Cambridge University Press
978-0-521-03957-4 - History of the Australian Vegetation: Cretaceous to Recent
Edited by Robert S. Hill
Excerpt
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1 The Australian fossil plant record: an introduction

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The living Australian flora is a complex mixture of species with widely varying distributions and interactions, covering the range from arid zone grassland to rainforest, alpine heath to mangrove swamp. The latitudinal range of Australia spans tropical to cool temperate climatic zones, and this is reflected in the extant vegetation, which is enormously complex (see Groves, 1981). Attempts to explain the distribution of Australian vegetation based solely on prevailing variables have been less than satisfactory. Australia, in all its aspects, is a product of its past. That is especially true of its flora and, unless the fossil record is properly considered, all attempts to explain vegetation patterns will be incomplete. Despite the complexity of the living vegetation, there has been a tendency to consider the past vegetation, especially that of the pre-Quaternary, as consisting in widespread, monotonously uniform communities. The recent explosion in information on Australian fossil plants shows that this perception was largely the result of a highly incomplete database, where the unknown areas were assumed to be the same as the small areas that were relatively well understood. It is now clear that past vegetation complexity, at least during the Cenozoic, was as high as, or possibly higher than, that seen at present. The past complexity is abundantly illustrated in this book, which may well represent the last occasion on which a thorough review of such a large period of time can be accomplished for the whole of Australia. Data are accumulating at a rapid rate, and almost every new site produces much that is novel, causing a reassessment of the prevailing hypotheses.

There is a long history of attempts to explain the origin and evolution of the Australian flora; some of these are well known, others more obscure. Hooker's (1860) discussion of the Australian flora provided a base of the highest quality, which slowly evolved into the invasion theory, perhaps best argued by Burbidge (1960). However, this theory crumbled soon after Burbidge's work, due to the broad acceptance of plate tectonics and the massive new collection of fossil data. Unfortunately, the fossil record has been given scant treatment by most Australian botanists, but the angiosperm fossil record has a long history, beginning in earnest with the work of von Ettingshausen (1888). The cosmopolitan theory espoused by von Ettingshausen led to a bitter debate, particularly involving Deane (e.g. 1900), which was well summarised by Maiden (1922). This seems to have gone largely unnoticed outside the palaeobotanical world, and in Australia had little impact on other areas of research. Palaeobotanical research that impinged on the living flora went through the doldrums following the early activity of Deane and of Chapman (e.g. 1921) in particular, but was almost single-handedly resurrected by Isabel Cookson, who set palaeobotanical studies on their modern course (for a list of her publications, see

Baker, 1973). There are currently many researchers working on plant remains in post-Jurassic Australian sediments. While their results, which are summarised here, suggest an increasingly complex picture, they also show an exciting prospect, where the enormous changes in Australia's past position and climate will make it a fertile ground for syntheses on factors involved in plant evolution at all levels in the years to come.

There are a number of features of this book that require a brief introduction, which will be attempted here. Some areas are incomplete or absent, but that is more the nature of current knowledge than a deliberate omission. The breadth of the topic of this book is such that some aspects are bound to be covered in less detail than may have been desired by some readers.

GEOLOGICAL TIME

There is not a standard time scale in use throughout this work. While that is desirable in theory, it proved impossible in practice because different research groups are tied to different interpretations of geological time. The inconsistencies are, however, relatively small, and in my view do not substantially affect the vegetation history presented here.

More critical is the choice of starting time for this work. The beginning of the Cretaceous was selected for two main reasons. Firstly, few pre-Cretaceous plants had a major, direct impact on the extant flora, and this work is meant primarily to explain the underlying causes of the make-up of the living vegetation. While some pre-Cretaceous genera, e.g. *Glossopteris* and *Dicroidium*, are very well known, they belong to another era of earth's history and cannot really be considered as 'Australian' plants in any meaningful way. Secondly, the history of Australia as an individual entity is a post-Jurassic phenomenon and therefore it seems legitimate to consider the Australian flora as having roughly that starting time.

ENVIRONMENTAL VARIABLES

Climatic change

Since the Jurassic, Australia has separated from Gondwana and moved over thousands of kilometres to its present location. Movement of Gondwanic land masses has, coincidentally, caused major climatic shifts, which have been vitally important for the development of the extant flora. Those changes are detailed in this book, although there is still much to be learned. There is a strong impression that climatic change has been the major factor shaping the extant vegetation, but there have been other factors that are more difficult to document, and the effects of which are more difficult to predict.

Photoperiod

One of the critical features of the Australian environment that has changed dramatically since the Cretaceous is photoperiod. For a long time the extreme southern part of Australia was at more than latitude 60° S (Wilford & Brown, Chapter 2, this volume). This means that the vegetation was growing under conditions of winter darkness and continuously light summers. The effect of this on the vegetation is difficult to predict, since there is no comparable situation in the modern landscape where the climate is suitable for large-tree growth. However, there is a good fossil record from both high southern (e.g. Jefferson, 1982) and northern (e.g. Francis & MacMillan, 1987) latitudes that suggests large trees were able to thrive as long as there was a suitable climate. Since the sun remains quite close to the horizon during much of the growing season, the trees must have been widely spaced and probably cone shaped to intercept the maximum possible incoming radiation (Francis & McMillan, 1987). The canopy layer is therefore effectively vertical or subvertical instead of horizontal as in modern tropical forests. While there is good evidence for the spacing of trees in these forests, the canopy shape can only be inferred. However, this suggests a forest structure very different from that which currently prevails in Australia, and this may have had many subtle but far-reaching effects. There are as yet no direct data on the extent of these effects.

Carbon dioxide levels

Evidence is accumulating for widely fluctuating CO_2 levels during the Cretaceous–Recent, from extreme highs of about 1000 (Walker *et al*., 1981) or even more than 1500 p.p.m. (Berner, 1990) during the Cretaceous to lows of just over 180 p.p.m. between 40 000 and 160 000 years ago (Barrett, 1991). Such levels of CO_2 must have had extreme effects on plant growth. Many of the broad-leaved conifers from Cretaceous and early Tertiary sediments in southern Australia have extraordinarily thick cuticles (e.g. Cantrill, 1991), which are well beyond the range of that exhibited by any extant conifers. The leaves are often quite intact and well preserved, suggesting the presence of clean abscission, and sometimes leaf bases demonstrate a clean abscission zone. The robust nature of the leaves and their extremely thick cuticles, in the context of extant CO_2 levels, suggest they were evergreen, since leaves of extant deciduous plants tend to be very thin, with an almost insignificant cuticle. However, with CO_2 levels above 1000 p.p.m., growth rates may have been so rapid that other features (e.g. resistance to herbivory) may have been more critical than seasonal loss of carbohydrate. Certainly the winter darkness in a mild climate would seem to suit the deciduous habit, and more effort should be directed toward determining whether these leaves were in fact winter deciduous.

There is evidence, largely unpublished, that winter deciduousness was more prevalent in Australia during the early Tertiary than at present. Only one winter deciduous species survives in Australia today (the Tasmanian endemic *Nothofagus gunnii*).

NOMENCLATURE

There are few major nomenclatural problems in Australian palaeobotany, since most researchers work to a common system. Occasional conflicts in this book do not increase the difficulty of understanding the data presented. However, there is one exception which must be explained in some detail. One of the dominant genera in the Australian fossil record, particularly that of pollen, is *Nothofagus*. Pollen of this type was initially split into two morphological types by Cranwell (1939), with a third added later by Cookson (1952) and Cookson & Pike (1955). These types were informally categorised as the *Nothofagus brassii*, *N. fusca* and *N. menziesii* types. One of the major problems with these pollen types was that the species assigned to the types did not closely match the formal infrageneric divisions of the time (van Steenis, 1953). Dettmann *et al.* (1990) revised the pollen of fossil and living *Nothofagus* and recognised eight types, four of which were produced by extant species. At about the same time Hill & Read (1991) revised the infrageneric classification of the extant species and proposed four subgenera, which, in species make-up, matched the new pollen groupings exactly. This paved the way for the use of formal subgeneric names in place of the informal pollen names, and that procedure has been adopted in this book. Unfortunately, the history of the infrageneric nomenclature of *Nothofagus* is very complex, and there are errors in Hill & Read's names. Hill & Jordan (1993) have corrected two of the subgeneric names, so that the names used here and their equivalents in Hill & Read's nomenclature are as follows (Hill & Read's names in parentheses where they differ): *Nothofagus* subgenus *Nothofagus*, *N.* subgenus *Fuscospora* (*Fuscaspora*), *N.* subgenus *Lophozonia* (*Menziesospora*) and *N.* subgenus *Brassospora*. These four subgeneric names are used throughout the text for fossil pollen and macrofossils.

THE CURRENT STATE OF RESEARCH

Research on various aspects of Australian Cretaceous and Cenozoic palaeobotany is proceeding at an all time high. However, not all areas are at the same level of understanding. This is very strongly reflected in this book. Some topics, such as Paleogene palynology, may be reviewed on the basis of an enormous data set. However, at the other end of the spectrum, Neogene macrofossil palaeobotany is very poorly known and is represented here by a combined study of the micro- and macrofossil record of the Latrobe Valley brown coal. While this flora is very well understood, there are only a few isolated and poorly studied macrofloras in this age range outside of southeastern Australia. The range between these extremes is clear in the various chapters. Our understanding of the evolution of the flora is expanding, but such is the complexity of the problem that it will be many years before an overall sense of order prevails.

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2 Maps of late Mesozoic–Cenozoic Gondwana break-up: some palaeogeographical implications

G. E. WILFORD & P. J. BROWN

The nature and positions of neighbouring land areas have been significant factors in the evolution of the Australian flora, both directly in determining migration routes and indirectly in influencing ocean currents and climate. The maps (Figures 2.3 to 2.10) show the approximate positions of the continents at 10 million years (Ma) intervals from 150 Ma onwards, based on the data of Scotese & Denham (1988), with modifications referred to in the notes below. Separation of continental fragments by sea-floor spreading was commonly preceded by rifting. Where the relative motion of the fragments was oblique, some fault blocks were uplifted and eroded and others were deeply buried by sediment, resulting in zones with a varied and changing mosaic of complex environments by comparison, for instance, with adjacent interior areas. These zones, peripheral to the Australian land mass, are shown together with some of the larger areas of sedimentation and volcanicity (from BMR Palaeogeography Group, 1990) which would have influenced soil type and vegetation. The time scale shown in Figure 2.1 has been used for the reconstructions. The key for Figures 2.3–2.10 is shown in Figure 2.2.

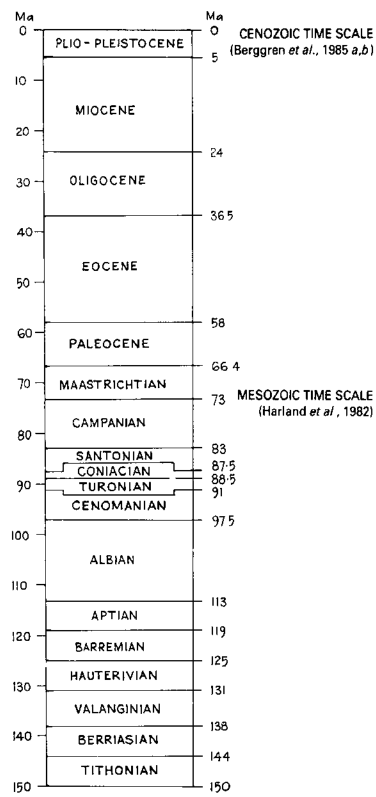

Figure 2.1 Time scale on which the following palaeogeographical maps are based.

150 Ma (Figure 2.3)

At about 150 Ma the 'Antarctic' coastline of Gondwana was positioned close to the South Pole

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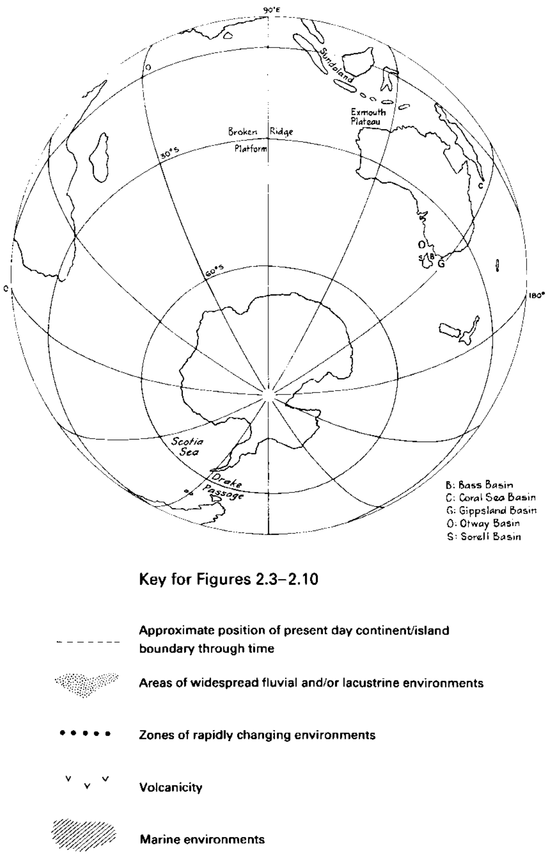


Figure 2.2 Reference to localities referred to in the text, and the key to symbols used in Figures 2.3–2.10.

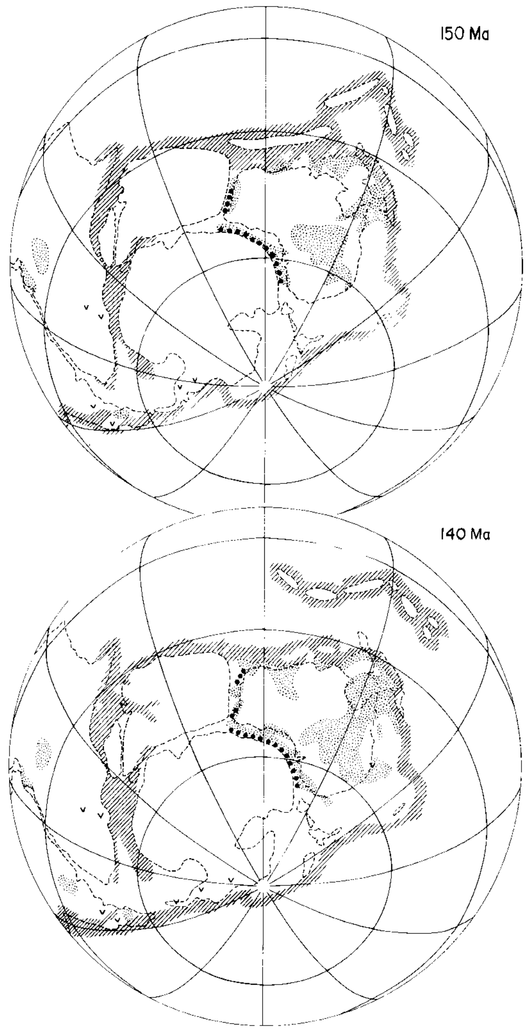


Figure 2.3

and western Tethys was connected to the proto-Pacific Ocean. Continental slivers from the northeast margin (Northwest Shelf region of Australia) and eastern tip (New Guinea region) of Gondwana may have rifted off periodically and been carried northwestwards from Permian time onwards. Such fragments now lie in South Tibet and various parts of Southeast Asia, but little definitive information exists on their time of movement and even less on their palaeogeographical configuration during transit across Tethys. Following Audley-Charles *et al.* (1988), who favoured a later, rather than earlier migration of fragments, the maps show them as a string of possible islands, assuming most departed after the Callovian (*c.* 167 Ma) sea-floor spreading event along that part of the edge of Gondwana. The fragments accreted to the southeastern part of the then Asian continent to form a promontory (Sundaland), which has remained in equatorial latitudes to the present day. It is shown on the maps by a group of 'hypothetical' islands to indicate possible 'stepping stone' links between Australian Gondwana and the Asian mainland, although the palaeogeography of the area will have changed quite dramatically with time.

At about 150 Ma, the present-day eastern Australian coastline was separated from the proto-Pacific Ocean by a strip of terrain now marked by the present-day Lord Howe Rise, Queensland Plateau and New Caledonia.

Gondwana break-up was preceded, in early to mid-Jurassic time, by widespread basaltic magmatic activity (dolerites of Tasmania, southeastern Australia; Karoo dolerites of South Africa; Ferrar Super Group, Dufek Intrusion in Antarctica), reflecting a major thermal event. By 150 Ma, movement between Africa–South America (West Gondwana) and Antarctica–Madagascar–Greater India–Australia (East Gondwana) had been initiated. However, the break-up was dominated by strike–slip movement, narrow basins were formed and it is likely that land connections between the two major fragments existed from time to time. Rifting along the southern margin of Australia was initiated at about this time (Willcox & Stagg, 1990).

140 Ma (Figure 2.3)

By 140 Ma narrow seaways existed along much of the split between Africa and Antarctica–Madagascar–Greater India–Australia and the fragments from the northeastern margin of Gondwana had moved towards the Equator. The incipient separation of Australia from Antarctica and Greater India was marked by the continued developments of rifts along the former's western and southern boundaries, although evidence for sedimentation in East Antarctica is virtually restricted to recycled palynomorphs (Truswell, 1983). Rifting along Australia's southern margin was accompanied by initial extension in a northwest to southeast direction of about 300 km and this was accomplished by about 120 Ma (Willcox & Stagg, 1990). New Zealand at this time was part of a considerable land mass flanking East Antarctica and southeast Australia. This land mass probably reached its greatest extent in the Early Cretaceous as a result of the Rangitata Orogeny (Stevens, 1989).

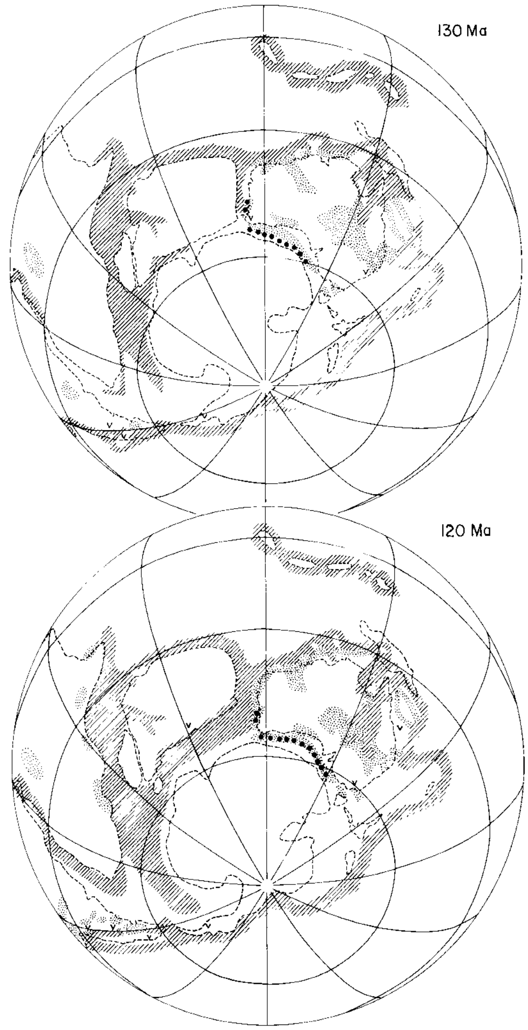


Figure 2.4

130 Ma (Figure 2.4)

By 130 Ma, Greater India, Australia and Antarctica had begun to move apart, although no significant seaways had developed between them (Powell *et al.*, 1988), the rate of separation between the last two being of the order of only a few millimetres per year. Break-up began at the southwest margin of the Exmouth Plateau at about 132 Ma and progressed southwards, then eastwards along the southern margin of Australia. The South Atlantic started to open about this time, propagating northwards (Nurnberg & Muller, 1991).

120 Ma (Figure 2.4)

By 120 Ma, substantial seaways existed along the east coast of Africa and between Greater India and Antarctica–western Australia. The slow continental extension between Australia and Antarctica continued but the earlier NW–SE direction changed to NNE–SSW with movement in the east of 120 km leading to the formation of the Gippsland and Bass Basins and modifying the development of the Otway and Sorell Basins (Willcox & Stagg, 1990).

110 Ma (Figure 2.5)

The map shows the Australian continent at the height of the marine transgression that culminated in the Aptian (*c.* 116–113 Ma), when extensive areas were covered by shallow seas. At about this time rifting commenced along the southeastern ('Australian') margin of Gondwana, and along the western margin of New Zealand, the former eventually leading to the formation of the Tasman Sea (Stevens, 1989). Rifting, together with the rotation of crustal blocks locally, affected the Antarctic Peninsula and adjacent areas of West Antarctica until about 100 Ma but had no major effect on the overall geography (Storey *et al.*, 1988). Spreading between Australia and Antarctica allowed the proto-Indian Ocean to enter from the west, initiating the formation of the Southern Ocean.

100 Ma (Figure 2.5)

By 100 Ma, erosion and subsidence had reduced the land masses around New Zealand, allowing the sea to flood a number of rift zones, although a land connection to Antarctica persisted in the south (Stevens, 1989). Uplift of the Australian Eastern Highlands may have started about this time, associated with the subsequent opening of the Tasman Sea (Wellman, 1987). At about 95

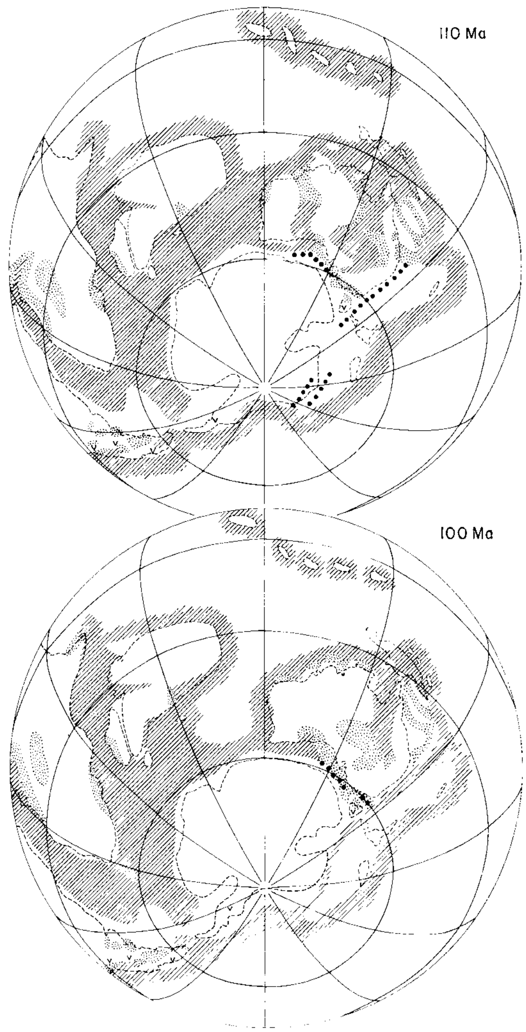


Figure 2.5

Key for Figures 2.3–2.10

- - - - -	Approximate position of present day continent/island boundary through time
(stippled)	Areas of widespread fluvial and/or lacustrine environments
• • • • •	Zones of rapidly changing environments
v v v	Volcanicity
(hatched)	Marine environments

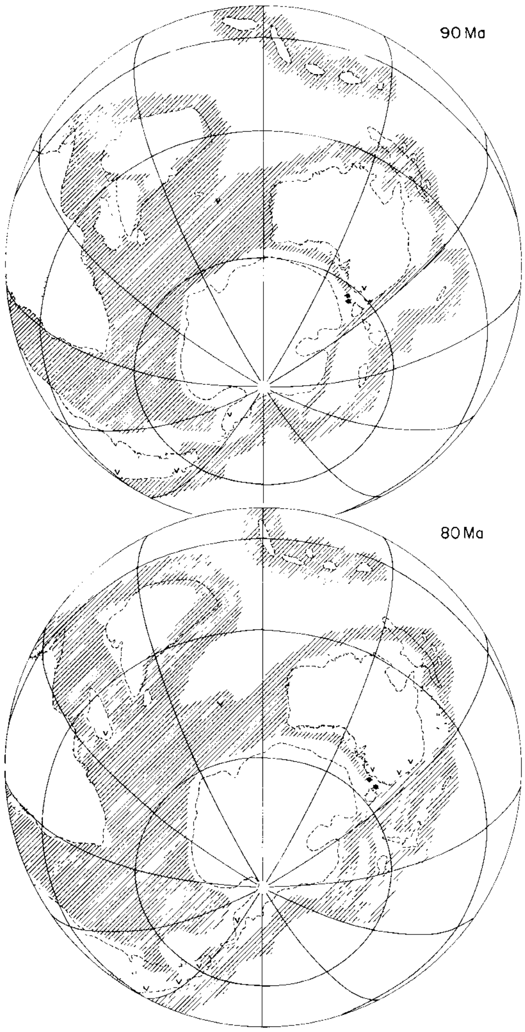


Figure 2.6

Ma the rate of Greater India's northward movement rapidly increased.

90 Ma (Figure 2.6)

Slow sea-floor spreading in a NNW direction between Antarctica and Australia continued until, by about 90 Ma, a tongue of the proto-Southern Ocean extended almost to Tasmania. Sea-floor spreading also resulted in the establishment of open ocean in the Tasman Sea and to the south of New Zealand isolating 'New Zealand' and 'New Caledonia' from the remainder of Gondwana (Stevens, 1989). Following Stevens (1989, figs. 5, 6), we show a land link between 'New Zealand' and 'New Caledonia' until about 70 Ma, although direct evidence for this is lacking. Subaerial volcanism existed in the open ocean west of Australia from 90 to 60 Ma, sited at the northern edge of the Broken Ridge platform (Rea *et al.*, 1990), and might have provided a 'stepping stone' for floral migration.

At about this time sea-floor spreading was under way between northeastern Australia and eastern New Guinea, leading to the formation of the Coral Sea Basin by the end of the Paleocene. Coeval sea-floor spreading in the vicinity of eastern New Guinea may have given rise to the separation of continental fragments that, in post-Paleocene times, were carried westwards by Pacific plate movements and are now located in the eastern islands of Indonesia (Pigram & Symonds, 1991).

80 Ma (Figure 2.6)

Madagascar separated from greater India at about this time, both being isolated in a surrounding ocean. Tasmania was still close to Antarctica and connected to Australia, the present-day Bass Strait area being occupied by mainly lowland, depositional environments until flooded by the sea in the Oligo-Miocene.

70 Ma (Figure 2.7)

The paucity of clastic sediments of this and earlier Late Cretaceous ages on and around the Australian continent (except for parts of the tectonically active southern margin), together with the widespread presence of thick, weathered profiles, indicate that relatively uniform humid climates were typical of much of Late Cretaceous time (G. E. Wilford, R. P. Langford & E. M. Truswell, unpublished data).

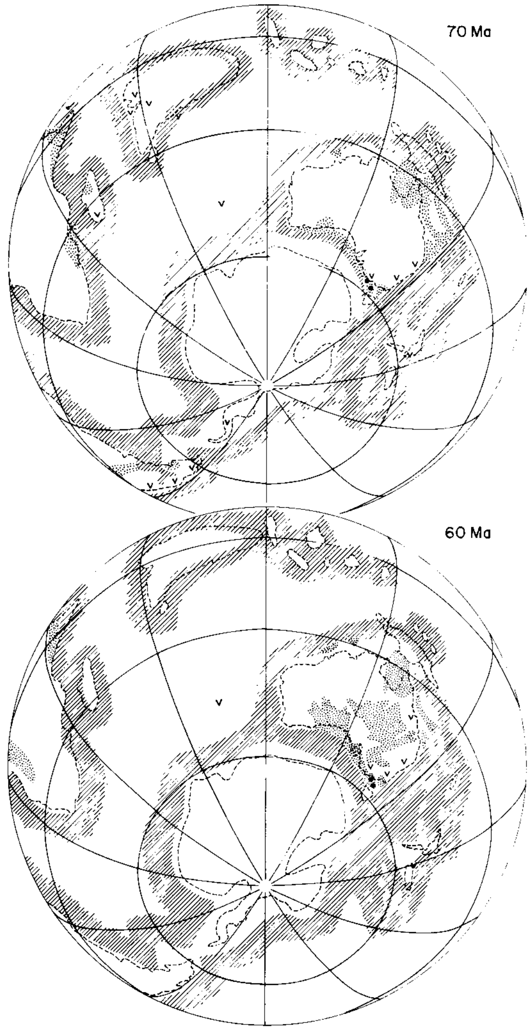
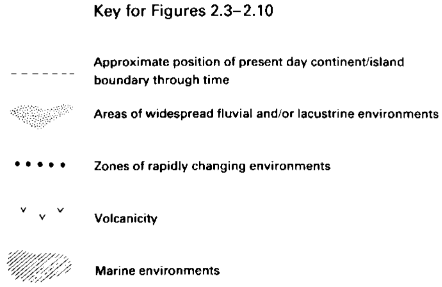


Figure 2.7



60 Ma (Figure 2.7)

By about 60 Ma, sea-floor spreading ceased in the Tasman Sea, although Australia's slow northward drift away from Antarctica continued. In the early Cenozoic, one or more cooling events, probably associated with ice build-up on Antarctica, triggered widespread erosion and deposition across much of Australia. Broad, swampy, alluvial channels were formed in the west, and extensive sandy fans accumulated in the east (G. E. Wilford, R. P. Langford & E. M. Truswell, unpublished data). These conditions continued intermittently until about Early Oligocene.

50 Ma (Figure 2.8)

Uplift of the Transantarctic Mountains at about this time (Fitzgerald & Gleadow, 1988) would have encouraged accumulation of snow and ice which was to become a major feature of Antarctica for much of the remainder of the Cenozoic.

40 Ma (Figure 2.8)

At about this time movement of the Pacific Plate changed from a northerly to a more west-northwesterly direction, resulting eventually in collision with the Australian Plate in New Guinea and mountain building there from the mid-Oligocene onwards (Pigram & Symonds, 1991) and subduction of the Australian Plate beneath Sundaland. At about 44 Ma, the spreading rate between Australia and Antarctica increased as the former moved northwards, and by about 38 Ma a deep marine strait had formed between Tasmania and Antarctica (Kennett, 1980), allowing circum Antarctic oceanic flow for the first time and resulting in the increased cooling of Antarctica and the adjacent oceans.

Until about this time microcontinental blocks formed a link between the Antarctic Peninsula and South America. They have subsequently become dispersed by plate movements and sea-floor spreading, associated with the opening of the Scotia Sea. However, considerable uncertainty