CHANGING CENOZOIC BARRIERS AND THE AUSTRALIAN PALEOBOTANICAL RECORD¹

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ABSTRACT

The first part of this study reconstructs the changing Cenozoic environment of continental drift, tectonics, and climate. The northward movement of Australia brought it into collision with Southeast Asia in Miocene time. Throughout the Cenozoic, New Zealand has remained in approximately the same relative position and the same distance from Australia. Tectonics within Australia have been minor, gentle, and the main topographic features have probably existed in much the same form all through the Cenozoic.

The climate of the early Tertiary was wetter and warmer than that of today, and although the start of desiccation is debated, the present degree of aridity has existed only since the late Pliocene. In the Quaternary, glaciation has been restricted to very small areas in Australia and the glacial periods were more arid than the interglacials. Sea levels have changed throughout the Tertiary as well as the Quaternary. Today, the arid center of the continent is the major feature of the climate. Soils are generally low in fertility, and have been low all through the Cenozoic, when some soils may have been even less fertile than those of today.

In the vegetation today, there are small and disjunct areas of closed forest (= rainforest) in the better watered northern and eastern coastal regions. *Eucalyptus* dominated forests and scrublands cover the major area. Grasslands and shrublands are found in the arid center.

The second half presents the paleobotanical record of all reliable identifications of macro- and micro-fossils, first appearances and the quantitative relationships of the abundant pollen groups. The vegetation must have been closed forest for most of the Tertiary. The nature of these closed forests changes, but open forests only start developing in the Pliocene. The first evidence of grasslands is found in the Miocene of Central Australia, and open savannah and/or grasslands became dominant in southeastern Australia in the Pleistocene. The vegetation was not necessarily more uniform than that seen today, for there is considerable evidence of geographic and time-related variation in the Tertiary floras.

The Quaternary shows cyclic changes of a more open and drier kind of vegetation in glacial periods and a more forested, wetter vegetation in the interglacials.

A comparison of the Australian and New Zealand paleobotanical records shows a general similarity. A number of fossil taxa appear first in Australia and later in New Zealand. The paleoclimate of both has been similar, and distance has not been an insurmountable barrier. The paleobotanical record of Southeast Asia is different, and limited migrations after the Miocene are probably associated with uplift. During the Miocene, there is an increase in Myrtaceae in both Australia and Southeast Asia. It is thought that new availability of soils of low fertility is the cause of this increase in Southeast Asia, whereas both low soil fertility and the developing aridity has been responsible for the increase in Australia.

Climate is the most important environmental factor, for the paleobotanical and paleoclimatic records usually go together. Climate has probably not been a barrier within Australia for most of the Cenozoic, when habitats suitable for closed forest existed in Central Australia, although not necessarily continuous. Some drier areas have probably existed long before the development of the present degree of aridity, allowing adaptations of the flora to develop before these conditions became widespread. Within Australia, tectonics and topography have not been barriers, although they have been important in maintaining habitat diversity. These factors may have been more important as barriers between Australia and Southeast Asia.

This study shows a complex, continuously changing, interwoven environment and flora, rather than migrations stopped or permitted by changing barriers. The concepts of barriers and migrations

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come from historical biogeography, and they seem inappropriate in this study, which essentially follows paleoecological principles.

INTRODUCTION

Areas unfavorable to the growth of plant species constitute barriers to the spread of those species. Fosberg (1963) separates most barriers into the categories of water, topography, climate, and vegetation. Distance may also be regarded as a temporary barrier. Soils, an important factor in Australian phytogeography, may constitute a barrier also. During the Cenozoic, continental drift changes the barriers of water and distance. Tectonic uplift changes topography and climate has been changing continuously. The flora and vegetation have also been changing continuously throughout the Cenozoic. By the beginning of the Cenozoic, the time under consideration in this symposium, the angiosperms had diversified greatly and were a major element in all floras. However, there has been much evolutionary change since the beginning of the Cenozoic, with the appearance of new taxa and extinction of old taxa.

The first part of this paper presents the Cenozoic environment, which is a necessary background to understanding the paleobotanical record. Because a plant taxon requires a suitable environment for growth, its distribution is, for the greater part, controlled by the environment, of which climate is the most important single factor. Some distributions may be adequately explained by a single environmental factor, but frequently a combination of factors produces a more satisfactory explanation. Fossil plants may be used as indicators of past climates. If paleoclimate is reconstructed in such a way and then used to explain past distributions, it would lead to a circular argument. Consequently, the paleoclimate must be reconstructed from independent evidence. Paleobotanical evidence is not admitted here although other biological evidence is admissible. This part of the paper reconstructs the paleogeography, tectonic changes and paleoclimate through the Cenozoic. An attempt is made to reconstruct changes in soil fertility but the evidence available for this is very limited.

In the second part of this paper, the Australian paleobotanical record is presented and possible reasons for changes discussed. The paleobotanical record of New Zealand and Southeast Asia is compared with that of Australia to test the effect of distance as a barrier. Finally, the effectiveness of the barriers discussed above are assessed.

THE CENOZOIC ENVIRONMENT

PALEOGEOGRAPHY

The break-up of Gondwanaland is well known and only movements directly related to Australia and its nearest neighbors are reiterated here.

Separation of Australia from Antarctica commenced at the end of the Paleocene with the formation of a narrow strait, but it was the mid-Oligocene before a deep water channel was formed between the two continents. Australia has moved north some 27° of latitude during the Tertiary (Fig. 1) (McElhinny, 1970; Crook, 1981; Powell et al., 1981).

FIGURE 1. Paleogeography showing the relationships of Australia to other continents in the southern hemisphere during the Tertiary. For more detail of the relationships with New Zealand, see Fig. 2 and with Southeast Asia, see Fig. 3.

At the beginning of the late Cretaceous, New Zealand, New Caledonia, and the Lord Howe Rise were closer to each other and to Australia. The opening of the Tasman Sea and the New Caledonian Basin in the late Cretaceous moved these regions further apart. They have remained at approximately the same distance from each other and from Australia for the whole of the Cenozoic (Fig. 2). The distance between Australia and New Zealand is about 2,000 km (Crook & Belbin, 1978; Coleman, 1980; Crook, 1981).

To the north, southern New Guinea has always been part of the Australian plate. The Banda Arcs are very complex and include some fragments from New Guinea. Parts of Timor originate from the Australian continent (Hamilton, 1979). In the early Tertiary, about 3,000 km of deep ocean separated the northern edge of the Australian plate from the southern edge of Southeast Asia. The Australian plate came into collision with the Sunda Arcs of Southeast Asia in Miocene time (15 million years ago). Southeast Asia was probably 2–3,000 km further east and has moved westward, starting about 20 million years ago, but it has always been at the same latitude as the present (Fig. 3) (Powell & Johnson, 1980; Powell et al., 1981).

These movements described above simply present the changing spatial relationships through time, and the latitudinal change of the Australian plate has been the most important (see paleoclimate). Continental drift should not be considered in isolation from other environmental factors that may be more important for biogeography (McGowran, 1979). Climate is the most important environmental factor and there have been global changes throughout the Cenozoic, quite apart from the effect of the changing latitude of Australia. These other environmental factors are presented below.

TECTONICS

Tectonically, the Australian continent has been relatively stable throughout the Cenozoic. Timing of uplift of the Southeastern Highlands is controversial (Bishop & Young, 1980; Wellman, 1980). One school of thought considers that uplift was well advanced by the early Tertiary and was virtually completed by

FIGURE 2. Changes in the distance of New Zealand and Antarctica in relation to Australia, constructed from Crook, 1981. Australia is treated as fixed. The boundary of Antarctica for 60 and 38 million years and the present show increasing distance between the two continents. New Zealand has remained at approximately the same distance of 2,000 km from Australia. New Caledonia and New Guinea have remained in approximately the same position, relative to Australia.

Oligocene time (Young, 1977). Another school of thought concludes that uplift has been going on continuously at a steady rate all through the Tertiary (Wellman, 1979). Uplift in the east, in South Australia, and in the west has been going on in stages during this time, and is probably still going on, as indicated by the occasional earthquake. There has been subsidence in central Australia and upwarping of parts of Western Australia. A series of lakes in central Australia was fed by the great internal drainage system. Shallow seas encroached from parts of the western and southern coasts but these marginal basins have been only slightly disturbed. All of these movements have been episodic, relatively small, and moderate (Brown et al., 1968; Ollier, 1977). Relief may have been higher in the early Tertiary (e.g., Young, 1977) but was probably not substantially greater than the present in the late Cenozoic (Galloway & Kemp, 1981). Various lines of evidence suggest that upland areas and drainage patterns of the early to mid-Tertiary were much the same as those of today (Nix, 1981). Australia is a low, flat land mass with most of the relief less than 1,000 m. The highest point, Mt. Kosciusko, is 2,228 m.

PALEOCLIMATE

Continental movement has had a major effect on climate through the initiation of the circumpolar current. With Australia and South America attached to Ant-

FIGURE 3. The position of Australia in relation to Southeast Asia. The position of the Australian and Indian Plates for present and 10, 20, 30, and 60 million years ago are shown. In the early Tertiary there was 3,000 km of deep ocean between the Australian and Southeast Asian Plates. The two came into contact 15 million years ago, in the Miocene. Modified from Powell and Johnson, 1980.

arctica, this current could not operate and the warm equatorial currents travelled to higher latitudes along the eastern margins of the southern continents, effecting a greater heat transfer from the low to the high latitudes. Once the circumpolar current came into operation, it effectively blocked the equatorial currents from travelling into the higher latitudes, thus limiting the heat transfer to these regions.

During the initial drift of Australia away from Antarctica the seas between the two land masses were shallow and the circum-Antarctic current was blocked by the South Tasman Rise, which linked Tasmania to Antarctica. To the end of the Eocene, the Southern Ocean was relatively warm and Antarctica largely nonglaci-ated. In the early Oligocene, substantial sea ice began to form and widespread glaciation developed on Antarctica. The clearing of the South Tasman Rise about mid-Oligocene time and the opening of Drake Passage between South America and Antarctica about the Oligocene-Miocene boundary (Barker & Burrell, 1977) allowed complete circumpolar circulation. The Antarctic ice cap formed about mid-Miocene time. The volume of ice has increased since this time and was greater than that of the present in the late Miocene (Kennett, 1977; Kemp,

FIGURE 4. Oxygen isotope paleotemperatures, modified from Shackleton and Kennett, 1975. $\delta^{18}O$ is the correction for the change of the ratio of the isotopes in sea water through the Cenozoic. Note: Sites 277 and 279 on the Campbell Plateau were about 50°S in the early Tertiary. The composite curve presented here represents the paleotemperatures of latitudes 40–50°S, for the whole of the Cenozoic.

1978, 1981). The decline in temperature during the Cenozoic is shown by the oxygen isotope temperature curve from deep sea cores on the Tasman Rise and Campbell Plateau, which have remained at latitudes of 40–50°S for the whole of the Tertiary (Fig. 4). There was an overall decline through the Eocene and substantial drops in temperature during the early Oligocene and after the mid-Mio-

FIGURE 5. Cenozoic changes in sea level in the Australian region, from the sedimentary cycles of Loutit and Kennett, 1981, and Chappell, 1978. The two Tertiary curves show sedimentary cycles on the continental margins and changes in sea level have been the major factor determining deposition. There is an overall agreement but they are not identical because of slightly different histories of deposition. The Quaternary curve for sea levels is for the last 250,000 years only. For further explanation, see text.

cene (Shackleton & Kennett, 1975). Throughout the overall decline, there are many fluctuations. That these fluctuations are important, biogeographically, is shown by the foraminiferal record. Tropical foraminifera show a number of short-lived excursions into the higher latitudes, and these excursions show a good fit, on the whole, with the oxygen isotope curve (McGowran, 1978).

Changes in sea levels through the Cenozoic have alternately exposed and drowned the continental shelves. Figure 5 shows two Tertiary sea level curves taken from Australian sedimentary cycles. A third, from the Western Australian continental shelf (Quilty, 1980), is very similar to the southern Australian curve shown on Fig. 5. The two curves show an overall agreement, but are not identical because of the different histories of deposition (Loutit & Kennett, 1981). These cycles in sea levels can be equated, in a general way, with world wide changes (Vail et al., 1977). It is thought that geotectonics, variations in rates, and directions of sea floor spreading, etc., have been the cause of these changes. The eustatic glacial cycles of the Quaternary are superimposed on the longer term cycles, although there was some glacial influence on sea levels before the Quaternary. At times of high sea levels, shallow flooding of the continental shelves and low lying areas results in a warm, wet climate. At times of low sea level, the low lying areas are drained and the continental shelves exposed, resulting in a climate that is cooler and drier.

The long term changes in sea level through the Cenozoic are measured in

terms of millions of years while the glacial cycles of the Quaternary can be expressed in terms of thousands of years. Figure 5 shows the sea level changes over the last 250,000 years (Chappell, 1978). This curve has been constructed from coral reefs in New Guinea, Timor, and the Barbados and shows a number of fluctuations between the major interglacial high levels.

Oceanic circulation and the development of the ice cap on Antarctica has had a major influence on Australian paleoclimate. Kemp (1978, 1981) used data from deep sea sediments to model atmospheric circulation. There are, however, many indications on the land itself as to the nature of the paleoclimate, although much of it is not as reliably dated as that of the deep sea cores. There is abundant evidence that inland Australia was once much wetter than today. Residual laterite and kaolinized profiles are widespread in Australia, including the arid region. The chemical weathering required to produce these profiles would require a warm, humid climate with a much higher rainfall than that received in inland Australia today. The ages assigned to laterite in the various regions are different, because there has been more than one episode of lateritization (Hayes, 1967; Alley, 1977; Idnurm & Senior, 1978). Paleomagnetic dating suggests that the dominant period of lateritic weathering over a large area of Australia was late Oligocene to early Miocene (Schmidt et al., 1976). The Cenozoic stratigraphy of the Lake Eyre Basin indicates an alternation of relatively humid and dry periods, but the present degree of aridity did not appear until the Quaternary (Jessup & Norris, 1971). In the Lake Frome area, the climate of the Miocene was subtropical or warm temperate with a relatively high rainfall and, at times, seasonal dry periods became a part of the weather pattern. Arid and pluvial climates alternated in the late Tertiary and Quaternary (Callen & Tedford, 1976). River systems in the arid region of Western Australia have been inactive since middle Miocene time and are now reduced to a chain of salt lakes (van der Graaff et al., 1977).

The aridity of the Australian continent reached its present proportions in late Pliocene-Pleistocene time, about 2.5 million years ago (Bowler, 1976). There is some debate as to how the present state of aridity was reached. One school of thought places the first beginnings of a drier climate in the Eocene, using the notion that offshore terrigenous sediments infer river drainage (Quilty, 1974) and that the change from terrigenous to carbonate sedimentation is an indication of the cessation of efficient drainage from the land. (This hypothesis contradicts the paleomagnetic dating of laterites, discussed above, if the possibility of fluctuations in climate is ignored.) Another school of thought interprets the same evidence as indicating drainage from a flat, well-vegetated terrain with a consequent lack of erosion. This second school of thought places the start of desiccation in the late Miocene (Bowler, 1976). There is general agreement, however, that at least localized dry areas have probably existed in inland Australia long before the present state of aridity was reached. If, during the Tertiary, very small pockets of aridity existed amid large areas of better watered country, they may be very difficult to detect by normal geological and paleontological methods. Such small pockets would be biologically very important, for they would allow the evolution of a genetic complement suited to the arid environment, forming a nucleus for later expansion.

The climatic changes of the Tertiary are described in terms of million of years, but those of the Quaternary may be described in terms of thousands of years. Bowler et al. (1976) have reviewed evidence of the climates of the last 60,000 years. From 25,000 to 15,000 years B.P., which includes the last glacial period, it is estimated that the mean annual temperature was lowered by 6–10°C. Glaciation was restricted to Tasmania and small areas in the Snowy Mountains, although periglacial activity extended much further in the Eastern Highlands. There is considerable evidence of a drier climate throughout the whole time, although in southern Australia lakes filled at the time that temperatures were lowest, probably as a result of reduced evaporation. In the last 10,000 years, the climate has been relatively stable.

Nix and Kalma (1972) have constructed models of changes that have occurred since the last glaciation. These models (see Fig. 6) include the postulated type of vegetation that would result from the climate prevailing at the time, but they have been built from the climatic controls of the vegetation. These models reflect the major influence of lowered sea levels that accompanied maximum glaciation. With the sea level at the margin of the continental shelf, the continentality of a low land mass such as Australia would be increased considerably. With deeper, colder seas surrounding Australia, evaporation and hence precipitation would be less. Changes similar to these must have happened many times during the Quaternary as the sea level oscillated with the glacials (see Fig. 5). Evidence from soils (Butler, 1967) and hydrologic regimen (Schumm, 1968) indicate alternating phases of unstable erosion/deposition and stable non-erosion/non-deposition during the Quaternary. It is thought that the disturbing effect of an unfavorable climate reduces the vegetation cover and erosion is accelerated. Such cycles of instability and stability of only a few thousand years duration must have had a profound effect on the biota.

THE CLIMATE TODAY

Aridity is the major feature of the climate of the Australian continent today. More than two thirds of the continent receives a mean annual precipitation of less than 500 mm and a third has values of less than 250 mm. Precipitation zonation is roughly concentric with the highest values across the northern edge and down the eastern coastal strip. Even the well-watered coastal regions receive a seasonal precipitation so that 80% of the continent has at least three months of the year without effective precipitation. Roughly the northern half of the continent receives summer precipitation and the southern half winter precipitation. New Guinea and Western Tasmania are the only significant areas of a humid climate receiving more than 2,000 mm mean annual precipitation.

For biogeographic purposes, the extremes of temperature are perhaps more instructive. All but the highest elevations near the coast of continental Australia receive mean daily maxima exceeding 30°C during the hottest part of the year. In the coldest part of the year, freezing temperatures and frosts occur regularly over roughly half the continent. For a more detailed discussion of the climate, see Nix (1981).

FIGURE 6. The main types of vegetation that might result from the climate postulated for stages since the last glacial period, from Nix and Kalma, 1972. 1. For the period of maximum sea level lowering. The loss of warm shelf water has greatly reduced precipitation and continentality has increased. The arid vegetation would have expanded and the closed forest (= rainforest) contracted, with a corresponding shift of the intermediate types. 2. For the period of rapid rise in sea level and rapid warming of very shallow shelf water, resulting in a greatly increased precipitation. Temperatures are slightly higher than those of today. The closed forest would have expanded considerably and the

SOILS

“There is probably no continent with soils so generally low in key plant nutrients as Australia . . .” (Bowen, 1981). Soils of high and moderately high nutrient status are restricted to an archipelago of islands on the Australian continent although they are fairly extensive in New Guinea. Soils of low and very low status are widespread and probably cover more than half the area of the continent. Gross deficiencies exist in both major and minor nutrient elements (Nix, 1981).

The low nutrient status of the soils is attributed partly to the mainly sedimentary parent material, and mostly to the prolonged deep weathering of the landscape and the stripping and reworking of older soil profiles (Nix, 1981). Since the present low status results from the once wetter climate and resultant processes of lateritization that were in progress during the early Tertiary, then the soils must have had a low nutrient status all through the Cenozoic.

There is some evidence of change in nutrient status of the soils during the Cenozoic. Volcanism has provided restricted areas of new parent material and has produced the islands of higher nutrient soils. In a second example, numerous water bores in western New South Wales have revealed two formations in the Cenozoic alluvium. The older, underlying formation contains sands and gravels that are almost entirely quartz and it is predominantly grey in color. The younger, overlying formation is varicolored, frequently red-yellow-brown and the sands and gravels are an admixture of the various rock types exposed in the catchment today. It is thought that the quartz in the underlying formation came from extensive quartz gravels that once blanketed the region but have now been eroded away except for remnant hill-cappings (Williamson, 1964). However, the transition between the two formations is time transgressive; about mid-Miocene in the western region on the riverine plain and late Pliocene–early Pleistocene in the eastern region in the river valleys. The pollen assemblages of the two formations always indicate a wetter climate for the lower and a drier climate for the upper formation (Martin, 1973, 1977a). This evidence suggests that there is at least a climatic component in the development of the two formations. Although there are no direct measurements, soils formed on predominantly quartz, under a wetter climate, are likely to have had a lower nutrient status than those of today that are formed on a variety of rock types with less weathering. Thus the little evidence available suggests that during the Tertiary, some soils were even less fertile than those of today.

THE VEGETATION TODAY

So that past changes in the environment and the vegetation may be fully appreciated, a brief outline of the phytogeography and the factors controlling the

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arid vegetation would be much reduced. 3. Present day, with deeper, cooler shelf water and the cooling effects of the current through Torres Strait. Temperatures and precipitation are slightly lower. There is a slight retreat of closed forest and an expansion of the arid vegetation. W, woodland. LW, low open woodland. WF, woodland/open forest. S, shrubland. A, arid vegetation.

FIGURE 7. The floristic zones (from Burbidge, 1960) and major categories of vegetation (simplified from Specht, 1970 and Webb & Tracey, 1981b). 1. Tropical zone. 2. Temperate zone. 3. Eremaean zone. 4. Interzone areas. 5. Closed forests (= rainforest). 6. The boundary between *Eucalyptus* dominated communities and those with a mixture of dominants. 7. Areas where *Nothofagus* may be found in the closed forests. For further explanation, see text.

vegetation today are presented. Figure 7 shows the three main floristic zones recognized by Burbidge (1960), the discontinuous distribution of rainforest, and the approximate limits of the dominance of *Eucalyptus*. In most of the Eremaean Zone, *Eucalyptus* is present but not dominant. *Acacia* is one of a mixture of dominants here, but it is also very common in the understory where *Eucalyptus* is dominant.

There are small areas of rainforest (= closed forest) along the northern and eastern coast (see Fig. 7). Although the rainforests are located in areas dominated by *Eucalyptus*, the latter is not a normal constituent of mature rainforests and there are few floristic affinities between adjacent rainforest and eucalypt communities. Tree species of mature rainforest must be able to regenerate under a well-developed or only slightly disturbed canopy. The rainforests are monsoonal and tropical in the north, subtropical and warm temperate along the east coast,

and cool temperate in the southern limits of their range. Tall closed forests require about 1,500 mm of precipitation per annum for extensive development (Francis, 1951), although rainforest elements growing as low forest with emergent *Araucaria* may receive only 900 mm p.a. (see Webb, 1978). Small pockets of rainforest may be found outside of the general climatic limits where the available moisture is supplemented, e.g. by seepage, mountain fog, or soils of higher fertility, especially in fire shadows that are protected from wild fires. These pockets may be only a few hectares in area, too small to be mapped, but biologically they are very important. In areas that are climatically favorable, the most complex rainforest is restricted to the soils of higher nutrient status or niches favorable for nutrient accumulation. Provided rainfall is high, soils of lower nutrient status may support simple evergreen types of rainforest that are typically mixed with sclerophylls. *Eucalyptus* and sclerophylls are dominant on the lower nutrient soils, which do not support rainforest especially where exposed to wildfires. *Nothofagus*, which is so conspicuous in the paleobotanical record (discussed below), is restricted to the areas shown on Fig. 7 where it is one of the few taxa of trees in mature temperate rainforest (Webb & Tracey, 1981a, 1981b; Howard, 1981). *Eucalyptus* requires light for germination and, even under a disturbed canopy, usually requires exposure of mineral soil for establishment.

The region dominated by *Eucalyptus* may be divided into (1) tall open forest, (2) open forest, (3) woodland, and (4) scrubs and shrublands. These divisions broadly follow the rainfall gradient with the tall open forests in the wettest and the scrubs and shrublands in the driest regions.

In tall open forests (or wet sclerophyll), the eucalypts are from 40 m to 100 m in height and there is a shrub layer of mesic taxa. In many places, eucalypts are emergent above well-developed rainforest. Such forests are clearly successional and are potentially capable of developing into rainforest. Tall open forests are found in the higher rainfall areas or the more protected sites. Because *Eucalyptus* requires light for germination and rarely regenerates under a closed canopy, fire regenerates and shapes the development of these forests. If fire is too frequent, i.e. before the eucalypts reach flowering age, it will eliminate *Eucalyptus*. Fire also prevents the succession proceeding towards rainforest (Ash-ton, 1981).

The eucalypts in open forests (or dry sclerophyll) are quite variable in height but less than 30 m. Moisture relationships appear to be the most important factor for tree growth and density. The hard-leaved shrubby layer, so distinctive of the dry sclerophyll forests is found on the more infertile soils, whereas the understory is grassy on soils of a better nutrient status (Gill, 1981). Efficient nutrient cycling is important on the infertile soils. Nitrogen fixation, mycorrhiza, and proteoid roots enhance the mineral status of the sclerophyllous communities (Bowen, 1981). At least one species of *Eucalyptus* utilizes insoluble phosphate (Mullette et al., 1974). Added fertilizers may increase growth of sclerophyllous shrubs, but then the shrubs may also become more drought susceptible (Specht, 1963). The slower growth rate imposed by low soil fertility may confer drought resistance (Parsons, 1968). In general, any means of increased drought resistance involves a cost to the plant in a reduced growth rate (Cowan, 1981). Thus the mechanisms of coping with low nutrient status and water stress may not be independent.

Grassy woodlands (savannah woodlands) characterized by well-spaced trees

are generally found on the better soils. Almost all of the woody taxa belong to either *Eucalyptus* or *Acacia* (Gillison & Walker, 1981).

Scrubs and shrublands (or mallee) are dominated by *Eucalyptus* with many stems arising from an underground lignotuber (mallee growth habit). Some species of *Eucalyptus* may grow both as a tree or a mallee, depending on growing conditions. The dominants are 2 m to 8 m in height. *Acacia* is also common here. The understory consists of sclerophyllous shrubs on the infertile soils, sparse grasses on the more fertile soils and chenopodiaceous shrubs in the drier regions (Parsons, 1981).

Shrublands and grasslands are the major vegetation types in the Eremaean Zone. Species of *Eucalyptus* are present but not usually dominant. Shrublands may have both large and small shrubs. The abundant large shrubs include *Acacia* and, less frequently, the mallee form of *Eucalyptus* (Johnson & Burrows, 1981). Chenopodiaceous shrubs are common in the southern part of this zone (Leigh, 1981). Tussock (*Astrebla*) and hummock (*Triodia* and *Plectrachne*) grasslands are found in the northern part of the arid region (Groves & Williams, 1981). Throughout, the low and erratic rainfall is the controlling factor. Nutrient status is generally low because the soils have been formed on the highly weathered and leached parent material. However, the most important soil characteristics are those that control the amount and availability of water (Perry & Lazarides, 1962).

THE PALEOBOTANICAL RECORD

Reconstructions of the flora and vegetation presented here come mainly from pollen studies. Work is in progress on macrofossils and provides much valuable evidence but it is not yet sufficient to be used for the reconstructions that are possible from pollen. When relying on evidence from pollen, it is important to bear in mind that there is a bias. When pollen and leaves have been identified from the same deposit, the two assemblages may contain quite different taxa. For example, mid-Eocene deposits contain pollen of *Nothofagus* and Myrtaceae but no leaves of these taxa (Christophel, 1981a). The reason for this difference is that leaves are derived mainly from the margins of the site of deposition of clastic sediments so that stream-side taxa are overrepresented. In coals and peats, however, leaves are produced on site. Most leaves do not transport well. On the other hand, pollen in a sediment is derived from a much greater area, probably the whole of the catchment of the depositional basin although most of it is produced locally. The heavy pollen producers, which are wind pollinated, are usually overrepresented in the assemblage. Water-transported pollen may constitute a significant fraction (Birks & Birks, 1980, p. 179). Additionally, some leaves do not preserve well, e.g. *Quintinia*, which is highly underrepresented in the leaf litter although it is relatively common along streams (Christophel, pers. comm.). Some pollen does not preserve, e.g. the Lauraceae, an important family in some parts of Australia. These differences result in apparent discrepancies between the interpretations from macrofossil and from palynological evidence. However, these two lines of evidence are complementary, not in competition, and when they can be integrated into one paleobotanical interpretation a more balanced and complete story will emerge.

Another important bias results from the conditions necessary for the preser-

vation of plant remains, viz., the anaerobic swamps, bogs, lake bottoms. Such requisites are abundant in high rainfall areas but exceptional under a dry climate or a strong seasonal drought. Consequently, the paleobotanical record is largely that of the wetter climates.

The level of identification in the fossil record is quite variable, particularly for pollen. Fossil populations are easily identified, but they rarely coincide with extant populations. Thus the fossil type may be found in several related genera but not necessarily in all species. Frequently, identifications can be made only to the family or a higher level.

A reliable age for the fossils is essential, but dating is frequently a problem. Many of the fossiliferous deposits are isolated and thin, and palynology is often the only means available for dating such deposits, with consequent dangers of a circular argument. The ages of some deposits are still being debated.

TAXA IDENTIFIED IN THE AUSTRALIAN TERTIARY

The list below includes pollen and macrofossils. The older macrofossil work which based identifications on gross morphology only is considered as unreliable and not included here. For references to the older work, see Duigan, 1950. Cookson and her co-workers consistently used epidermal and other cellular detail as confirmation of identifications. Their work and that of subsequent authors is included here. Botanical names are preferred and the reader is referred to the reference for fossil names and the proof of identification. Taxa listed without a reference have been reviewed in Martin (1978) and this reference is not repeated. Where a taxon has not been reviewed in Martin, 1978, and the fossil name is necessary to follow the literature, then it is included here in brackets. Throughout the rest of the text, fossil names are only used where necessary for clarification. Where there have been taxonomic revisions, only the latest reference is given. Where the identification and Australian occurrence are found in separate references, both are given. The qualifications and suffixes are those used by the original authors, viz.

Type—a good fit with reference material but it may not be restricted to the particular taxon

Comp—compares favorably with existing reference material

Sim—a strong similarity between fossil type and the present day taxon

Like—strong evidence for the identification

No suffix—a reasonably certain identification.

Type of fossil indicated thus:

P—pollen

L—leaves or leafy shoots

C—cones or cone scales of gymnosperms

K—flowers

F—fruits of angiosperms

S—seeds

W—wood.

GYMNOSPERMAE

- ZAMIACEAE: *Bowenia* L Hill, 1978; *Lepidozamia* L Hill, 1980.
 TAXODIACEAE: *Athrotaxis* L Townrow, 1965b.
 CUPRESSACEAE: Cupressaceae P not identified further; *Callitris* sp. L Blackburn, 1981b; three forms related to *Papuacedrus* L Offler, 1969.
 PODOCARPACEAE: *Phyllocladus* P & L Cookson & Pike, 1954, ? W Patton, 1958; *Dacrydium* type 1, *D. franklinii* P; *Dacrydium* type 2, Section B of the genus P, L & S Cookson & Pike, 1953b; three forms of *Dacrydium* related to sections A, B and C respectively L Offler, 1969; *Podocarpus* type 1, section *Dacrycarpus* P & L Cookson & Pike, 1953a, Townrow, 1965a; *Podocarpus* type 1, most other sections in the genus, P & L Townrow, 1965a, L Blackburn, 1981a, at least 5 spp. Blackburn, 1981b; *Microcachrys* P; *Microstrobos* L Townrow, 1965a.
 ARAUCARIACEAE: Araucariaceae P not distinguishable to generic level; *Araucaria* L & C Cookson & Duigan, 1951; *Agathis* L & C Cookson & Duigan, 1951, W Patton, 1958.

ANGIOSPERMAE Subdivision DICOTYLEDONAE

- WINTERACEAE: *Tasmania* (= *Drimys*) P.
 MORACEAE: Moraceae comp P Luly et al., 1980.
 FAGACEAE: *Nothofagus*, the *menziesii* pollen type P; *Nothofagus*, the *fusca* pollen type P; *Nothofagus*, the *brassii* pollen type P.
 CASUARINACEAE: *Casuarina* P & F Pike, 1953, W Patton, 1958. Both *Cryptostomae* and *Gymnostomae* L & F Christophel, 1980, Blackburn, 1981b.
 GYROSTEMONACEAE: Gyrostemonaceae P Luly et al., 1980.
 PORTULACACEAE: *Montia* P.
 CHENOPODIACEAE/AMARANTHACEAE: P of Chenopodiaceae and some Amaranthaceae are indistinguishable.
 POLYGONACEAE: *Polygonum* pantoporate pollen type (Martin, unpubl.).
 ELAEOCARPACEAE: *Elaeocarpaceae* F Blackburn, 1981b; *Elaeocarpus* P Luly et al., 1980.
 BOMBACACEAE: Bombacaceae (*Bombacidites bombaxoides*) P Couper, 1960, Stover & Partridge, 1973.
 MALVACEAE: Malvaceae P.
 ERICACEAE/EPACRIDACEAE: Ericaceae/Epacridaceae P is very similar.
 SAPOTACEAE: Sapotaceae P not identified further.
 EVENACEAE: Ebenaceae aff. *Diospyros* K & L Christophel, 1981b.
 SYMPLOCACEAE: *Symplocos* P.
 EUCRYPHIACEAE/CUNONIACEAE (dicolpate): *Geissois-Eucryphia* comp P Luly et al., 1980; *Ceratopetalum* comp P Luly et al., 1980.
 CUNONIACEAE (tricolporate): Cunoniaceae P Luly et al., 1980.
 ESCALLONIACEAE: *Polyosma* sim P Luly et al., 1980; *Quintinia* P.
 MIMOSACEAE: *Acacia* P & L Cookson, 1954.
 LEGUMINOSAE (= PAPILIONACEAE): Leguminosae P Luly et al., 1980.
 HALORAGACEAE: *Haloragis* P; *Myriophyllum* P.
 GUNNERACEAE: *Gunnera* P.
 MYRTACEAE: Seven pollen types not reliably identifiable further, *Acmena* comp Luly et al., 1980; *Baeckea* comp Luly et al., 1980; *Rhodamnia* comp Luly et al., 1980; *Syzygium-Cleistocalyx* comp Luly et al., 1980; *Eucalyptus*-like F Lange, 1978a; *Leptospermum*-like F Lange, 1978a; *Calothamnus*-like F Lange, 1978a; F like *Melaleuca-Callistemon* Lange, 1978a; *Angophora*-like F Lange, 1978a.
 ONAGRACEAE: *Jussiaea* (*Corsinipollenites*) P Traverse, 1955, Hekel, 1972; *Fuchsia* P, A. D. Partridge, pers. comm., D. Hos, pers. comm.
 PROTEACEAE: *Adenanthos*-type P. TRIBE BANKSIEAE P & L Cookson & Duigan, 1950, L Blackburn, 1981a, 6 spp. of L Blackburn, 1981b; *Banksia* P Luly et al., 1980, F Cookson & Duigan, 1950, Pike, 1953, W Patton, 1958; *Beauprea* P. TRIBE GREVILLEAE L Blackburn, 1981a; *Grevillea*-type P; *Helicia*-type P; *Isopogon*-type P; *Orites* comp P Luly et al., 1980; *Xylomelum*-type P; *Xylomelum* comp P Luly et al., 1980; Proteaceae comp P Luly et al., 1980. Many pollen forms attributed to the family have not been identified further. cf. Proteaceae I, II, III and IV L Lange, 1978b.
 RHIZOPHORACEAE: Rhizophoraceae (*Zonocostites ramonae*) P Germeraad et al., 1968, Hekel, 1972.
 ALANGIACEAE: *Alangium* (*Alangiopollis*) P Traverse, 1955, Hekel, 1972.
 OLACACEAE: *Anacolosa* P.
 SANTALACEAE: *Santalum* P.
 LORANTHACEAE: *Amylotheca* P; *Decaisnina*-type P; Lorantheae P Luly et al., 1980.
 AQUIFOLIACEAE: *Ilex* P.

- EUPHORBIACEAE: *Austrobuxus-Dissiliaria*, the spiny type P; *Austrobuxus-Dissiliaria*, the non-spiny type P; *Choriceras* comp (non-spiny) P Luly et al., 1980; *Austrobuxus* (= *Longetia*) (spiny) P Luly et al., 1980; *Coelebogyne* P; *Macaranga-Mallotus* P; *Micrantheum-Neoroepera* P; *Omalanthus* comp P Luly et al., 1980; *Petalostigma* P; Euphorbiaceae P Luly et al., 1980.
- RHAMNACEAE: Rhamnaceae P Luly et al., 1980.
- VITACEAE: Vitaceae P Luly et al., 1980.
- SAPINDACEAE: Tribe Cupaniae P; *Diplopeltis* P; *Dodonaea* P; *Dodonaea* cf. *D. triquetra* P, Martin unpub.
- RUTACEAE: *Melicope* comp P Luly et al., 1980; Rutaceae P Luly et al., 1980.
- GERANIACEAE: *Geranium* P; *Pelargonium* P.
- POLYGALACEAE: Polygalaceae P.
- ARALIACEAE: Araliaceae P Luly et al., 1980; between *Fatsia* and *Harmsioplanax* L Blackburn, 1981a.
- GENTIANACEAE: *Gentiana* sim P Luly et al., 1980.
- OLEACEAE: Oleaceae P & L Cookson, 1947; *Jasminum* comp P Luly et al., 1980.
- RUBIACEAE: '*Randia*' *chartacea* type P.
- COMPOSITAE: Compositae P.

ANGIOSPERMAE Subdivision MONOCOTYLEDONAE

- RESTIONACEAE: *Hypolaena*-type (with centrolepidoid pore) P; *Restio*-type (with graminoid pore) P; Restionaceae/Centrolepidaceae P Luly et al., 1980.
- CYPERACEAE: Cyperaceae P not identified further.
- GRAMINEAE: Gramineae P not identified further.
- SPARGANIACEAE: *Sparganium* P; *Sparganium*-type 2 P.
- PALMAE: *Nypa* (*Spinozonocolpites prominatus* = *S. echinatus*) P Muller, 1968, Stover & Evans, 1973, Hekel, 1972.
- LILIACEAE: *Rhipogonum* comp P Luly et al., 1980; Liliaceae comp P Luly et al., 1980.

FIRST APPEARANCES, SOUTHEASTERN AUSTRALIA

The first appearance and approximate time range of the Tertiary taxa are shown in Fig. 8. Some gymnosperms extend from the middle Mesozoic through the Tertiary. The first angiosperm that can be reliably identified with a modern taxon is *Ilex* (Martin, 1977b). Other angiosperms that first appear in the late Cretaceous are *Nothofagus* and the proteaceous type. The Myrtaceae, perhaps the most important family in Australia today, is first seen in the Paleocene. Taxa appear almost continuously through the Tertiary. In the late Tertiary, there are more herbaceous taxa making their first appearance. It is not known whether the first appearances are the result of evolution or migration (probably a mixture of both).

QUANTITATIVE ASPECTS, SOUTHEASTERN AUSTRALIA

The quantitative aspects through the Tertiary of the major pollen types grouped according to their taxonomic affinities are shown in Fig. 9. As well as the abundant pollen types, there are many other types only found in low frequencies and not shown in Fig. 9. A detailed interpretation and the methods involved are discussed in Martin, 1978. The main points are summarized here:

Paleocene. The gymnosperm group, consisting of ten different pollen types is most abundant in the oldest of the assemblages. The proteaceous group, which may consist of up to 23 different pollen types, is also abundant. Many of these proteaceous types become extinct during the Tertiary. Myrtaceae is present but not abundant. *Nothofagus* is present only in low frequencies. Judging from the present day pollen dispersal behavior of *Nothofagus* (Martin, 1978), these low

FIGURE 8. Range chart showing the first appearances of fossil pollen taxa through the Tertiary, for southeastern Australia. Modified from Stover and Partridge, 1973, and Martin, 1978.

frequencies probably indicate that it was not very common and growing at some distance from the areas of deposition. Angiosperms other than these major groups continue to diversify.

Eocene. The early Eocene assemblages are generally like those of the Paleocene, there is a marked change about mid-Eocene time when *Nothofagus* becomes the dominant pollen group. This great increase in *Nothofagus* must represent an increase in this taxon in the vegetation, but not to the extent suggested by the pollen frequencies, because *Nothofagus* is a very heavy pollen producer. Many of the proteaceous types and some other angiosperms became extinct during the mid-late Eocene.

FIGURE 9. General quantitative relationships of the pollen floras through the Tertiary. Only the abundant pollen types are shown, grouped according to their taxonomic affinities. The three types of *Nothofagus* are shown thus: m, *menziesii* f, *fusca* b, *brassii*.

Oligocene. The pollen floras are dominated by *Nothofagus* with most other types present in low frequencies. The abundance and diversity of the proteaceous group is lower.

Miocene. The early part of the Miocene is quantitatively similar to the Oligocene. About mid-Miocene time, the abundance of *Nothofagus* decreases and the Myrtaceae group becomes the dominant. The precise timing of this change is

earlier inland and later near the southeast coast. There are 8 different pollen types in the Myrtaceae group, but these cannot be identified reliably with extant genera in the family. The 'eucalypt pollen type,' which may be found in other genera besides *Eucalyptus*, is present but not abundant. The greater proportion of the Myrtaceae pollen is more like that found in *Tristania*, *Backhousia*, *Baeckea*, *Syzigium*, and *Acmena* (and possibly other genera). Molds and casts of fruits that are like *Eucalyptus*, *Leptospermum*, *Calothamnus*, *Melaleuca-Callistemon*, and *Angophora* (Lange, 1978a) show these genera exist in the fossil record, but they can only be dated as Eocene-Oligocene or Miocene (Ambrose et al., 1979).

Pliocene. Myrtaceae is dominant, although there are small amounts of *Nothofagus* and a few of the early Tertiary pollen forms are still present. Gramineae and Compositae are usually present but in low frequencies.

Pleistocene. *Nothofagus* and most of the gymnosperms have disappeared from most of the Australian continent. Myrtaceae continues as the dominant and abundance of Gramineae and Compositae have increased greatly. For further detail of the Quaternary, see Kershaw, 1981.

As well as these abundant groups, there are many pollen types found only in low frequencies (about 5% or less). These types probably come from plants with a low pollen production and insect pollination, e.g. *Acacia*, which is important in the vegetation today. Thus a consistent presence of a low frequency taxon is thought to indicate that it may have been important in the vegetation. Many of these low frequency taxa show changes about the time of change in the dominant groups.

These quantitative relationships must represent vegetation that was closed forest through most of the Tertiary, judging from the low herbaceous content (Gramineae and Compositae). A physiognomic analysis of some Eocene leaf floras of southeastern Australia shows them to be most similar to Simple Mesophyll Vine Forest, Complex Notophyll Vine Forest, and Simple Notophyll Vine Forest. These forest types are found today in the rainforest along the east coast of Australia between the latitudes of 15°S–25°S, 20°S–35°S and 15°S–37°S (at higher altitudes), respectively (Christophel, 1981a). The modern rainforests are classified into these physiognomic types on the size of mature, exposed, 'sun' leaves from the tree layers only (Webb, 1959). Fossil leaf floras would contain some of the larger 'shade' leaves, which would inflate the perception of tropicality/subtropicality. However, the diversity of angiosperms represented suggests a complexity now found only under warmer conditions, and certainly not in temperate forests (Webb et al., 1982). If the Eocene pollen and leaf floras are compared, then the latter indicate a much greater diversity in the flora (Christophel, 1981b), but this may be a reflection of the regional versus local representation, respectively, of the two types of fossils.

The nature of these closed forests change through the Tertiary, but it is not until the Pliocene that the forest started opening up to allow the development of a herbaceous stratum of Gramineae and Compositae, at least in southeastern Australia. Open woodlands and/or grasslands did not develop until the Pleistocene (Martin, 1978) in southeastern Australia although the timing of this major change in the vegetation is earlier in inland regions and in Queensland (discussed more fully below).

VARIATION IN THE TERTIARY FLORAS

The general quantitative relationships of the Tertiary floras shown in Fig. 9 are usually recognizable in pollen assemblages of the same age. However, this does not imply that the vegetation was more uniform than that of today. Attempts to identify pollen assemblages from surface samples of moss polsters, surface lake muds, etc., with the parent vegetation have shown that they are identifiable at the "vegetation-landform unit" level, i.e. large vegetation units. When individual plant associations are sampled, little distinction could be made below the level of vegetation-landform unit (Birks & Birks, 1980, p. 243). Consequently, these Tertiary pollen assemblages shown in Fig. 9 should be viewed in the light of large vegetation units. However, with the use of improved methods, more precision in identifying plant communities in the fossil assemblages is possible (see Luly et al., 1980). Even so, when sufficient samples of the same age are compared, they reveal some time-related and geographic variation in the Tertiary floras, although the problems of dating (discussed previously) should be remembered.

Mid-late Eocene Comparisons. Figure 10 compares four mid- and late Eocene assemblages. Three sites are late Eocene, one (St. Vincent's Basin) is mid-Eocene. Figure 10 shows that the spores of pteridophytes are less frequent in inland locations. Trapping of modern pollen has shown that fern spores form a greater proportion of the catch from water transport than from aerial transport (Birks & Birks, 1980). Narrow gullies are more favorable habitats for ferns, so there may be other environmental reasons besides climate for these differences. Only Albany would have been coastal-oceanic (or near coastal) on Eocene paleogeography. Casuarinaceae may have been more abundant elsewhere in Australia with up to 62% in one sample of the Officer Basin. It is not possible to distinguish *Gymnostoma* from *Casuarina* on pollen morphology (Kershaw, 1970a). If Casuarinaceae grew in or along the margins of the swamps or lakes, then it could produce a higher pollen representation. *Nothofagus* may have been more abundant in southeastern Australia, particularly when the Murray Basin is compared to the Officer Basin. The low values in the St. Vincent's Basin are not strictly comparable for these may pre-date the mid-Eocene rise in abundance of *Nothofagus*. Similarly, the high values of 'Proteaceae' in St. Vincent's Basin may pre-date the mid-late Eocene decline of this group, but the high values of 'Proteaceae' at Albany are unusual for the late Eocene (Hos, 1975, 1977, 1978; and Martin, 1978).

Variation in Late Eocene to Early Miocene Assemblages Eastern Murray Basin. Numerous bores penetrating strata of this time range have been studied. Figure 11 shows one of the gymnosperms, the *Dacrydium franklinii* pollen type (= *Phyllocladidites mawsonii*) plotted as a ratio of the total gymnosperms count alongside the percentage of gymnosperms in the total pollen count. While the percentage of total gymnosperms does not vary much, the relative proportions of the different gymnosperms may change. In the late Eocene-early Oligocene, *Dacrydium franklinii* is the most common single gymnosperm pollen type in the group. A rise in abundance of *D. franklinii* may be seen in the Gippsland Basin of southeastern Victoria where this pollen type may constitute up to 80% of the total count in some late Eocene-early Oligocene coals (Stover & Partridge, 1973). Figure 12

FIGURE 10. Comparison of the abundant pollen groups, in the mid-late Eocene. Spores of pteridophytes and 'Proteaceae' are more abundant at Albany. Casuarinaceae is less abundant in the Murray Basin, the easternmost location.

shows one of the *fusca* pollen type, *Nothofagus flemingii*, plotted in the same way. While the percentage of the *Nothofagus* group varies little, *N. flemingii* shows two peaks of greater abundance, one in the early Oligocene and the other probably in the early Miocene. These two peaks in *N. flemingii* abundance may be recognized in the same stratigraphic position over the whole area studied. These examples illustrate how the grouping of the taxa in Fig. 9 may mask the variation present.

The ratio of Myrtaceae to *Nothofagus* pollen is presented in Fig. 13 and shows a gradual increase where the sampling interval is sufficiently close. This increase in Myrtaceae is earlier and more marked in bores to the west than those in the south and east of the study area, which is approximately 250 km × 250 km (Martin, unpubl.).

Mid-late Miocene Comparisons. Figure 14 shows that the Myrtaceae reaches the highest values in the Castlereagh River Valley and Jemalong Gap—the two most westerly locations. Latrobe Valley in the most southeastern part of Australia has lower values for Myrtaceae. A reciprocal pattern is seen with *Nothofagus*, highest in the southeast and it has practically disappeared from Queensland. In the Latrobe Valley, two definite habitats may be identified in the coals; (1) open water, which accumulates mainly wind blown pollen and especially *Nothofagus* and (2) swamp, accumulating pollen from the plants on site as well as wind blown

FIGURE 11. The ratio of *Dacrydium franklinii* to total gymnosperms. While the percentage of gymnosperms varies little, *D. franklinii* is the most abundant in the late Eocene-early Oligocene.

pollen. The latter has appreciable quantities of Restionaceae/Centrolepidaceae pollen (Luly et al., 1980). Macrofossils indicate a sclerophyllous vegetation in these swamp habitats (Blackburn, 1980). Assemblages from the Namoi and Castlereagh River Valleys may be very rich in unidentified tricolpate/tricolporate pollen types. Most of the taxa that can be identified in the latter sites are found today on the east coast of northern New South Wales and it is thought that the late Miocene vegetation here was more akin to the subtropical rainforest (Martin, 1980, 1981). Compositae, Gramineae, and the chenopod pollen type (Chenopodiaceae and Amaranthaceae) are present in low frequencies to the north.

Pliocene Comparisons. Figure 15 shows that the Myrtaceae was more abundant to the west, in Jemalong Gap. Gymnosperms may be quite abundant and particularly the Araucariaceae, which may reach 50% of the total count on the Mooki River Valley. It is not clear whether the Araucariaceae was abundant in the Queensland site, for there is a problem of identification with the fossil pollen type *Dilwynites granulatus*, which may belong to the Araucariaceae but is also like *Cinnamomum* (Harris, 1965a). It is thought that these assemblages with high Araucariaceae are akin to the present day low microphyll vine forests with emergent *Araucaria* ('hoop pine scrubs') of southeastern Queensland. There is a little *Nothofagus* in the Pliocene, mostly the *menzeisii* and *fusca* pollen types. The

FIGURE 12. The ratio of *Nothofagus flemingii* to total *Nothofagus* pollen. There are two peaks where the ratio exceeds 0.25, indicating change within the *Nothofagus* flora.

brassii type, which accounts for the greatest proportion of the *Nothofagus* count up to the mid-Miocene, is occasionally present but in very minor amounts, 1–2%. Such small quantities could result from long distance dispersal or reworking of the older Tertiary sediments. *Nothofagus* in the Pliocene may be traced over most of southern New South Wales where it forms a valuable stratigraphic datum plane, but it is rarely encountered in the northern regions (Mooki and Castlereagh River Valleys). Compositae may be abundant, particularly to the north. The samples from Jemalong Gap with the high Compositae may be close to the Pleistocene boundary, judging by their distance above the *Nothofagus* horizon. Gramineae is usually present but not abundant and the chenopod pollen type is more abundant in the Queensland assemblage. In southwestern Australia, Myrtaceae or Casuarinaceae may be abundant. Restionaceae is usually well represented and *Gyrostemon* is important in some samples. Pteridophytes and gymnosperms are rare.

Other reports give further indication of variation across Australia at different time intervals during the Tertiary. A pollen flora from Central Australia, 170 km northwest of Alice Springs, is reported to be mid-late Eocene in age by Kemp (1976). It has many features in common with those of southeastern Australia, but there are some differences. Cupressaceae, Cyperaceae, and *Micrantheum*, which are found in the Central Australian assemblages (Kemp, 1976), are rarely seen in southeastern Australia until the late Miocene–Pliocene. Early-mid Miocene assemblages near Lake Frome in inland Australia contain abundant grass pollen and have been interpreted as representing riverine rainforest with grasslands or

FIGURE 13. The ratio of Myrtaceae to *Nothofagus* pollen. There is an increase in the early Miocene, indicating a replacement of *Nothofagus* by Myrtaceae as the abundant pollen type.

grassy woodlands on the drier slopes and hillsides (W. K. Harris, pers. comm. in Callen & Tedford, 1976). This contrasts with southeastern Australia where grasslands did not develop until the Pleistocene (Martin, 1969). These Central Australian records probably indicate the early stage of desiccation and contraction of closed forests. Unfortunately, once a dry climate or a strong seasonal climate is established, the permanently wet bogs, lakes, etc., which are necessary for preservation of plant material, disappear so there is no record of the development of the arid flora.

Queensland assemblages have been compared with others where relevant, but there are other differences as well. *Anacolosa* and *Santalum* pollen types, which disappear from southeastern Australia by the end of the Eocene, are found in early Miocene assemblages in Queensland. *Nothofagus* does not become abundant until early Miocene time, and the peak is short lived. It is thought that this Miocene peak is associated with a climatic change or uplift (Hekel, 1972) and suggests that the north was not as suitable for *Nothofagus*.

Comparisons with Quaternary Changes. The Tertiary shows the development of the flora and vegetation to roughly the present day status. In contrast to the Tertiary, the Quaternary shows changes within what is essentially the present day flora and vegetation. Nevertheless, these changes have been quite considerable, for while reasonable analogues of the fossil pollen assemblages may be found in the present vegetation, they are not precise and indicate that plant communities of even 10,000 years ago may no longer exist today.

There have been some extinctions on the Australian mainland as well, for example, *Dacrydium* Sect. B (cf. *D. cupressinum*) in northeastern Queensland

FIGURE 14. Comparison of mid-late Miocene assemblages. Myrtaceae is least abundant in Latrobe Valley, the southern-most site. *Nothofagus* is most abundant at the same site. Restionaceae and other sclerophyllous taxa are important in the Latrobe Valley (see Text for further discussion).

up to about 25,000 years B.P. (Kershaw, 1978), *Dacrydium* Sect. B and *Podocarpus* Section *Dacrycarpus* in northeastern New South Wales, in the Pleistocene (Martin, unpubl.) and *Phyllocladus* in Holocene southwestern Victoria (Dodson, 1974; Churchill & Dodson, 1980). Of the many Quaternary records (Kershaw, 1981), only the two that extend back to the last interglacial period of 125,000 years ago or beyond will be mentioned here.

Lake George in the Eastern Highlands has the longest pollen record of 350,000 years. There are four wooded periods alternating with five non-wooded periods (Singh *et al.*, 1981a, 1981b) and these periods correspond to interglacials and glacials, respectively. The character of the wooded periods changes from wet sclerophyll in the oldest to open sclerophyll and finally dry sclerophyll in the youngest and present wooded period. In an intriguing study of fire history, as reconstructed from the abundance of charcoal particles, fire frequency is always higher in the wooded periods, but increases along with the development of open sclerophyll during the last glacial period. During the non-wooded period of the last interglacial, the fire frequency does not drop, unlike the preceding three non-wooded periods, and this is attributed to Aboriginal man's activities (Singh *et al.*, 1981a).

A record of 123,000 years in northeastern Queensland extends back to the last interglacial period. There is a full cycle of change in which the oldest

FIGURE 15. Comparison of Pliocene assemblages. A = Araucariaceae; D = *Dilwynites granulosus*; which may have affinities with the Araucariaceae (see Text). Araucariaceae may be abundant in Mooki and Castlereagh River Valleys. Myrtaceae is the most abundant in Jemalong Gap, the western-most site.

and youngest part of the profile are similar, with rainforest angiosperms the major group. The intervening period shows an increase of rainforest gymnosperms then sclerophyllous taxa, with the latter accounting for almost all of the pollen in the sediments of the last glacial period (Kershaw, 1978). The last 20,000 years of this pollen diagram are in agreement with the models proposed by Nix and Kalma (see Fig. 6).

In summary, where the Quaternary record extends back far enough, it shows periods in which two types of vegetation alternate; these periods may be linked with the glacial/interglacial cycles. Vegetation of a drier environment or of a more open nature is always found during the glacial times. The vegetation shows progressive change with the repetition of the cycles. There is some evidence of the effect of man on the vegetation through his penchant for starting fires. The oldest confirmed date for the presence of man in Australia is 32,000 B.P. (Barbetti & Allen, 1972), but he may have been present at 40,000 B.P. or even earlier (Bowler, 1976).

COMPARISONS WITH NEW ZEALAND

Mildenhall (1980) has reviewed the Cenozoic plant biogeography of New Zealand and made comparisons with Australia. The main points are summarized here. The late Cretaceous floras of Australia and New Zealand are very similar.

The same palynological zones and datum planes may be used. *Nothofagus* appears in the late Cretaceous in Australia, New Zealand, and South America, and is scarce. In the Paleocene, podocarps are very common, all three pollen groups of *Nothofagus* are present but not abundant. Proteaceae, *Casuarina*, and the *fusca* pollen type of *Nothofagus* are the next most common to the podocarps. Myrtaceae appears in the Paleocene. The assemblages are essentially temperate, with rare occurrences of some tropical elements, e.g. *Anacolosa* and palm pollen. The Paleocene floras are similar to those of the late Cretaceous.

The Eocene is a time of widespread change, just as it is in Australia, and many new forms appear. *Nothofagus* becomes dominant, supplanting the podocarps. First the *fusca* group becomes more abundant, followed by the *brassii* group. *Phyllocladus* and pollen of *Podocarpus* section *Dacrycarpus* appear in the Eocene and there is an increased diversity in the Proteaceae and other angiosperms. At the end of the Eocene, the tropical and subtropical elements disappear, e.g. *Anacolosa* and the palms, including *Nypa*.

In the Oligocene, the *brassii* type of *Nothofagus* is dominant, with *Casuarina* often abundant. Myrtaceae, palms, podocarps, and the *fusca* type of *Nothofagus* are also prominent. Although *Dacrydium franklinii* is present, an abundance in the early Oligocene comparable to some of the high values seen in southeastern Australia has not been found in New Zealand. The *Macaranga-Mallotus* pollen type (Euphorbiaceae) may have been locally abundant. There is an increase in temperate taxa and a decrease in species diversity probably as a result of continued cooling.

In the early Miocene, low lying swamps are common in which *Sparganium* and palm pollen are abundant. The flora is very rich, indicating subtropical forests. The assemblages are dominated by the *brassii* type of *Nothofagus*, Myrtaceae (including ? *Eucalyptus*), *Casuarina*, podocarps, and *Macaranga-Mallotus*. The late Miocene shows a dramatic change with many herbaceous taxa appearing (Mildenhall, 1980). *Acacia* also appears in the early Miocene, approximately the same time as its first appearance in Australia (Pocknall, 1981) and temperate taxa become prominent in most assemblages. The *brassii* type of *Nothofagus* is still common and occasionally dominant, as is *Casuarina*, but the *fusca* type of *Nothofagus* and podocarps are more often dominant. Many new taxa appear in the Miocene.

In the Pliocene, a mosaic of different forest types occurs, both in space and time. Glaciation reduces some forests to scrubland or grassland. The *brassii* pollen type of *Nothofagus* is still prominent in the north. Palm pollen ceases to be important in the early Pliocene. Ferns become more diverse and abundant. In the South Island, middle Pliocene assemblages contain abundant grasses, Compositae, and other herbaceous taxa, indicating grassland. There is, however, a wide range of floral characteristics indicating rapid environmental change. Many tropical taxa disappear during the Pliocene. Many of the taxa appearing in the Miocene disappear before the Pleistocene glaciations. A number of shrubby and herbaceous taxa appear, including *Acacia*, which disappears from New Zealand in the Pleistocene. In the Pleistocene repeated glaciations wipe out many taxa.

Mildenhall (1980) also cited a number of examples of trans-Tasman migration. One of the best examples is seen in the different pollen types of *Nothofagus*.

TABLE 1. Comparison of first appearances in Australia and New Zealand.

Taxa Appearing First in Australia		
First Appearance		
	Australia	New Zealand
<i>Ilex</i>	Late Cretaceous	Eocene
<i>Nothofagus flemingii</i>	Paleocene	Late Eocene
<i>N. falcata</i>	Mid-Eocene	Oligocene
<i>Polycolpites reticulatus</i>	Early Eocene	Late Eocene
Restionaceae, 'Restio' pollen type	Early Eocene	Mid-Eocene
<i>Micrantheum</i>	? Eocene ¹	Late Mio-Pliocene
<i>Macaranga-Mallotus</i>	? Eocene ²	Oligocene
Polygalaceae (<i>Polycolpites esobalteus</i>)	Early Eocene	Miocene
<i>Banksia</i>	Early-mid-Paleocene	Late Eocene
Bombacaceae (<i>Bombacacidites bombaxoides</i>)	Early Eocene	Late Eocene
Cyperaceae	? Eocene	Oligocene
Cunoniaceae	Eocene ³	Oligocene
' <i>Randia</i> ' <i>chartacea</i>	Mid-late Miocene	Early-mid-Pliocene
Taxa Appearing First in New Zealand		
First Appearance		
	New Zealand	Australia
<i>Nothofagus, menziesii</i> type	Paleocene	Early Eocene
<i>Anacolosa</i>	Paleocene	Eocene

Time ranges from Mildenhall (1980), Stover and Partridge (1973), and ¹ Kemp (1976), ² Martin (unpubl.), ³ Christophel (pers. comm.).

Some types appear first in Australia, some first in New Zealand (see Table 1). Because *Nothofagus* has a very limited seed dispersal (see Martin, 1977b), Mildenhall thinks that long distance dispersal has been accomplished by means of viable pollen to a still receptive gene pool (i.e. windblown pollen from Australia fertilized female flowers in New Zealand). Table 1 lists the taxa common to Australia and New Zealand that appear first in Australia and first in New Zealand. Although not all-inclusive, more taxa make their appearance first in Australia than in New Zealand. Work in progress will change some of the time ranges, but the general conclusion that a number of taxa appear first in Australia will probably remain valid (D. Pocknall, pers. comm.). There are many other taxa that appear about the same time in both. As discussed previously, Australia and New Zealand have remained at approximately the same distance apart, 2,000 km, throughout the Cenozoic, although there have been relative changes in latitude.

COMPARISON WITH SOUTHEAST ASIA

The most complete record comes from Borneo. Paleocene-Eocene floras of Borneo are distinctive and 60% have not been recorded outside of Sarawak. Twenty-six percent of the remainder are world wide. Only 11% can be referred to living genera. Nine percent are exclusively pantropical. One pollen type has northern hemisphere affinities. None of the extremely characteristic Australian groups such as *Proteacidites*, *Nothofagus*, or the southern hemisphere gymno-

FIGURE 16. Pollen taxa common to Borneo and Australia in the early Tertiary. The broken line for Queensland through the Eocene and into the late Paleocene indicates imprecise dating (see Text for further discussion). The Eocene of Borneo is poorly known (J. Muller, pers. comm.) hence is represented by the broken lines. The numbers represent taxa, see Table 2.

sperms are present. When compared with the latitudinal equivalents in Africa and South America, the Bornean floras are rather depauperate in contrast to the present day, where it has the richest floras (Morley, 1977). Thus the early Tertiary floras of Borneo were very different to those of Australia, as would be expected from the 3,000 km, latitudinally, between the two regions. However, there are a few taxa in common and these are shown in Fig. 16, in which floras of Borneo, Queensland, and southeast Australia are compared (Table 2). Unfortunately, the early Tertiary unit from Queensland is not dated more precisely than Paleocene to Oligocene (Hekel, 1972) (although it probably covers this time range), and this is shown by the broken line on Fig. 16. The *Ilex* pollen type, which has had a world wide distribution since the beginning of the late Cretaceous (Martin, 1977b), is present in Borneo, Queensland, and southeast Australia. Myrtaceae is found in Borneo, Africa, and South America in the Cretaceous (Muller, 1981), before its first appearance in southeast Australia in the Paleocene (Stover & Partridge, 1973). It is rare in the pre-Miocene of Borneo. In the early Miocene there is a marked increase and it remains abundant thereafter (Muller, 1972), just as it does in southeast Australia. It is also present in the oldest Tertiary flora in Queensland.

TABLE 2. Pollen common to Borneo, Queensland, and SE Australia in the Tertiary. Key to the taxa shown in Fig. 16.

Botanical Affinity	Fossil Name(s)	References
1. <i>Ilex</i>	<i>Gemmatricolporites permagem-matus</i> <i>Ilexpollenites</i> spp.	Muller, 1968 Martin, 1977b; Hekel, 1972
2. Myrtaceae	<i>Myrtaceidites</i> spp.	Muller, 1968; Stover & Partridge, 1973; Hekel, 1972
3. <i>Anacolosa</i>	<i>Anacolosidites</i> spp.	Germeraad et al. 1968; Stover & Partridge, 1973; Hekel, 1972; Harris, 1965b.
4. Unknown	<i>Striatocolporites minor</i>	Muller, 1968; Hekel, 1972
5. Rhizophoraceae	<i>Zonocostites ramonae</i>	Germeraad et al., 1968; Hekel, 1972
6. <i>Nypa</i>	<i>Spinozonocolpites prominatus</i> = <i>S. echinatus</i>	Muller, 1968; Stover & Evans, 1973; Hekel, 1972
7. <i>Alchornea-Coelebogyne</i>	<i>Psilatricolporites operculatus</i>	Germeraad et al., 1968; Martin, 1974; Hekel, 1972
8. Compositae	<i>Echitricolporites spinosus</i> <i>Tubulifloridites antipodica</i>	Germeraad et al., 1968; Stover & Partridge, 1973; Hekel, 1972
9. <i>Austrobuxus</i> (= <i>Longetia</i>)- <i>Dissiliaria</i>	<i>Malvacipollis diversus</i>	Muller 1972; Stover & Partridge, 1973; Hekel, 1972

Anacolosa does not appear in northeast Queensland until the late Oligocene (Hekel, 1972), although it is present in the Paleocene Brisbane microfloras of southeast Queensland (Harris, 1965b). Other pollen types found in both Borneo and Queensland before the Miocene are shown also in Fig. 16 (Muller, 1968; Germeraad et al., 1968; Hekel, 1972) and include Rhizophoraceae, *Nypa*, *Alchornea/Coelebogyne*, and Compositae. In southeastern Australia in the early Eocene, at a time of low sea level, *Nypa* probably formed extensive mangrove forests on the exposed continental shelf, particularly in the Bass Strait between Tasmania and mainland Australia. A rapid rise in sea level subsequently inundated these forests (Partridge, 1976).

Mangrove pollen of the *Sonneratia* type and Rhizophoraceae become important in Borneo in the Oligocene. The ancestral type of *Sonneratia* may extend into the latest Eocene. *Nypa* and the *Brownlowia*-type pollen are the only mangroves present in the Eocene, perhaps suggesting that mangrove vegetation was not well developed then. In the late Miocene, other mangrove taxa become important. These include *Acanthus*, *Aegialites*, *Avicennia*, and *Camptostemon*. There is thus a history of the gradual appearance of the modern mangrove vegetation (Muller, 1964; Morley, 1977).

Pollen of Asiatic montane taxa become common and abundant in the Oligocene-early Miocene of Borneo. These taxa include *Pinus*, *Picea*, *Tsuga*, and *Alnus*. Some of these pollen types are notorious for long distance dispersal but their abundance indicates that they must have been growing locally. The montane pollen is found in assemblages with the tropical lowland mangrove pollen. Geological evidence indicates mountain building in the areas bordering the depositional basins, and that these mountains had been reduced by erosion by the late

Miocene when there was further uplift (Muller, 1966, 1972). Apart from these selected taxa, there are no other published accounts of Oligocene floras for south-east Asia.

A Miocene coal from Borneo has been studied in detail and compared with a Holocene peat and the present-day swamp vegetation. There are some 76 spore and pollen types and the floristic composition of the coal and peat is closely comparable. Any minor differences can be attributed to ecologic variation, etc. Only one pteridophyte spore, *Stenochlaena areolaris*, has become extinct since the Miocene (Anderson & Muller, 1975) although it is present elsewhere in the Philippines today. Thus the flora takes on a modern aspect in the Miocene (Morley, 1977) and has remained much the same to the present day in this particular location. In the montane record, however, the austral taxa *Podocarpus* sect. *Dacrycarpus* and *Phyllocladus* appear in the late Pliocene-Pleistocene (Muller, 1966). In the Pliocene, pollen of Acanthaceae, Balsaminaceae, Compositae, Gramineae, and Loranthaceae increase in frequency and diversity (Morley, 1977). In the Quaternary, several lines of evidence indicate a more seasonal climate in the Sunda area (Morley, 1977) but the palynological record is very meager for this period.

In New Guinea, pollen floras from the Central Delta region of Papua extend back to the late Miocene and consist mostly of contemporaneous taxa. Spores of pteridophytes generally dominate the counts. Gymnosperms are present in very low frequencies and include *Microcachrys* and/or *Microstrobis* (which disappeared in the late Tertiary), *Podocarpus* section *Dacrycarpus* and other *Podocarpus* spp., *Dacrydium*, Araucariaceae, and probably the cycad-type. Of the angiosperm pollen, the mangroves Rhizophoraceae and Sonneratiaceae are the most abundant together with Palmae. *Nothofagus*, the *brassii* pollen type (now growing in the New Guinea highlands) is present but usually 10% or less of the total pollen counts, suggesting that it was probably transported into the area of deposition. There are a few grains of the *fusca* type of *Nothofagus* and it is uncertain whether this represents long distance dispersal or a rare presence in New Guinea. Small quantities of Rubiaceae, Proteaceae, Casuarinaceae, Myrtaceae, and Malvaceae are present (Khan, 1974). This region of New Guinea has always been part of the Australian plate. The oldest record, however, dates from a time when the southeast Asian and Australian plates were in contact. The pollen flora largely reflects the deltaic environment of deposition with some pollen being transported in from the surrounding regions.

DISCUSSION

The Australian paleobotanical record shows major changes in the mid-late Eocene, the Miocene, and the end of the Pliocene. These changes coincide broadly with major declines in the oxygen isotope temperature curve (Fig. 4). The mid-late Eocene changes are associated with the opening of the seaway south of Australia. The Miocene change is associated with the Antarctic ice-cap reaching major proportions and developing aridity in Australia. The changes at the end of the Pliocene are associated with the onset of the glacial cycles and aridity in Australia reaching its present dimensions. These changes are shown clearly in

the abundant pollen groups shown in Fig. 9, but many of the low frequency pollen types show changes about the same time.

The Tertiary pollen assemblages show general and distinctive patterns for any one geological age. Some changes in the Australian flora through the Tertiary may be postulated thus:

Early Paleocene: Gymnosperms are probably the major element and angiosperms are still increasing in importance. There are many extinct taxa.

Late Paleocene–Eocene: 'Proteaceae' are more abundant and very diverse. This abundance is surprising, given the low pollen production of this taxon today (Martin, 1978). If these Tertiary 'Proteaceae' were trees, then more pollen would be produced when compared with a sclerophyllous shrub layer, especially if the trees were those of the high canopy (Birks & Birks, 1980). Some proteaceous trees are found in Queensland rainforests today, but pollen counts are low (Kershaw, 1970b). It is possible that these ancient 'Proteaceae' were one of the dominants in the vegetation. Many of the taxa are extinct.

Late Eocene, Oligocene, and Early Miocene: *Nothofagus* is the dominant pollen type in the pollen assemblages but, given its heavy pollen production, it may not have been the dominant in the vegetation, although more abundant than formerly. Other low pollen producers that are usually present in the assemblages may have been just as abundant in the vegetation.

Miocene and Pliocene: Myrtaceae becomes the dominant. The eucalypt pollen type (which may include other genera) is present but not abundant, except perhaps in southwestern Australia (Bint, 1981), assuming reliable identification of *Eucalyptus*.

Late Pliocene and Early Pleistocene: The present floristic zones and vegetation probably became established about this time, but this assumption is based on the climatic evolution, for the fossil record is too scanty to support it. Besides these overall trends, there are shorter fluctuations in the pollen record (see Figs. 11, 12), which are probably the result of climatic fluctuations, but the 'resolution' of dating is not sufficient to allow any correlation with a causal factor such as the oxygen isotope curve or sea level changes.

Most of the variation seen in the Tertiary assemblages is consistent with the hypothesis that there was a Tertiary climatic gradient parallel to that seen today, i.e. drier inland and wetter on the coast, particularly in the southeast corner of Australia. (The inland region was, however, relatively well watered through most of the Tertiary when compared with its present state.) Myrtaceae becomes abundant first in inland New South Wales and later in southeast Victoria, whereas *Nothofagus* declines first in Queensland, then inland Australia, and last in southeast Victoria, where small remnant stands of *Nothofagus cunninghamii* are still present today. The development of open woodland and/or savannah started first in Central Australia, then possibly in the north, and finally in southeast Australia. Some present-day patterns appear to be fore-shadowed even in the early Tertiary, following the climatic gradient. *Dacrydium franklinii* was more abundant in southeastern Victoria, during the late Eocene early Oligocene, close to its present distribution in Tasmania. Not all taxa fall into this category. *Ilex* found today across the north of Australia does not extend south of latitude 18°10'S in Queens-

land yet it is present in the early Tertiary in southeast Australia when it was adjacent to Antarctica.

There are general similarities between the Australian and New Zealand paleobotanical record, even though these two land masses have remained at approximately the same distance of 2,000 km from each other throughout the Tertiary. The increase in abundance of *Nothofagus* in the Eocene is seen in both. New Zealand was as much affected by the opening of the seaway around Antarctica as was Australia, so these similarities are not surprising. The Miocene was also a time of major change in New Zealand, for it too was influenced by the ice cap development on Antarctica. However, the Miocene marks a divergence, New Zealand being subjected to heavy glaciation that probably started in the Pliocene whereas Australia suffered increased aridity. This difference probably results from New Zealand remaining at the same latitude whereas Australia continued on its path northwards, although a small, insular landmass such as New Zealand is not strictly comparable to a continental landmass. This floral similarity is illustrated by the extinct Tertiary angiosperm taxa in New Zealand. Of the 200 or so extinct taxa in the palynological record, 70% occur in the Australian record also. About 20% are restricted to New Zealand, mostly in the Miocene (Mildenhall, 1980).

The early Tertiary floras of southeast Asia and Australia are quite different although the evidence from northern Australia, the most relevant region in this context, is very scanty. This difference is to be expected for two reasons: the different floristic inheritance and the different climatic zones that must have existed with a latitudinal distance of 3,000 km between the two continents. There are, however, a few taxa in common with both continents, even with southeast Australia. The most notable common taxon is the Myrtaceae, which appears first in Borneo, before Australia. There are more taxa in common, from Miocene time when the two continents came into collision, but there remain many differences which may be attributed to environmental differences.

Today the dry monsoonal climate and infertile soils of northern Australia are very limited in New Guinea, whereas the habitats for the complex lowland humid rainforests of New Guinea are restricted to a "small archipelago" of habitats on the Australian mainland (Webb & Tracy, 1972). Areas of seasonal drought and dry pockets are very restricted in the island archipelago of southeast Asia (see van Steenis, 1979, p. 107). This environmental difference is largely the result of different geological evolution, more active tectonism in New Guinea and elsewhere than on the Australian mainland. It is likely that this difference extended back into the Tertiary. With one published account for New Guinea and two for Queensland, the fossil record is too inadequate for further comparisons.

The increase in Myrtaceae in Borneo in the early Miocene, about the same time as it started increasing in Australia, is most interesting. The increase in Australia may be attributed to developing aridity, although independent evidence for the timing of this event is uncertain. However, it is unlikely that aridity was the cause of the increase in Borneo. In the vegetation of Borneo, Myrtaceae may be abundant on the infertile soils (J. Muller, pers. comm.). Although not studied in detail, Specht and Womersley (1979) described "heathlands" in Malesia. 'Heath forests' are considered as an edaphic climax rainforest developed on very infertile

soils. With increasing site severity the forest is replaced by open scrubland. Species of *Baeckea*, *Leptospermum*, *Eugenia*, *Tristania*, *Rhodamnia*, *Rhodomyrtus*, and *Xanthostemon* of the Myrtaceae are involved. A diagram of the heath-forests and scrublands in Bako National Park, Sarawak, shows Tertiary Sandstone as the parent rock (Specht & Womersley, 1979). Thus the increase in Myrtaceae in Borneo may be related to newly available infertile soils.

The hypothesis above, which accounts for the increase in Myrtaceae in Borneo, also questions the developing aridity as the cause of the increase in Australia. As discussed previously, there is evidence, such as quartz sands and gravels in the lower sediments in western New South Wales, that the soils may have been less fertile than those of today. *Nothofagus* and other rainforest taxa would have had to exist on these infertile soils as well as the Myrtaceae. However, some sites, such as narrow gullies, favor nutrient accumulation. In any given topography, a mosaic of soil fertility and available moisture would exist, even with a uniform parent rock material and climate (respectively). Consequently the different components of the pollen assemblage may not have been growing together, but the palynological method would not detect this. As discussed previously, adaptations to a low nutrient status lowers the growth rate, which appears to confer added drought resistance as well. Now, any taxon with a slower growth rate is at a serious competitive disadvantage if the climate is suitable for faster growing species. It is likely that the long history of infertile soils allowed the evolution of mechanisms of coping with infertility. Such taxa would be relegated to the most unfavorable sites while the climate was suitable for faster growing species, for some kinds of rainforest are capable of growing on relatively infertile soils, provided that rainfall is adequate (Webb, 1978). Once the climate started to become drier, the taxa on the unfavorable sites expanded their area. This expansion of Myrtaceae starts earlier in the west of western New South Wales, thus paralleling the climatic gradient. Independent evidence from the sediments, viz., that the carbonaceous content decreases about the time of the Myrtaceae increase, is interpreted as a decrease in swamp vegetation that would follow a drier climate. Most of the early Miocene Myrtaceae are not the *Eucalyptus* type. The whole assemblage indicates closed forest, even into the Pliocene and there is no known analogue in Australia for these myrtaceous forests. It is a matter for conjecture whether these Miocene-Pliocene myrtaceous closed forests were akin to the "heath forests" of Borneo today.

So far this paper has dealt with the barriers of water, topography, climate, soils, and distance. Reconstruction of the barriers of vegetation are more difficult because the palynological method is not suited for the detection of vegetation that may exist as a mosaic. Identifications are rarely to specific level and the ecological tolerances of a genus may encompass more than one vegetation type. It is possible to reconstruct the vegetation mosaic from the pollen assemblage, given incompatible ecological tolerances, but not with any great precision. *Acacia* in New Zealand provides a good example. In the early Miocene, *Acacia* is found on the eastern coast of the South Island in assemblages with abundant *brassii* pollen of *Nothofagus*. The whole assemblage indicates rainforests. *Acacia* is usually found in open vegetation, so it may have existed in exposed coastal situations subject to wind desiccation (Pocknall, 1981). However, there are a few

species of *Acacia* that are found in certain rainforests today (Webb & Tracy, 1981b) so this Miocene *Acacia* in New Zealand may have been a rainforest species also. *Acacia* appears in the Pliocene on the west coast of the North Island of New Zealand and becomes extinct during the Pleistocene (Mildenhall, 1975). The pollen assemblages in which it is found indicate coastal swamp sedges together with scrub and grassland species. Tree pollen is relatively rare and trees may have been restricted to the surrounding hills. Thus this second occurrence of *Acacia* in New Zealand is more in agreement with the ecological requirements of most Australian species today. Obviously, interpretations of pollen assemblages rely on a knowledge of the pollen behavior of the present vegetation. In a southeastern Australian study of some surface samples from small pockets of rainforest in vast areas of eucalypts, the rainforest was hardly detectable, quantitatively. (This study has important implications, viz., that very small areas of a different kind of vegetation that are biologically very important, may be almost undetectable by the quantitative palynological method.) Moreover, *Acacia*, regarded as one of the dominants in the *Eucalyptus* vegetation, was not recorded in the surface samples (Ladd, 1979). *Acacia* is a low pollen producer with very limited dispersal and it is never found in any quantity. These are examples of the problems of interpretation of pollen assemblages, particularly those of Tertiary age for which the present vegetation is not a good analogue.

Long distance dispersal is a controversial subject, but experience with the paleobotanical record leads to the conclusion that it has occurred. The best illustration of this is the similarity of the Australian and New Zealand Tertiary record. It is not known how this was accomplished, for much of the knowledge gleaned from present day observations of dispersal seems inapplicable to the fossil record. The reason for this probably lies in the vast geological time where the million-to-one chance has probably occurred many times. There are, however, mechanisms that make long distance dispersal possible. Birds transport seeds either in the gut or stuck to feet and feathers (Carlquist, 1981). Some birds migrate regularly. Birds may travel long distances in relatively short times. An example may be seen in opportunistic waterfowl, which rapidly move into flooded areas in inland Australia. Flooding may occur anywhere in the arid region after exceptional rains. When the floodwaters dry up, the birds disperse to the coast (Braithwaite, 1975) or as far away as New Zealand, Christmas Island or MacQuarie Island (G. van Tets, pers. comm.). The second mechanism is wind. Raven (1973) quotes a number of direct measurements of transport by the prevailing westerly winds of pollen, dust, smoke, and possibly pathogens from Australia to New Zealand. The prevailing westerlies probably could transport small seeds but would be unlikely to carry larger seeds. However, birds also use winds and some (e.g. albatross) regularly circle the globe in these latitudes. In New Zealand, the more recently arrived land birds are almost exclusively Australian (McDowall, 1969). Tropical cyclones produce winds that are much stronger than those of the westerlies. Tracks of the cyclones in the Australian region generally travel across the north, down the west coast and down the east coast, some of the latter eventually end up in New Zealand (Coleman, 1972). New Caledonia is well within the cyclone area. Tropical cyclones cause a great deal of damage and create the disturbance that may allow new introductions to become established. They also

carry birds off course. There are plovers in Tasmania and New Zealand, and it had long been assumed that they were the same. However, a more critical examination of the New Zealand plover showed its affinities with a Queensland form. It is thought that tropical cyclones assisted the plovers in their journey to New Zealand (G. van Tets, pers. comm.). It is not intended to pursue this topic further, but simply to establish the following points: (1) The paleobotanical record indicates long distance dispersal has occurred; (2) mechanisms exist for long distance dispersal; and (3) the vast geological time where the most unlikely of probabilities may have occurred a number of times. In any case, dispersal does not succeed unless the environment at the end of the journey is suitable for growth and establishment. It appears that the environment of New Zealand and Australia was sufficiently similar to allow long distance dispersal to succeed.

CONCLUSIONS

Throughout this study, climate emerges as the most important environmental factor, for changes in the paleobotanical and paleoclimatic records usually go together. It is doubtful whether climate has acted as a barrier within Australia, through most of the Cenozoic. The arid center, a conspicuous barrier today, only reached full development in the late Tertiary, some 2.5 million years ago. Through most of the Tertiary, habitats suitable for closed forest existed in central Australia, though not necessarily continuous. Although the center was relatively well watered, there is evidence of a Cenozoic climatic gradient parallel to that of today, i.e. drier in the center and wetter on the coast. Such a gradient would provide a diversity of habitats. There may have been a north-south temperature gradient during the Tertiary, judging from the greater abundance of *Nothofagus* in southeastern Australia when compared to Queensland, but there is no independent evidence to support this.

Climate appears to have been no great barrier between Australia and New Zealand. Both of these land masses have been in the same latitudinal zone through most of the Tertiary and subjected to the same major influences on climate, viz., proximity to and ice cap development on Antarctica. The paleobotanical record is generally similar through most of the Tertiary, becoming less similar in the Pliocene when glaciation becomes increasingly important in New Zealand. The difference in climate between Australia and Southeast Asia must have been a barrier, as would be expected from a latitudinal distance of 3,000 km in the early Tertiary. The paleobotanical records are quite different as well. There is evidence of very limited migrations after these two land masses came into collision in the Miocene, for the seasonally dry habitats, so widespread in Australia, are very restricted in Southeast Asia. As well, such seasonal habitats may have had a relatively late development.

Soil fertility has probably played an important role, in conjunction with climate. Although documentation of Cenozoic changes in fertility is sparse, the limited evidence suggests that, during the Tertiary, some soils were even less fertile than those of today. Adaptations to low fertility through a slower growth rate may enhance drought resistance. Hence some of the Tertiary flora may have possessed adaptations before the development of aridity. Low fertility soils are widespread in Australia but probably not so common in Southeast Asia. The

increase in Myrtaceae in both Australia and Borneo is thought to be due to a combination of low fertility soils and perhaps developing aridity in Australia, but to newly available infertile soils in Borneo. That these two events both occur in the Miocene is probably only a coincidence.

The major topographic features in Australia have remained more or less the same through most of the Cenozoic. Tectonics have been very minor and gentle. Rather than acting as barriers, these factors have probably been important in maintaining habitat diversity. Tectonism has been more active in Southeast Asia, and topographic differences much greater, so these two factors may have been greater barriers to migration between Australia and Southeast Asia after these two plates came into collision.

Continental drift has had a major influence on the evolution of climate and this has been its most important effect within Australia throughout the Cenozoic. New Zealand has remained at approximately 2,000 km from Australia for the whole of the Cenozoic, but this distance appears to have had little effect as a barrier. The 3,000 km between Southeast Asia during the early Tertiary appears to be a barrier, which, however, may have been more of climate than of distance. After these two plates came into collision, there has been only limited migration, for the barriers of climate and soils remained and are seen today.

Barriers and migrations are concepts derived from historical biogeography, which is essentially the study of present day distributions. Historical biogeographers have traditionally held the hypothesis that a taxon originates somewhere (by evolution) and then spreads its range by dispersal, which may be stopped by barriers or channelled along migratory pathways. By closely studying some characteristics of the taxon and its distribution, they then work this hypothesis backwards to arrive at some explanation of how the present distributions came to be. The unstated assumption of this practice is: provided all other factors remain equal and stable. This study shows clearly that all other factors are not equal or stable, but that there is a complex, interwoven and continuously changing environment and flora. Although I have attempted to use the concepts of barriers and migrations, they seem inappropriate in this study, which essentially follows paleoecological principles.

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