus bugaldiensis* from the middle Miocene Chalk Mountain Formation in the Warrumbungle Mountains of New South Wales, based on impressions of umbel-shaped infructescences. They also described two *Eucalyptus* leaf types from impressions, noting that at least two of the phylogenetic lines proposed by Johnson (1972) for *Eucalyptus* were present at the site. They concluded that the fossils exhibited some features of advanced states in both fruits and leaf venation.

Deane (1902) described seven species of *Eucalyptus* from middle Miocene sediments at Berwick in Victoria, and Holmes *et al.* (1982) noted the presence of a leaf with *Eucalyptus*-like cuticle and an impression of a eucalypt-like fruit in the flora. This site was extensively re-collected by Pole *et al.* (1993), and several leaves with reasonably well-preserved cuticle were recovered that have clear affinities with *Eucalyptus*. *Eucalyptus* macrofossils have also been recovered recently from Miocene sediments in northern New South Wales (R.S.Hill, unpublished data) and there are also Pliocene leaves named *E. pluti* from Daylesford in Victoria (McCoy, 1876). McCoy noted that these leaves are almost identical in size and shape to extant *E. globulus*, but he noted some minor differences in the venation pattern.

Figure 69. The Neogene pattern of rainforest decline. Modified from Kershaw *et al.* (1994).

The macrofossil record of *Eucalyptus* from central Australia is very important but frustratingly uncertain. Lange (1978b) described several excellent casts of eucalypt-like fruits, which are only part of a more diverse collection from Island Lagoon, near Woomera. Unfortunately, there is poor age control on this diverse assemblage of eucalypts, which may be either Eocene-Oligocene or Miocene in age (Ambrose *et al.*, 1979). Greenwood (1991) reported 'the earliest record' of *Eucalyptus* macrofossils from the middle Eocene silcretes in the Eyre Formation in central Australia, but he neither described nor illustrated these macrofossils, and in his earlier work on the flora (Greenwood *et al.*, 1990) he only mentioned leaves assigned to *'Eucalyptophyllum'*, about which he concludes 'it is not possible to determine the affinities of this leaf type'. If unequivocal *Eucalyptus* fossils have been found in middle Eocene sediments in central Australia, their formal description should be a high priority.

Eucalyptus macrofossils are absent from several near-coastal south-eastern Australian Paleocene to Early Oligocene floras. It is also notable that *Eucalyptus* has not been reported from the Latrobe Valley coal macroflora (Blackburn & Sluiter, 1994). Allied to this is the argument presented by Archer *et al.* (1991) that the relative rarity of early koalas in Oligo-Miocene rainforests may have been due to the rarity of eucalypts in that vegetation.

Current evidence, sparse as it is, favours the hypothesis of Lange (1980) that in the mid-Tertiary the continental margins of Australia supported only mesic non-eucalypt vegetation, while eucalypts contributed to the more xeric vegetation in the interior. With progressive development of central Australian aridity, it is likely eucalypts were displaced to the continental margins while most mesic vegetation was eliminated altogether. It is informative that the late Oligocene-Miocene coastal sites where *Eucalyptus* has been recorded do seem to contain rainforest vegetation which is less mesomorphic in character and may represent a transition to drier climate forest (Hill, 1994a).

The early pollen record of *Eucalyptus* is even more enigmatic than the macrofossil record, partly because fossil pollen which has sometimes been referred to *Eucalyptus* is also similar to *Angophora*, *Syncarpia* and possibly *Metrosideros* (Martin, 1978). Cookson & Pike (1954) described *Myrtaceidites eucalyptoides* for pollen grains with probable affinities with *Eucalyptus* and noted its range as Pliocene to Pleistocene. However, this pollen type, which is referred to as the *Angophora*/*Corymbia*-type of pollen (Martin, 1989, 1994) is now recorded from the Late Paleocene of the Lake Eyre Basin in inland Australia. Harris (1965) described *Myrtaceidites tenuis,* and noted that this species is a very rare form, similar to forms related to *Eucalyptus* by Cookson & Pike (1954). *Myrtaceidites tenuis* does not persist beyond the Eocene, and its possible affinity with *Eucalyptus* is particularly interesting, since the eucalypt-type does not appear again in south-eastern Australia until well into the Oligocene (Hill, 1994a).

In more recent sediments, there is excellent evidence for a dramatic increase in abundance of *Eucalyptus* associated with increased charcoal levels. Although this occurs at different times in different parts of Australia, this is compelling evidence for the influence of Aborigines in artificially increasing the fire frequency (Singh *et al.*, 1980; Kershaw, 1986). Thus the current superdominance of *Eucalyptus* in Australia may be a relatively recent phenomenon, the result of the extraordinary adaptation of the genus to fire (Jackson, 1968) coupled with an artificial increase in ignition associated with the arrival of Aborigines. A drying climate probably assisted this event, since the vegetation was then much more prone to burn once it was lit (see Flannery, 1994, for a detailed discussion of the effect of Aborigines on the vegetation).

An important aspect of the *Eucalyptus* fossil record is its apparent presence in both South America and New Zealand. Frenguelli (1953) described *Eucalyptus patagonica* from a group of three fruits in Miocene (now considered to be probably Eocene, E.J.Romero, pers. comm.) sediments in Patagonia. Johnson & Briggs (1984) discussed this fossil and others which had been collected since, noting that Frenguelli's specimen 'could conceivably belong among the more generalised members of *Symphyomyrtus*', but they did not consider that the other specimens they saw belonged to the *Eucalyptus* alliance. Future research on these fossils will be particularly important to those with an interest in the origin and evolution of *Eucalyptus*.

Pole (1989) described leaves from Early Miocene sediments in the South Island of New Zealand which are 'identical to many *Eucalyptus* species', and noted their occurrence with eucalypt-like fructifications. This record is far more reliable than that from South America, especially when it is considered in conjunction with the pollen record. Mildenhall (1980) lists the stratigraphic range of *Eucalyptus* pollen in New Zealand as Miocene-Early Pleistocene, suggesting a relatively recent extinction.

These extra-Australian records are of great significance in tracing the history of the genus. The New Zealand records either represent long distance dispersal from Australia, in the Miocene or earlier, or they represent part of an ancient lineage which was present across at least part of Gondwana prior to separation of New Zealand and Australia, but which did not assume prominence (and thus appear in the fossil record) until climatic changes favoured its expansion (Hill, 1994a). It is impossible to decide between these options at present, although long-distance dispersal is now being invoked for *Nothofagus* from Australia to New Zealand (Martin & Dowd, 1993; Macphail *et al*., 1994; Hill *et al*., 1996) and perhaps for much more of the flora (Pole, 1994), but for *Eucalyptus* the South American record will prove crucial. If further work confirms a link between the South American fossils and *Eucalyptus*, then an ancient (Cretaceous?) Gondwanic distribution for this now characteristically Australian genus would have to be considered the most likely hypothesis (Hill, 1994a).

Latest Miocene to Pliocene

This interval is best dealt with as a single unit, because of the difficulties of separating late Miocene from early Pliocene deposits. The best evidence for trends in the vegetation comes from sequences in the river valleys draining westward from the Dividing Range; the Lachlan Valley preserves the most continuous record.

We see there, some time in the late Miocene, a marked decline in the abundance of *Nothofagus* in the pollen spectra; indeed there is a complete elimination of subg.
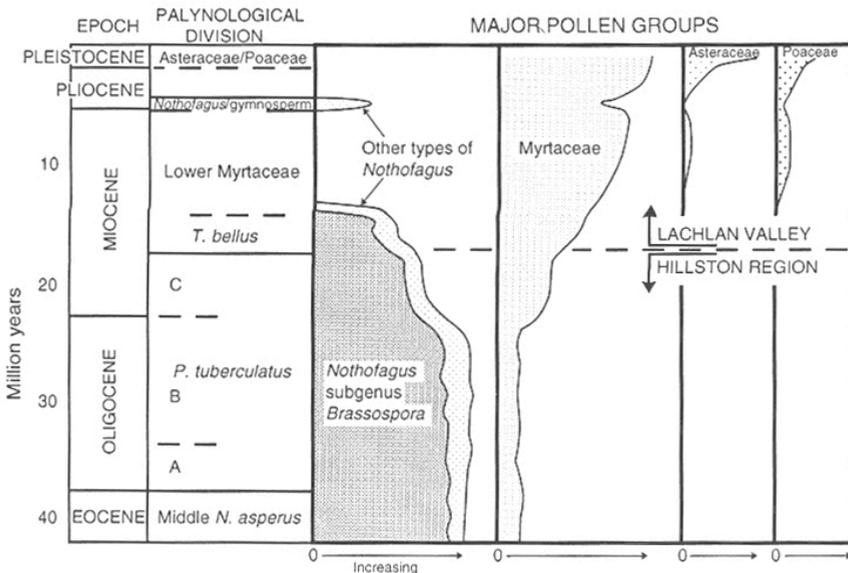

Figure 70. Major pollen groups for the late Miocene-Pliocene in the Lachlan region, northern New South Wales. Modified from Martin (1991) and Truswell (1993). *T. bellus* = *Triporopollenites bellus*; *P. tuberculatus* = *Proteacidites tuberculatus*; *N. asperus* = *Nothofagidites asperus*.

Brassospora and a corresponding increase in Myrtaceae (Fig. 70). The nature of this surge in Myrtaceae, which Martin (1987, 1991) called the 'Lower Myrtaceae phase' is problematic in terms of the vegetation it represents. Some of the increase in abundance represents eucalypts but other, more rainforest-related taxa are present too, including pollen that Martin assigned to *Tristania*, *Syzygium* and *Backhousia*. These now occur in wet sclerophyll forests. Here again there is evidence of fire (Fig. 71). Charcoal counts increase dramatically, probably under conditions of reduced precipitation and more seasonal rain. These communities seem to have been subject to more burning than phases that were clearly rainforest. This may strengthen the claim that this Myrtaceae phase reflects wet sclerophyll communities, possibly with a myrtaceous canopy above an understorey containing some rainforest taxa, and akin to communities bordering rainforests in northern Queensland today.

In the Pliocene, probably at different times according to geographic location, the trend from closed forests to open vegetation seems to have accelerated (Fig. 72), probably in response to climatic swings which were comparable to those of the Pleistocene. There are hints of savanna vegetation in north-western Australia. In pollen spectra from the Ocean Drilling Program site off the north-west margin there is substantial grass pollen at the beginning of the Pliocene (Kershaw *et al*., 1994), but we know little of the associated trees.

At Lake George near Canberra the record is better, but there are big gaps. Dating there has been by magnetic reversal stratigraphy (McEwen Mason, 1991). The sequence shows a fairly
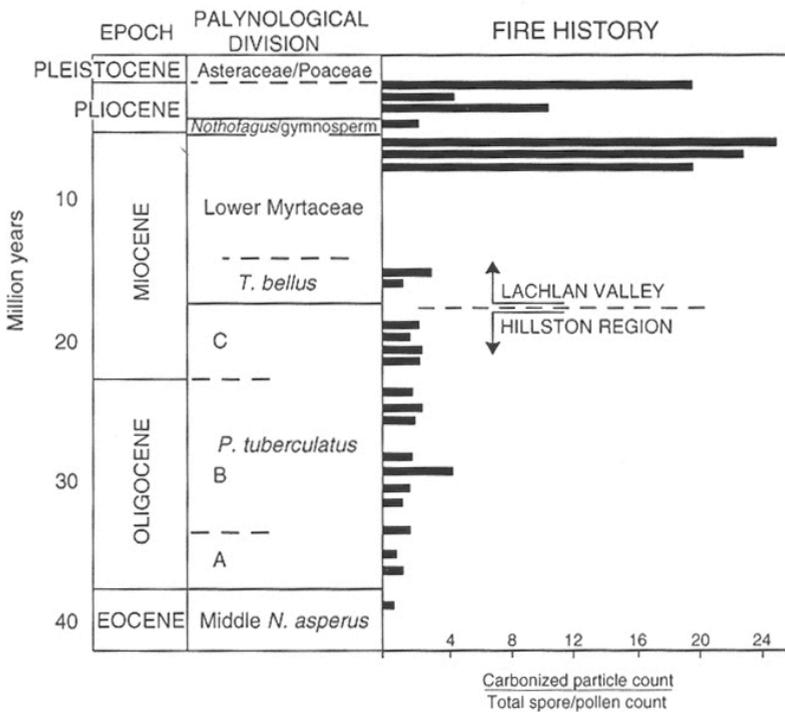

Figure 71. Suggested vegetation types represented by pollen spectra in the Lachlan region. Carbonised-particle content reflects changes in the fire history. Modified from Martin (1991) and Truswell (1993). *T. bellus* = *Triporopollenites bellus*; *P. tuberculatus* = *Proteacidites tuberculatus*; *N. asperus* = *Nothofagidites asperus*.
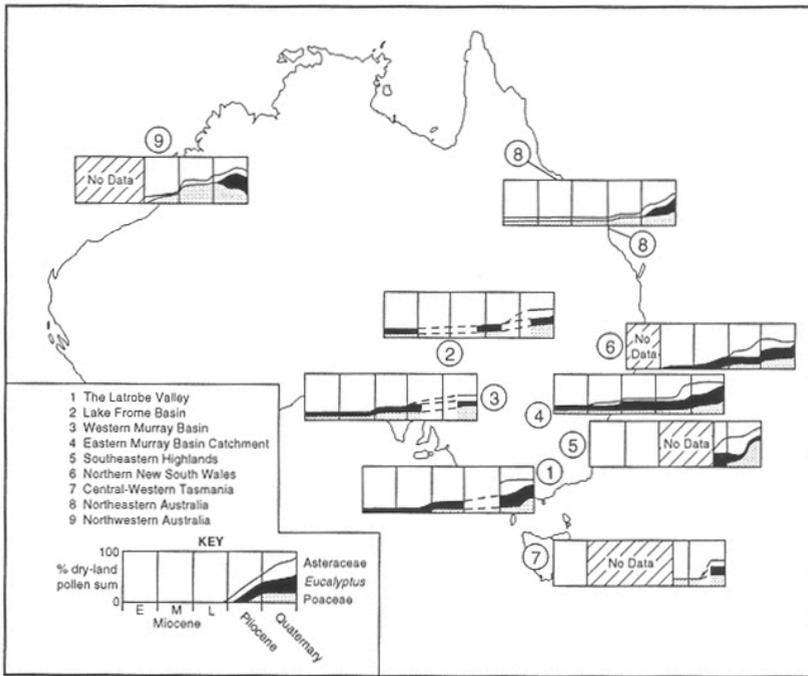
Figure 72. The Neogene increase in selected components of open vegetation. Modified from Kershaw *et al.* (1994).

dramatic shift in the late Pliocene from what seems to be temperate rainforest with *Nothofagus*, Podocarpaceae and some *Araucaria*, to a dominance by Asteraceae and grasses, in a landscape with very few trees. The Asteraceae pollen is mainly referable to the fossil species *Tubulifloridites pleistocenicus*, which is common in the Pleistocene but whose affinity is unknown (Macphail & Martin, 1991). The nature of this open vegetation remains problematic, as do the climatic conditions it reflects. Speculatively, conditions may have been cool and dry; they may reflect the first winter rainfall communities within this region.

Quaternary

The pollen record for the Quaternary consists mainly of extant Australian taxa, with a few exceptions, but there is a great deal of evidence for shifts in species' ranges and associations as glacial cycles progressed. There is certainly abundant palynological evidence for fluidity of plant communities during this time. However, the scant macrofossil evidence suggests that, in the Early Pleistocene at least, there were still many species present that are now extinct, and the glacial cycles must have been extremely important in sifting communities, especially at high latitudes (Hill & Macphail, 1985; Macphail *et al.*, 1993; Jordan, 1994, 1995; Jordan & Hill, 1994).

The Australian vegetation has been altered enormously in more recent time since the arrival of first Aboriginal and later European people. The detail of that change, which is largely the result of land clearance by fire and for agriculture has been summarised recently by Kershaw (1988), Flannery (1994) and Hope (1994).

Summary of Cainozoic vegetation

In summary, the record that we have now, in spite of its limitations, and its bias towards wet habitats and data from south-eastern Australia, gives a general picture of a transition from widespread, very diverse and complex-patterned rainforests, to predominantly open vegetation with rainforest restricted to wetter regions. There are aspects of the early Tertiary forests that we have not yet explored sufficiently. The constraints that the high latitude position must have placed on these are one such issue: in attempting to reconstruct these forests we may have been overly influenced by apparent similarities with present low-latitude vegetation.

The rainforest elements identifiable in the early Tertiary are now segregated along a latitudinal gradient in eastern Australia. The processes of change to cooler, more seasonal conditions are still elusive, but morphological changes are apparent in a number of important lineages (e.g. in conifers and *Nothofagus*). This process of opening out may go back a long way; *Banksia* in the Paleocene and Eocene may record the development of sclerophylly at that time, and *Acacia* is now known nearly as far back and was well-established in the Oligocene, but is unknown as macrofossils in pre-Quaternary sediments.

We know that by at least the mid-Miocene there was heath-like vegetation established locally in coal swamps and growing under particular fire regimes. The drier rainforests, with abundant *Araucaria*, seem to have been established first at inland localities, perhaps because *Nothofagus* subg. *Brassospora* could not compete effectively under more seasonal rainfall. We know little of the origins and structure of these forests.

There is evidence that fire was important in developing other communities in the Tertiary, perhaps including wet sclerophyll forests. These have been identified in the late Miocene, linked with increases in the quantity of charcoal in sediments. Grassland and savanna seem to have become established in the Pliocene, but their histories are sketchy and there are no data from northern Australia that can be linked in a continuous way with modern savanna vegetation. There is so far no recognised modern analogue for the enigmatic Pliocene and Pleistocene daisy-rich vegetation. The massive expansion of the eucalypts, probably at the expense of the drier rainforests and Casuarinaceae woodlands, is a more recent story and has possible links with human land-management practices, although there was apparently a much earlier shift of eucalypts from central to coastal Australia.

On the broader issues of phytogeography, there is sufficient evidence now to suggest that much of the present Australian vegetation is of Gondwanan stock. The record does, however, suggest that some interchange occurred with regions to the north during the Cretaceous and Tertiary. We cannot yet see any evidence for large scale invasions in the Miocene. The developing record from Antarctica indicates that this area formed a dispersal centre and migration route for many taxa which now have disjunct distributions in middle or low latitudes.

There are major gaps in our knowledge. We have far too little information, from either pollen or macrofossils, about Australia's north. There are very large numbers of macrofossils, mainly leaves, whose affinities remain unknown. But it is the present strength and the potential of the fossil record that leaves an impression. There will be major advances in Australian palaeobotany in the future, and for the first time there is a concentrated effort to frame questions in advance of the research. This will lead to major breakthroughs in our understanding of the history of the vegetation and provide a thorough framework for those researchers who base their work on the living flora.

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