Journal of Arid Environments 66 (2006) 533–563
Journal of Arid Environments
www.elsevier.com/locate/jnlabr/yjare

Cenozoic climatic change and the development of the arid vegetation in Australia

H.A. Martin*

School of Biological, Earth and Environmental Sciences, University of New South Wales, Sydney, Australia

Available online 7 March 2006

Abstract

Australia has not always been arid, and the central desert was once well watered. This paper traces the changes in climate and vegetation, leading to the present aridity. At the beginning of the Cenozoic, continental Australia had a warm and humid climate, and the vegetation was mainly meso–micro-thermal (warm to cool temperate) rainforest. Central Australia experienced seasonal rainfall and there may have been limited aridity in the northwest. By the mid–late Eocene, rainforest in central Australia was restricted to the well-watered valley bottoms, with sclerophyll vegetation on the slopes and ridges. In the latest Eocene–earliest Oligocene, there was an abrupt cooling of ocean waters and the diversity of megathermal angiosperms decreased.

The early–mid-Miocene was warm–humid and there was a considerable diversity of forest types. Woodlands and Casuarinaceae forests became more common. Central Australia was seasonal, with a very warm season of high evaporation. In Western Australia, regular flows in the palaeodrainage systems had stopped by the mid-Miocene and this marked the first major step towards aridity.

The late Miocene was cool and dry, with a major reduction of rainforests and an increase of *Eucalyptus*/casuarinaceous sclerophyll forests in inland southeastern Australia. Regular burning became a feature of the eucalypt forests. Rainforest persisted, however, along the east coast and highlands of Australia. Central Australia became more arid with dry woodland and chenopod shrublands. Rainforests continued to decrease during the Pliocene and grasslands developed in central northern Australia.

By the early Pleistocene, the modern climatic regime had been established, but precipitation was higher than today. Cycles of open, shrubland/grasslands/herbfields and wooded vegetation accompanied the arid glacial and humid interglacial cycles (respectively). About 0.5 Ma, there was a change to a drier climate, but it was still wetter than today. The last glacial period was particularly harsh, and the present interglacial period is drier than the previous interglacial. Aridity has thus increased in a number of steps, following the first major step towards aridity in the early Miocene.

*Tel.: +61 2 9385 8099; fax: +61 2 9385 1558.
E-mail address: h.martin@unsw.edu.au.

0140-1963/$ - see front matter
doi:10.1016/j.jaridenv.2006.01.009

Distinctive elements of the vegetation can be traced back to times when the arid zone was humid and supported rainforest. The elements, which have remained in arid regions, are the few that could tolerate or adapt to the drier climates. The taxa, which could not cope with these changing conditions, were eliminated from the arid regions.

Keywords: Australia; Cenozoic; Climatic change; Aridity; Vegetation history; Arid vegetation

1. Introduction

There is ample evidence from a number of different inquiries to show that central Australia was once well watered and the past vegetation was very different from that growing there today (Hill et al., 1999). This paper traces the development of the arid vegetation and the climatic changes that allowed these developments. The palaeovegetation is reconstructed from fossil evidence, and palaeoclimate is deduced from a number of different disciplines. The palaeovegetation of central Australia is best appreciated when compared with the palaeovegetation of the same age in other parts of Australia, and shows that the climatic gradients of today existed throughout the time under consideration here, and that the changes to a drier climate were not limited to central Australia: they registered throughout the continent.

This study concentrates on the Cenozoic, which commenced some 65 million years ago. Angiosperms, the flowering plants which dominate the vegetation today, first appeared in Australia some 120 million years ago but they were not common then. By the beginning of the Cenozoic, angiosperms had become common and in places, the dominant plant group, and thus more like the modern flora.

2. The arid climate today

The continent of Australia is essentially an arid one, with one-third of the land mass having an annual precipitation of 250 mm or less. Another one-third comes into the semi-arid category. The overall pattern of rainfall distribution is one of the concentric zones with increasing rainfall, outwards from a vast central desert. Rainfall is undoubtedly the over-riding environmental factor (Keast, 1959). The only regions that could be said to be well watered are the east coast strip and the southwest and southeast corners of the continent (Fig. 1). In northern parts, monsoonal influences and tropical cyclones bring summer rains and in the south, the winter cold frontal systems bring most of the winter rainfall. Irregular major droughts and periodic seasonal droughts characterize most of Australia (Nix, 1981; Hobbs et al., 1998).

A mean annual rainfall of 250 mm or less may define the desert, but it has practically no meaning in respect of plant growth. The mean annual rainfall may fall in a single shower, or it may be scattered in a number of small showers in such an amount that it does no more than wet the surface dust. Periods when the rainfall in arid regions is less than 50 mm frequently last for 2 years. Heavy rains may fall at any time, but they are more frequent in the summer months, coming from monsoonal troughs to the north. Winter rains are more common in the south (Specht, 1972; Allan, 1990).

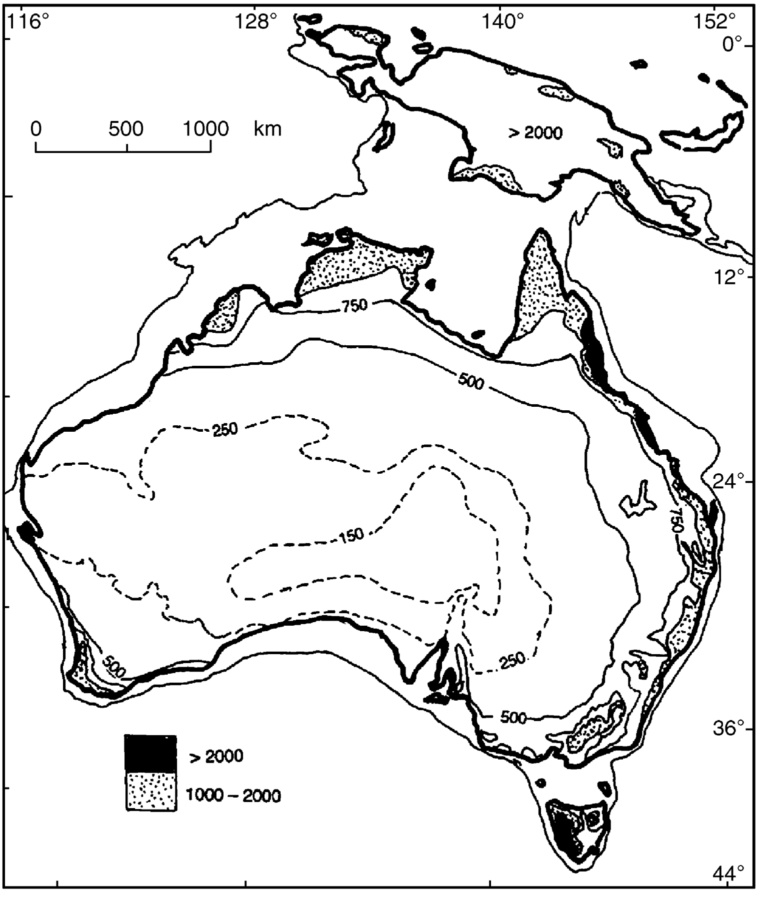

Fig. 1. Mean annual precipitation (mm). Modified from Nix (1981). The broken lines cover regions where few records are available.

During a dry period, falls of less than 6 mm are ineffective so far as the vegetation is concerned: the water does not penetrate as far as the roots of the plant before it is evaporated. During a wet period, smaller falls than these are, of course, beneficial. On the whole, the number of days with falls of rain greater than 6 mm is a useful index. In practically, the whole of the region, the number of days with such effective falls is 9 days/a (Specht, 1972).

Temperatures show a high diurnal range, in common with all desert and semi-desert regions. An important result of the high diurnal range of temperature is the change in the humidity during any 24 h. This occurs during all months of the year. During the day, humidity is low, but during the night the temperature may fall to the dew point and the air becomes saturated with water vapour. Dew condensing on leaves of droughted plants during the night can enter the leaf and help to restore turgor; stomata may then open for a short time at dawn, enabling carbon dioxide for photosynthesis to enter the leaf. However, the plant cannot survive on dew alone and when subjected to drought, is defoliated (Specht, 1972).

A glance at the map of Australia shows many inland lakes, fed by the inland drainage systems. Most of these lakes are dry for very long periods, only filling occasionally after exceptional rains. As an example, Lake Eyre, almost at the centre of the continent, has witnessed spectacular fillings in 1950, 1974 and 1984, with over 20 smaller flood events (Kolwicki, 2004).

3. The present vegetation

In the broadest sense, the native vegetation follows these climatic patterns (Fig. 2). Tall, dense plant communities are found in the high rainfall areas and stunted, open communities in the driest regions (Specht and Specht, 1999). Rainforest is restricted to areas along the east coast region where the precipitation is more than 1500 mm/a, although

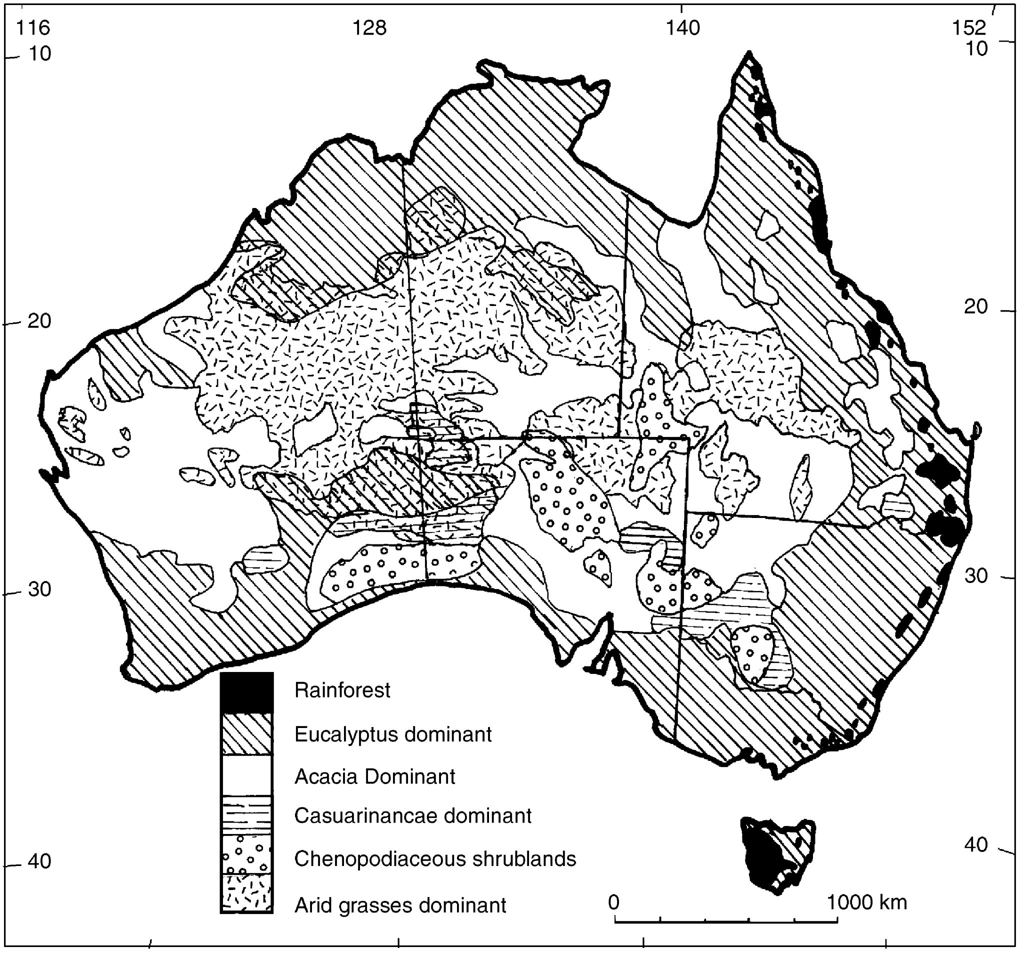

Fig. 2. Generalized map of the vegetation of Australia. Modified from Kershaw et al. (1994) and Groves (1999).

small isolated outliers may be found in favourable habitats down to 750 mm/a (Webb and Tracey, 1981). *Eucalyptus*, "the universal Australian" (Prior and Johnson, 1981, p. 501), is dominant over much of the continent and is found in forests, woodlands and tall shrublands (Fig. 2). In the arid zone, *Eucalyptus* is less prominent and occupies rather specialized habitats. Here, *Acacia*, Casuarinaceae, chenopods and grasses are the dominants in the arid plant formations (Groves, 1999).

The vegetation of Australia today (Fig. 2) is described here in terms of broad, general units that may be deduced from the fossil record.

Rainforests: Closed forests or rainforests are found in the better-watered environments that lack a significant seasonal drought and are usually structurally and floristically complex (Specht and Specht, 1999). *Eucalyptus* is not dominant in rainforests and is only found in special habitats such as ecotones on the edges of rainforests or in mixed forests. There are many different types of rainforest in tropical, subtropical and temperate regions (Specht and Specht, 1999). In Australia, tropical rainforests are the most complex and are best developed north of 21°S latitude, although small patches may extend further south. Subtropical rainforests are most common between 21° and 35°S and temperate rainforests are the dominant type south of 35°, although small patches may be found as far north as 28°, in more montane regions (Webb and Tracey, 1981; Specht and Specht, 1999). *Nothofagus*, so common in the fossil record, is found in temperate rainforests that are well developed in Tasmania (Busby and Brown, 1994), but confined to a few small regions on the Australian mainland where high humidity is maintained through the year.

The usage of rainforest here is very broad and includes all forest types that share many taxa and have the same physiognomic characteristics of forests that are climatically rainforests. Rainforests are in stark contrast to *Eucalyptus*-dominated sclerophyllous forests and woodlands.

Sclerophyll or open forests: These are most commonly dominated by *Eucalyptus* and/or *Casuarina/Allocasuarina* (Specht and Specht, 1999). Wet sclerophyll forests have an understorey of rainforest and other mesic taxa, and if left undisturbed, may revert to rainforest. The understorey of dry sclerophyll forests, however, contains sclerophyllous shrubs and rainforest taxa are lacking. Fire is an integral part of the environment of sclerophyll vegetation (Ashton and Attiwell, 1994; Gill, 1994).

Open vegetation: In forests, the tree canopy forms an almost continuous layer and if dense, insufficient light reaches the lower layers to support a good growth of understorey and ground cover. In woodlands, the trees are well spaced and hence with more light reaching the ground and shrubs and ground cover are more prominent (Specht and Specht, 1999). This applies particularly to grasslands which, by definition, are almost treeless (Mott and Groves, 1994). In the evidence based on palynology, open vegetation refers to mainly shrublands, grasslands and/or herbfields.

Arid and semi-arid vegetation: *Acacia* shrublands and low woodlands largely replace *Eucalyptus* communities in the drier regions of the continent. They become dominant in southern areas where the rainfall is winter incident and the annual precipitation is less than 250 mm. In northern regions, *Acacia* communities predominate in areas receiving less than 350 mm/a. Within the central and western arid zone, particularly in the northwest and in the drier desert areas, *Acacia* often forms only a sparse shrub layer over *Triodia* hummock grasslands (Johnson and Burrows, 1994; Mott and Groves, 1994).

Chenopod shrublands are dominated by various perennial and annual species of the family Chenopodiaceae and are best developed in southern arid regions. They are found in an environment receiving 125–266 mm/a where 30–50% of the precipitation falls in winter. The shrublands are composed of drought- and salt-tolerant xeromorphic halophytes (Leigh, 1994). In places, species of small tree *Casuarina* may be dominant (Specht, 1972).

4. Palaeogeography

At the beginning of the Cenozoic, Australia lay some 35–40° of latitude further south and was adjacent to Antarctica, which was essentially unglaciated. The rift between Australia and Antarctica remained an embayment which did not allow a through current until the latest Eocene–earliest Oligocene, when widening of the rift allowed the Circumpolar Current to develop (Wilford and Brown, 1994). This development had profound consequences: the Circumpolar Current isolated Antarctica and blocked the heat transfer from the low latitudes, allowing glaciation to develop. The oxygen isotope temperatures of surface oceanic waters reflect these changes (Fig. 3).

Australia is regarded as a very old continent and is tectonically stable. It was once thought that the uplift of the Eastern Highlands was relatively recent, but there is

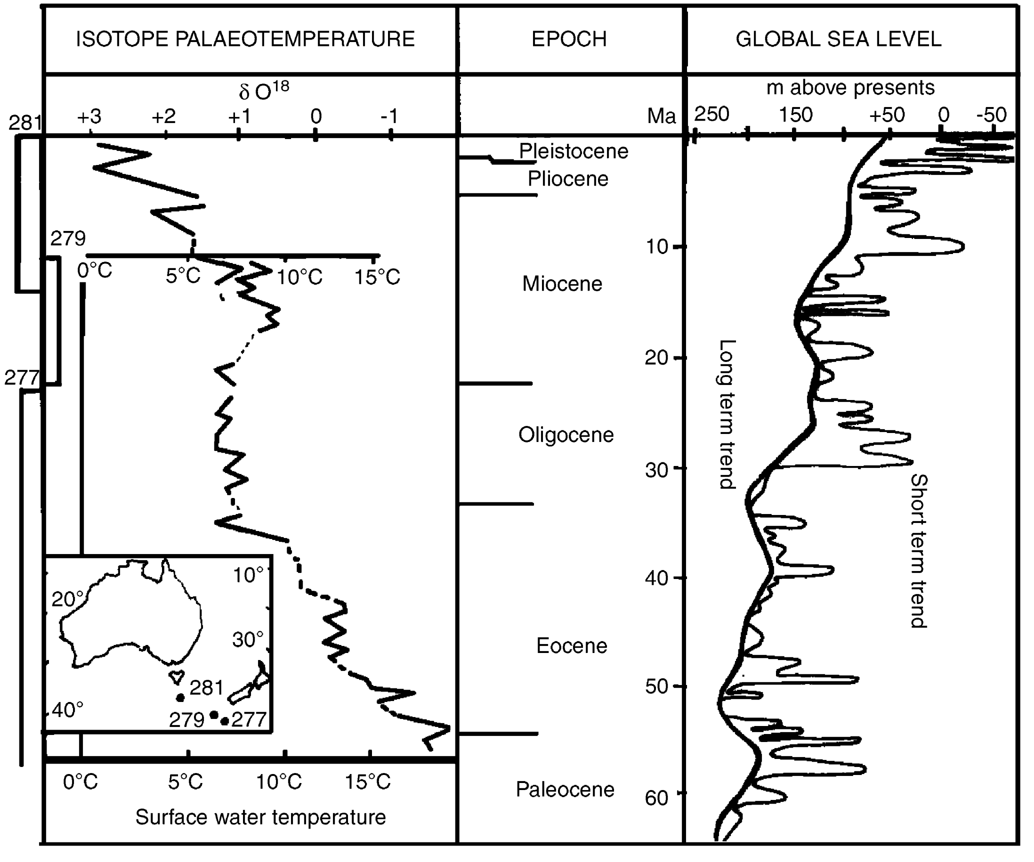

Fig. 3. Changes in sea level, from Haq et al. (1987) and oxygen isotope temperatures, from Shackleton and Kennett, 1975) through the Cenozoic. This oxygen isotope record relates directly to the Australian region, and does not differ in any substance from the global record (Zachos et al., 2001). Time scale from Ogg (2004).

consensus that most of the uplift is at least late Mesozoic and uplands in other parts of Australia are even older (Taylor, 1994). The last major tectonic episode occurred in the mid-Cretaceous (Veevers, 1991).

East of the Eastern Highlands, the drainage systems are short and steep, whereas on the western side, they are long with gentle slopes, the latter culminating in the large inland drainage basins. In the western part of the continent, drainage is largely chaotic (Taylor, 1994). The present drainage systems reflect even older systems and have been much the same throughout the Cenozoic (Wasson, 1982). Starting in the late Palaeocene–early Eocene, downwarping of the Lake Eyre Basin in central Australia lead to extensive deposition in sand sheets, braided streams, swamps and lagoons at a time when most of the continent was undergoing erosion (Benbow et al., 1995).

Changes in sea level have their impact on geography (Fig. 3). At times of high sea level, low lying coastal plains are flooded and with sluggish drainage, there are more swamps and floodplains. The climate is usually warmer and wetter. When the sea level is low, the drained coastal plains become available for recolonization. With a lowered base level to the rivers, drainage is more effective and there are fewer swamps and floodplains. Times of low sea level are usually drier and colder (Haq et al., 1987; Macphail et al., 1994). Although changes in sea level account for most inundation and draining of the land, minor tectonics may cause flooding of low lying regions (Quilty, 1994).

The global curve of changing sea level (Fig. 3) shows some major high and low stands, but there were almost continuous (in geological time) fluctuations. Thus, coastal vegetation would have been subjected to almost continuous disturbance. Macphail et al. (1994) suggest that the change of one plant community type to another may have been accomplished within 0.2 Ma. Such dynamic environments may have encouraged evolution and novel plant communities (Martin, 1997).

A consequence of the changes in sea level is that they largely determine where sediments are deposited. At times of high sea level, deposition occurs in the swamps on land and on the continental shelf. At times of low sea level, sediments are carried further out to sea. Thus, sedimentological and palaeontological studies of sites on land are mainly 'snapshots' of times of high sea-stands.

5. Evidence of climate change

The palaeoclimate may be deduced from a number of different lines of evidence, both in the marine realm and on land, as well as the palaeofloras. Marine sediments are usually better dated, and deposition is more continuous than terrestrial sediments, which are more fragmented. For a full discussion of developments and limitations of research in this field, see Truswell (1993) and Macphail et al. (1994). In this attempt to trace the development of the arid flora, there are serious limitations if relying on the palaeobotanical record alone. Plant parts require permanently wet lakes, swamps, bogs, etc. for preservation and as the climate becomes drier, these environments become fewer. Moreover, deposition of plant parts is biased towards swamps and lakeside environments. Once deposited in sediments, the plant must be buried deep enough to escape the destructive effect of the alternate wetting and drying of a fluctuating water-table. Studies of the sediments themselves yield evidence of the climate at the time of deposition and this evidence, together with the palaeobotanical record, give a better picture of the development of the arid climate and flora.

Not all of Australia is arid, but the climatic changes that lead to the development of the arid centre affected the whole of the continent. For this reason, climatic change over all of Australia is discussed here.

5.1. The Palaeocene

The Palaeocene was a time of warm marine conditions, with less tropical/polar differentiation of climatic zones than there is today (Quilty, 1994). Antarctica was essentially unglaciated.

On the North West Shelf (Fig. 4), studies suggest that the early Palaeocene climate was at least warm temperate, with a relatively wet climate to the south and drier to the northeast. In the late Palaeocene, the north of the Shelf was hot and fairly dry and

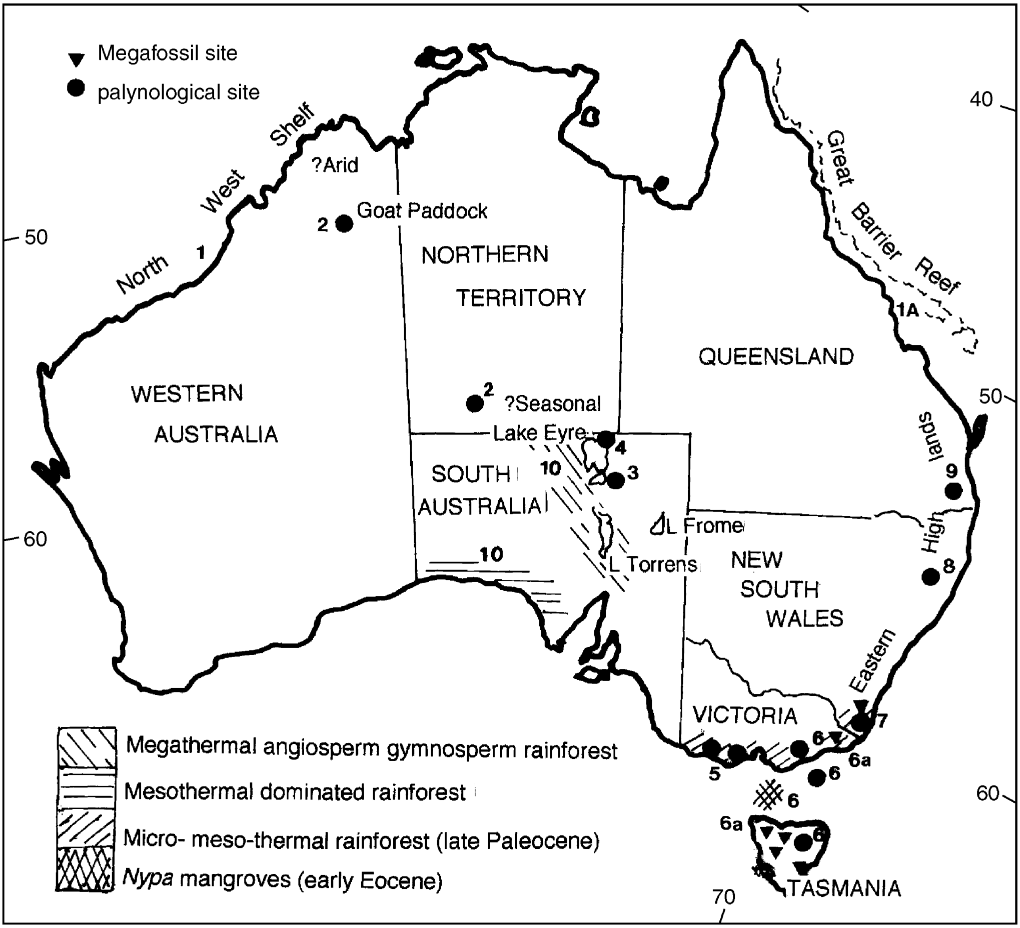

Fig. 4. Late Palaeocene–early Eocene localities and features. References: 1, Apthorpe (1988); 1A, Feary et al. (1991); 2, Truswell and Harris (1982); 3, Sluiter (1991); 4, Martin (1998a); 5, Harris (1965a); 6, Macphail et al. (1994); 6A, macrofossil sites, Hill (2004); 7, Taylor et al. (1990); 8, Martin et al. (1987); 9, Harris (1965b); 10, Benbow et al. (1995). Palaeolatitudes are for the late Palaeocene–early Eocene.

probably seasonal, but occasionally wet enough to support marsh and estuarine environments. Oceanic temperatures were tropical in the north and warm temperate or subtropical to the south of the Shelf (Apthorpe, 1988). In northeastern Australia, the northern part of the Great Barrier Reef would have had subtropical temperatures and the southern part was temperate (Feary et al., 1991).

In southeastern Australia, there was considerable precipitation and runoff (Quilty, 1994) and southern Australia was cool temperate (Benbow et al., 1995). Gymnosperms and Proteaceae species were prominent in the palynoflora, but *Nothofagus* (mainly the extinct ancestral type) was rare. Pteridophytes were also common inferring a year-round high humidity. The vegetation was a richly diverse cool temperate (meso–micro-thermal) rainforest. Coastal regions in the east, however, probably had more Casuarinaceae (Harris, 1965a; Macphail et al., 1994).

In the Eastern Highlands, gymnosperms were prominent, but there was appreciable *Nothofagus* (mostly the ancestral type) and a diversity of other angiosperms (Harris, 1965b; Martin et al., 1987; Taylor et al., 1990). Fossil wood of gymnosperms and angiosperms have well-defined rings that indicate strongly seasonal growth patterns, as would be expected from the high latitudinal position at the time. The vegetation was cool temperate (meso–micro-thermal) rainforest with rainfall of somewhere between 1200 and 2400 mm/a (Taylor et al., 1990).

Central Australia was warm temperate with seasonally high rainfall (Quilty, 1994). Late Palaeocene–early Eocene vegetation was characterized by Cunoniaceae-dominated forests with a significant gymnosperm content. Angiosperms were more diverse and abundant when compared with southeastern Australia (Sluiter, 1991; Martin, 1998a). From climatic requirements of comparable modern communities, the late Palaeocene mean annual temperatures was about 18–19 °C and mean annual precipitation greater than 1400 mm (Sluiter, 1991). The vegetation was meso–megathermal (terminology follows Nix, 1982) angiosperm/gymnosperm rainforests (Benbow et al., 1995).

In summary, the Palaeocene in Australia was warm and humid, the vegetation was largely rainforests and swamps, and the only evidence of possibly aridity is in the northwest. Central Australia experienced seasonality (Fig. 4).

5.2. Early Eocene

Globally, the early Eocene was the warmest period in the Cenozoic (Zachos et al., 2001). Marine surface waters were warm (Fig. 3) and bottom waters were about 14–15 °C warmer than today (Quilty, 1994).

In the north of the North West Shelf, the climate warmed progressively and the late Palaeocene aridity continued. The southern part of the Shelf, however, became cooler and wetter (a distance of some 1800 km is involved here), but it is unclear whether this cooling is the result of a global trend or a rearrangement of the currents (Apthorpe, 1988). This climatic pattern in the northwest is probably in accord with global trends: in the early Eocene, the high latitudes experienced enhanced humidity whereas the low and middle latitudes were subjected to increased aridity (Robert and Chamley, 1991). At Goat Paddock in the southern Kimberly region (Fig. 4), however, a palynoflora thought to be early Eocene in age, was typical of that commonly found at that time and indicative of a high rainfall, but *Nothofagus* was not present (Truswell and Harris, 1982). In the northeast of Australia, marine temperatures continued to rise from the Palaeocene, such that all of the Great Barrier Reef was within the subtropical range (Feary et al., 1991).

In southeastern Australia, temperate conditions, with considerable rainfall and runoff continued (Quilty, 1994). There is an upsurge of megathermal angiosperms and ferns, and the pollen/fern spore proportions are not dissimilar to that produced by tropical evergreen (non-seasonal, megathermal) rainforest containing emergent Auraucariaceae. There may have been some deciduous taxa, and the mean annual temperature is estimated to have been 16–22 °C and the mean annual precipitation >150 mm (Greenwood et al., 2003). Mangroves of the palm *Nypa* were present in tide-dominated environments. Most of the evidence comes from what would have been coastal/deltaic environments and the local dominants were quite variable (Macphail et al., 1994; Pole and Macphail, 1996).

In Tasmania, there was a rich macrofossil flora of mainly gymnosperms, including extinct types. *Nothofagus*, the more evolved *Brassopora* type, is the dominant pollen type. Megathermal elements are lacking (Carpenter et al., 1994; Macphail et al., 1994).

In central Australia, Cunoniaceae and Myrtaceae dominated the forests and there were many other angiosperms, but *Nothofagus* and Casuarinaceae were rare (Sluiter, 1991). These 'snapshots' were representative of the regional vegetation, for very similar pollen data is found in the Lake Torrens and Lake Frome Basins (Macphail et al., 1994).

In summary, the early Eocene was warmer than the Palaeocene and just as humid. Megathermal angiosperms were prominent on the mainland. The only possible aridity was in the northwest and central Australia had a dry season.

5.3. Mid–late Eocene

Australia was beginning to separate from Antarctica, but only by an embayment that did not allow a significant through current (Lawver and Gahagan, 2003). The mid–late Eocene was an interval of marked general decrease in oceanic water temperature. There was a short reversal of this trend in the late Eocene when conditions were tropical (Quilty, 1994) or warm temperate (Apthorpe, 1988) over much of the western margin of the continent.

Rainfall probably decreased further over the southern part of the North West Shelf (Apthorpe, 1988). A palynoflora at Glen Florrie (Fig. 5), thought to be mid–late Eocene in age, contained prominent *Nothofagus* (the *Brassopora* type), Casuarinaceae and other pollen types commonly found in the Eocene of central Australia (Truswell and Harris, 1982); thus, some parts of the west could support rainforest.

In northeast Australia, temperatures declined and by the end of the Eocene all of the Great Barrier Reef was temperate (Feary et al., 1991). Casuarinaceae, Araucariaceae and less frequently, Myrtaceae are the dominant pollen types. *Nothofagus* was present, but was less common when compared with the southeast. The vegetation was meso–mega-thermal rainforest (Macphail et al., 1994).

In southern Australia, surface marine temperatures in local waters were ~24 °C in the late Eocene warm peak, and about 7 °C cooler at the Eocene–Oligocene boundary (Kamp et al., 1990), when there was a major cooling and relatively arid phase (Benbow et al., 1995). Middle Eocene macrofloras in South Australia contain abundant and diverse leaves, fruits and flowers, and the majority of the leaves have affinities with plants in the meso- to mega-thermal rainforests (Christophel, 1994; Benbow et al., 1995; Greenwood et al., 2003). The macrofloras have abundant lauraceous leaves (Christophel, 1994; Hill et al., 1999),

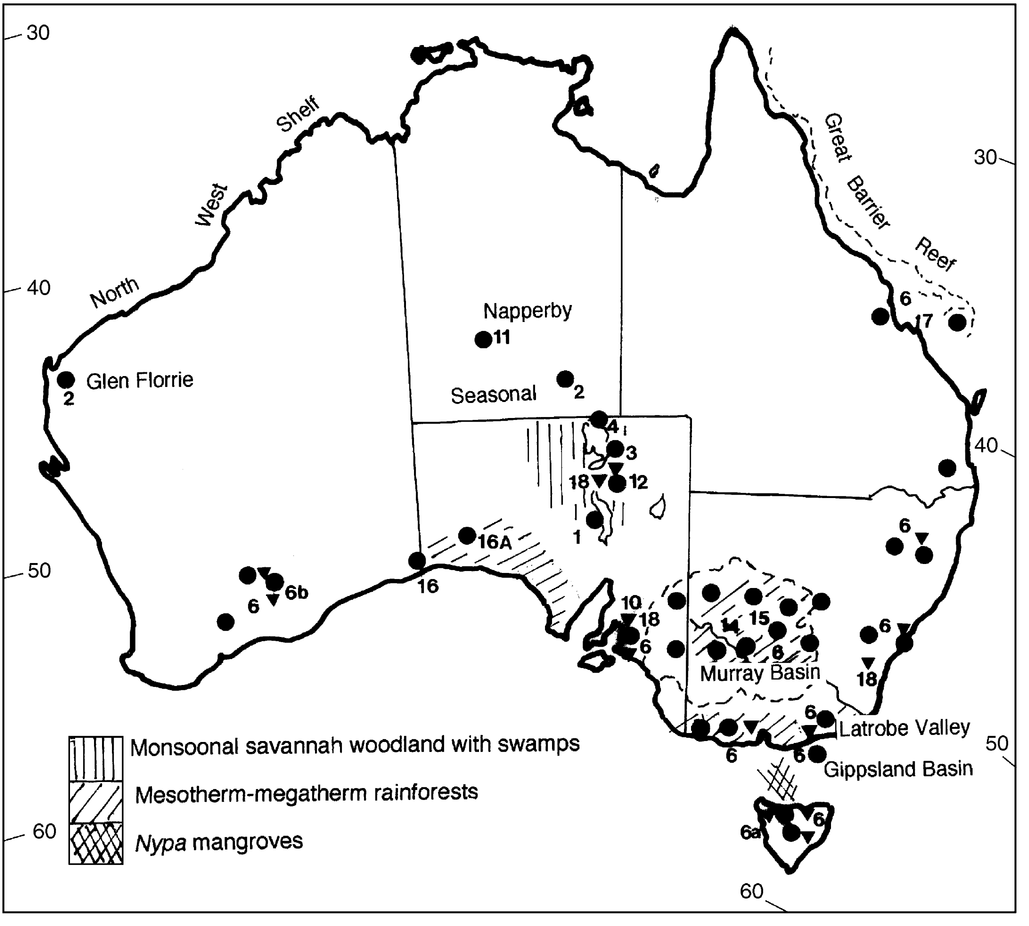

Fig. 5. Mid–late Eocene localities and features. References: 6B, macrofossil sites, Hill and Merrifield (1993) and Carpenter and Pole (1995); 11, Kemp (1976); 12, Alley et al. (1996); 13, Carpenter et al. (1994); 14, Martin (1993); 15, Macphail (1999); 16, Milne (1988); 16A, Alley and Beecroft (1993); 17, Hekel (1972); 18, Greenwood (1994). References to Fig. 4 apply here also. Palaeolatitudes are for the mid–late Eocene.

in contrast to the palynofloras which are dominated by pollen of *Nothofagus* sg. *Brassopora*, in the same sediments (Greenwood et al., 2003). Lauraceous pollen does not preserve.

In southeast Australia, the *Brassopora* type of *Nothofagus* became the dominant pollen type (Macphail et al., 1994). Casuarinaceae pollen is also common and macrofossils show the pollen would have come from *Gymnostoma*, a rainforest taxon. Gymnosperms are slightly more common than in the early Eocene and even more abundant in tableland regions, when compared with coastal lowlands. Most of the early Eocene angiosperms are present also, including a rich diversity of Proteaceae pollen types. Some of the angiosperms, which make their first appearance at this time, have affinities with sclerophyllous taxa, viz. *Banksia serrata* type, *Dodonaea triquetra* type and *Isopogon*. Some megathermal elements are found in the inland Murray Basin only. The vegetation was probably a mosaic of rainforest associations. At the end of the Eocene, the mangrove *Nypa* disappeared (Macphail et al., 1994; Pole and Macphail, 1996).

In the Lake Eyre Basin, central Australia, mid-Eocene macrofloras contained Proteaceae, Sterculiaceae (*Brachychiton*), abundant leaves of Myrtaceae (*Eucalyptus* and/or *Melaleuca*) and cones of *Gymnostoma* and *Casuarina* (Christophel et al., 1992; Greenwood, 1996), suggesting both rainforest and seasonally dry forests. Rare fruits of *Eucalyptus* (Lange, 1978) are probably the oldest record of this important genus (Benbow et al., 1995). A mean annual temperature of more than 20 °C is inferred (Greenwood, 1994; Alley, 1998; Hill and Christophel, 2001). Non-woody swamp vegetation of Cyperaceae, Restionaceae/Centrolepidaceae and Sparganiaceae/Typhaceae were present for the first time. The palynofloras suggest a mean annual temperature of 17–18 °C and precipitation at least 1500 mm/a in the mid-Eocene (Sluiter, 1991). In the late Eocene, Casuarinaceae and *Nothofagus* pollen became more common than previously, suggesting that it had become cooler, but *Nothofagus* was far less common in central Australia than in the southeast. There was also a wealth of other angiosperms (Martin, 1998a).

The Lake Eyre 'snapshots' are in general representative of the regional vegetation. At Lake Torrens (Fig. 4), *Nothofagus* pollen is present in low frequencies and would have been a very minor part of the vegetation. Its windblown pollen may well have come from the nearby ranges. Myrtaceae, including *Eucalyptus* pollen, is moderately common. Casuarinaceae and swamp taxa may be very common locally. Grasses were established in inland regions, but were not common and may have inhabited swamps. The pollen of rainforest taxa is low, suggesting that rainforest was confined to the well-watered valley bottoms and sclerophyll vegetation probably occupied the slopes and ridges (Benbow et al., 1995).

In southwest Australia, palyno- and macro-floras are similar to those in the southeast. The dominant pollen types are shared between Casuarinaceae, *Nothofagus* (*Brassopora*) and Proteaceae (Macphail et al., 1994), and the dominant leaf types are Lauraceae, Proteaceae and Myrtaceae (Hill and Merrifield, 1993; Carpenter and Pole, 1995). The precise mix of dominants varies with the locality. Although the Proteaceae as a group is prominent over most of Australia at this time, if all the fossil types are examined closely, different localities have distinctive suites of species (Macphail et al., 1994). The earliest record of *Acacia* type pollen is found here in the late Eocene in what was a near coastal location (Milne, 1988; Alley and Beecroft, 1993; Macphail and Hill, 2001).

In summary, the temperatures declined (overall) during the mid–late Eocene, but high humidity prevailed over most of Australia. The vegetation was predominantly rainforests, but some sclerophyllous elements have appeared, especially in central southern Australia. Hill (1998) presents evidence that sclerophylly first appeared in humid climates and suggests that it arose in response to low nutrient levels and low phosphorus levels in particular (in accord with eco-physiological work by Beadle, 1966). Sclerophylly then became adapted to a xeromorphic function when dry conditions arose. There may have been a decrease in rainfall in the northwest but the few palynofloras reported show that precipitation was high enough to support rainforest, at least in certain habitats, in the mid–late Eocene.

5.4. Latest Eocene– earliest Oligocene

This is a key interval that marks the transition from the Cretaceous–Eocene marine and atmospheric circulation to a markedly different regime that led directly to the modern climate (Quilty, 1994). Glacial climates were already established in Antarctica. The rift between Australia and Antarctica widened during the late Eocene, strengthening the Circum-Antartic Current and effectively reducing the heat transfer from the tropics to the high latitudes. In the earliest Oligocene, there was an abrupt cooling of ocean waters which was considerable in the high latitudes but only moderate in the lower latitudes (Feary et al., 1991; Wei, 1991; Quilty, 1994; Zachos et al., 2001). Deposition of sediments off the western and southern coasts of Australia had an increasing carbonate and decreasing terruginous content, suggesting decreased runoff from the land (Quilty, 1994).

In southeastern Australia, pollen of *Nothofagus* (mostly the *Brassopora* type) and gymnosperms were common, but the diversity of angiosperms was much lower than in the Eocene. The vegetation was largely cool temperate (microtherm) rainforest (Benbow et al., 1995). Swamp taxa became increasingly prominent in the Latrobe Valley freshwater swamps which later became brown coals (Macphail et al., 1994). Lignitic deposits are found in the Murray Basin also and attest to a very high rainfall.

In summary, the latest Eocene–early Oligocene was a cool and very wet period, at least in southeastern Australia. Angiosperm diversity declined and *Nothofagus* increased in prominence.

5.5. *Oligocene to early–mid-Miocene*

The cooling trend continued into the early Oligocene and sea levels varied widely. About the mid-Oligocene, there is a major drop in sea level. An hiatus in sedimentation is taken to coincide with extensive laterite formation in Western Australia, perhaps indicating seasonal climates (Quilty, 1994). The early–mid-Miocene was a time of high sea levels and flooding of marginal, shallow basins, e.g. the Murray and Eucla Basins, and warm, humid climates which have not been experienced since the mid-Miocene.

Northeast Australia was temperate during the Oligocene, becoming warmer in the early Miocene when coral reefs grew once again. At the end of the early Miocene, the waters in the north were subtropical to tropical (Feary et al., 1991; Quilty, 1994).

In Tasmania, *Nothofagus*, especially the *Brassopora* type, continued to be the dominant pollen type and gymnosperms were common in Oligocene palynofloras. Macrofossils indicate that the vegetation was microthermal/mesothermal rainforests (Macphail et al., 1994).

In the Latrobe Valley of southeast Australia (Fig. 6), palynofloras and macrofossil floras from freshwater swamp sediments suggest several plant associations, including a relatively open heath scrubland on highly acidic, infertile soils which was subjected to repeated wildfires. *Nothofagus* pollen is common in these sediments, but it did not grow in the swamps (Macphail et al., 1994). A late Oligocene to possibly earliest Miocene macroflora from Berwick has both rainforest and *Eucalyptus* leaves, suggesting a vegetation mosaic and a dry season (Pole et al., 1993).

The Murray Basin (Fig. 6) encompassed marginal marine, extensive floodplain, deltaic and dryland environments. The Oligocene range of plant communities included *Nothofagus* (*Brassopora* type) forests, gymnosperm-rich semi-swamp forests, Araucariaceae/Casuarinaceae forests near the coast of the marine incursion and herbaceous swamps in the northwest. Myrtaceae was common at times, probably in deltaic environments (Martin, 1993; Macphail et al., 1994). Even more diversity is evident in

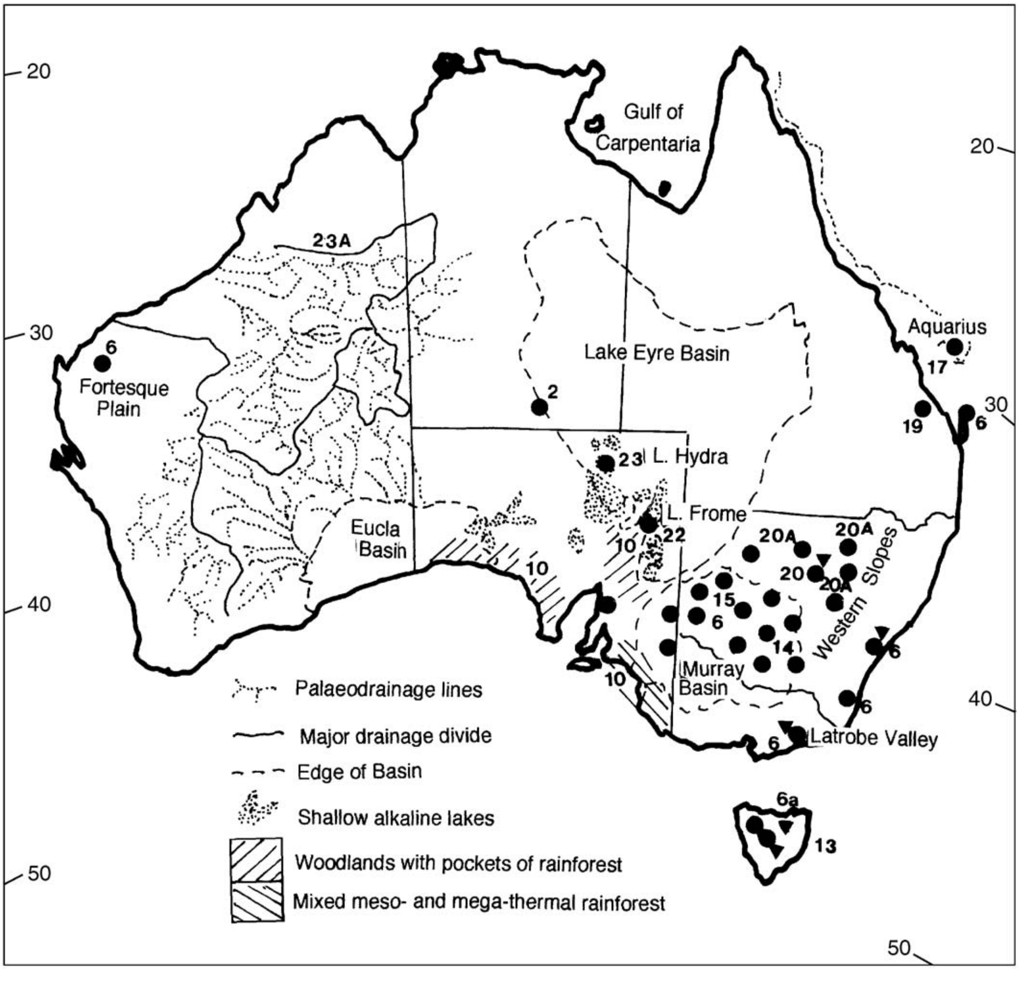

Fig. 6. Oligocene to early–mid-Miocene localities and features. References: 19, Dettmann and Clifford (2003); 20, Holmes et al. (1983); 20A, Martin (1990a); 21, Kershaw et al. (1994); 22, Martin (1990b); 23, Martin (unpubl.); 23A, van der Graff et al. (1977). References to Figs. 4 and 5 apply here also. Palaeolatitudes are for the early–mid-Miocene.

the early–mid-Miocene, with mixed angiosperm communities. At times of high sea level, the Murray Basin was partially flooded and in the early–mid-Miocene, the shallow estuaries became particularly warm, when *Polyshaeridium zoharyi*, the cyst stage of *Pyrodinium bahalmense*, a toxic dinoflagellate of tropical waters became abundant. A comparable abundance of this dinoflagellate is seen today in Port Morseby Harbour, New Guinea and the Gulf of Carpentaria (Martin, 1992).

Most of the Myrtaceae pollen in the Oligocene–early Miocene of the Murray Basin is unlikely to be *Eucalyptus* and is more like rainforest myrtaceous taxa (*Backhousia*, *Tristania*, *Syzygium*, etc.) and *Melaleuca*, the latter especially in deltaic environments (Martin, 1993). *Eucalyptus*, however, was present in the Eastern Highlands. Mid-Miocene macrofossils of *Eucalyptus* leaves and fruits show some features of advanced state when compared with extant species (Holmes et al., 1983).

Oligocene palynofloras in southern east coastal locations are similar to these inland palynofloras, but in coastal southeast Queensland, a late Oligocene–early Miocene assemblage has prominent Araucariaceae, with other gymnosperms and *Nothofagus* is less common, probably reflecting a warmer climate (Macphail et al., 1994; Dettmann and Clifford, 2003).

There are many indicators of warm marine conditions in southern waters, but extensive coral reefs are not present, hence it was not tropical. The vegetation in coastal regions would have been woodland/forests (Fig. 6) dominated by *Casuarina*, with a much reduced *Nothofagus* content, indicating a shift to a drier climate (Benbow et al., 1995).

In the early–mid-Miocene of central Australia, there were extensive, shallow, alkaline lakes (Fig. 6). The climate was significantly wetter than today, but evaporation must have been high to allow dolomite deposition, implying a well-marked dry season. Local ooids and stromatolites imply warmth as well as shallow lakes. Decreasing carbonaceous sediments and increasing dolomite to the northwest of Lake Eyre suggest increasing aridity in that direction (Benbow et al., 1995; Alley, 1998). Lake Hydra, close to Lake Eyre, has a rich palynoflora with abundant swamp/aquatic pollen (Cyperaceae, Restionaceae, *Myriophyllum* and unidentified monocotyledons like Juncaceae), saline/alkaline indicators (*Wilsonia*/*Cressa*), ephemeral swamps (*Meuhlenbeckia* cf. *florentula* (= *cunninghamii*, 'lignum'), sclerophyll communities (*Acacia*, *Eucalyptus*, *Casuarina*) and rare rainforest taxa (Martin, 2000; unpubl.). Mid-Miocene macrofloras yield leaves of *Eucalyptus*, *Brachychiton*, *Cochlospermum*, *Orites* (Rowett, 1997), *Callicoma* (Barnes and Hill, 1999) and *Banksia* (Greenwood et al., 2001). Rainforest was probably restricted to the wetter habitats and the drier forests/woodlands of *Casuarina* and *Eucalyptus* were prominent (Benbow et al., 1995).

A rich vertebrate fossil fauna reflected the environment. The numerous birds include many wetland species, land-dwelling browsing marsupials, fish, lungfish, dolphins, large crocodiles and turtles infer warm conditions and a substantial body of permanent water. Koala-like animals, phalangers, possums and native cats suggest that trees grew in the area (Benbow et al., 1995). Both the palaeobotany and the animal fossils suggest that widespread grasslands did not exist in the mid-Miocene (Martin, 1990b; Benbow et al., 1995). The middle Miocene marks the last time there was significant drainage in central Australia (Quilty, 1994).

At Fortesque Plain in Western Australia (Fig. 6), a palynoflora suggests mainly *Eucalyptus* and Casuarinaceae forests with small patches of rainforest (Macphail et al., 1994). Regular flows of water in the palaeodrainage systems of Western Australia (Fig. 6) had stopped by the mid-Miocene (van der Graaff et al., 1977).

In summary, the Oligocene was a cool, wet period, becoming warm and wet in the early Miocene. In Oligocene time, seasonality became apparent in southeastern Australia and probably in Western Australia. In the mid-Miocene, conditions were probably more equitable than at any time since. By the mid-Miocene, the first major step towards aridity, apart from evidence of localized or seasonal dryness became apparent: the cessation of regular flows in the palaeodrainage systems over much of Western Australia. The forest communities became increasingly diverse and in the drier inland regions, rainforest was restricted to small pockets.

5.6. Late Miocene

The upper mid- to late Miocene cool conditions correspond to global cooling, a lowered sea level and a major ice sheet expansion on Antarctica. Marine temperatures declined dramatically to the south of Australia (Shackleton and Kennett, 1975; Gallagher et al., 2001; Zachos et al., 2001) and the temperature decline was greatest in the high latitudes, less in the mid-latitudes, and even remaining constant or slightly increasing in the low latitudes (Savin et al., 1975). Sediments around Australia became more carbonate rich, generally reflecting a decrease in outflow to the oceans as the climate on land became more arid (Quilty, 1994).

Pollen in the offshore ODP site 765, northwest Australia (Fig. 7) was produced by the vegetation on land and indicates sclerophyll forests of Casuarinaceae, some Gyrostemonaceae (mainly desert shrubs), Restionaceae and a little Poaceae. There are no unequivocal rainforest taxa (Martin and McMinn, 1994).

Most of the pollen in the offshore sites 815 and 823, northeast Australia (Fig. 7), would have been produced by the coastal vegetation and suggests that it was araucarian forest and casuarinaceous sclerophyll forest. There is some indication of cyclic variation between the two (Martin and McMinn, 1993). Further south, near the end of the Great Barrier Reef (Aquarius well), the vegetation on land was similar, but with an appreciable Myrtaceae content (Hekel, 1972). The Great Barrier Reef was tropical/subtropical (Feary et al., 1991): a consequence of Australia's drift northwards that had placed it in lower latitudes.

Central Australia became more arid with dry open woodlands and chenopod shrublands. In southern Australia, pockets of rainforest with *Nothofagus* and podocarps persisted in suitable habitats (Benbow et al., 1995).

In southeast Australia, there was a major change: the *Brassopora* type of *Nothofagus* disappeared or became rare, although the subgenera *Lophozonia* and *Fuscopora* still persisted in highland and coastal regions. In the Latrobe Valley, the *Lophozonia* type of *Nothofagus* increased in the late Miocene, probably a response to cooler temperatures but still humid climate, near the coast. This type of *Nothofagus* is still present in the region as the modern species *Nothofagus cunninghamii*. Many other rainforest pollen types also disappeared or were severely restricted. *Eucalyptus* and other Myrtaceae, Casuarinaceae and herbaceous taxa, especially of the family Asteraceae and Poaceae became more common. All of these changes reflect an increasingly drier climate over the greater part of Australia (Kershaw et al., 1994; Martin, 1994).

Along the inland river valleys of the Western Slopes (Fig. 6), some rainforest taxa persisted but Myrtaceae and Casuarinaceae were the dominant pollen types. There is abundant charcoal in the sediment, showing that burning had become part of the environment, and suggesting that most of the hard to identify Myrtaceae pollen was probably *Eucalyptus*. These palynofloras suggest wet sclerophyll forest (Fig. 7), with a canopy of *Eucalyptus* and *Casuarina* and an understorey including some rainforest species. If left unburnt, it would revert to rainforest, but with regular burning, it remained wet sclerophyll forest (Martin, 1987, 1991). There must have been a well-marked dry season to allow regular burning.

In summary, the colder, drier conditions of the late Miocene are reflected in a considerable contraction of rainforest and an expansion of *Eucalyptus* and casuarinaceous sclerophyll vegetation. Concurrent with the change to eucalypt vegetation, regular burning became a feature of the environment.

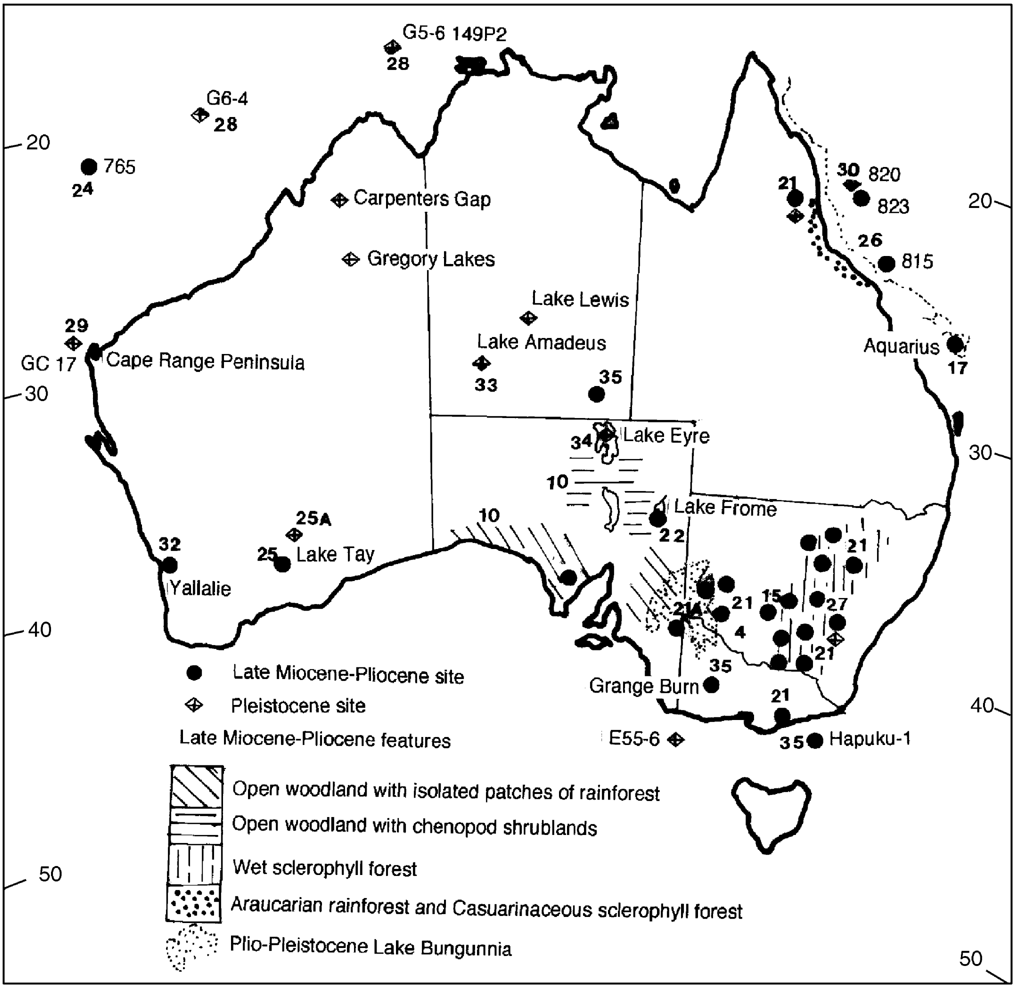

Fig. 7. Late Miocene–Pliocene and Pleistocene localities and features. References: 21A, Stephenson (1986) and Zhisheng et al. (1986); 24, Martin and McMinn (1994); 25, Bint (1981); 25A, Zheng et al. (2002); 26, Martin and McMinn (1993); 27, Martin (1987); 28, van der Kaars (1991); 29, van der Kaars and De Deckker (2002); 30, Kershaw et al. (1993); 31, Harle (1997); 32, Dodson and Ramrath (2001); 33, Chen and Barton (1991); 34, Magee et al. (1995) and De Vogel et al. (2004); 35, Macphail (1997). References to Figs. 4–6 apply here also. Palaeolatitudes are for the late Miocene–early Pliocene.

5.7. Pliocene

Around northern Australia, tropical conditions continued and in the northwest, early Pliocene marine temperatures were warmer than either the late Miocene or the late Pliocene. Some early Pliocene angiosperm fossils found in Antarctica suggest that the early Pliocene was a warmer interval there also (Quilty, 1994).

The palynofloras from site 765, northwest Australia (Fig. 7), indicate a decrease in the casuarinaceous tree cover and the gradual development of desert chenopod shrublands and grasslands (Martin and McMinn, 1994) on the land. This is the oldest palaeobotanical evidence of grasslands in Australia (Martin, 1998b) and it concurs with the increase of grazing animals in the vertebrate palaeontological record (Archer et al., 1994).

The coastal araucarian rainforest and casuarinaceous sclerophyll forest of northeast Australia show surprisingly little change from that seen in the late Miocene (Martin and McMinn, 1993). The Aquarius site suggests an increase in the herbaceous elements Asteraceae and Chenopodiaceae (Hekel, 1972). Phytoliths found in a deep sea site off on the Lord Howe Rise, off the east coast of Australia suggests that grasslands became prominent in the Pliocene (Locker and Martini, 1986; Martin, 1998b), at a similar time to that seen in the northwest.

In southeastern Australia, early Pliocene marine temperatures were warm and stable, but late Pliocene temperatures were cooler and variable (Gallagher et al., 2003). The offshore Hapuku-1 well (Fig. 7) registers Araucariaceae forest in the early Pliocene and a marked increase in Asteraceae and Poaceae in the late Pliocene. At the early Pliocene Grange Burn site, K-Ar dated to 4.46 Ma, there was a mosaic of Araucariaceae forest and sclerophyll communities. The early Pliocene temperatures were estimated to be about 20 °C and rainfall exceeded 1000 mm, significantly higher than that of today, viz. 13 °C and 680 mm/a, respectively (Macphail, 1997).

For a brief interval in the early Pliocene, there was a resurgence of rainforest in the river valleys of the Western Slopes in southeast Australia and sometimes *Nothofagus* (only the *Lophozonia* and *Fuscopora* types) was present. This resurgence of rainforest suggests a brief wetter period. The vegetation both before and after the rainforest resurgence was wet sclerophyll forest (Martin, 1987, 1991). The vegetation communities reflect a rainfall gradient, drier in the west and wetter in the Eastern Highlands (Kershaw et al., 1994). Most likely, *Nothofagus* and other rainforest taxa survived in small, favourable habitats in the Eastern Highlands during the cooler, drier late Miocene and expanded its distribution down the river valleys of the Western Slopes during the wetter interlude of the early Pliocene.

In the latest Pliocene of southeastern Australia, the few remaining rainforest taxa in the palynofloras disappeared and the vegetation became open sclerophyll forest. The Asteraceae and Poaceae content increased in the latest Pliocene, so that by Pleistocene time, the vegetation had become open woodland/grasslands (Martin, 1987; Kershaw et al., 1994).

Near Lake Frome in central Australia, a palynoflora thought to be early Pliocene in age suggests open Casuarinaceae sclerophyll forest. Freshwater and saline/alkaline swamps this were also present (Martin, 1990b). Another palynoflora from just north of Lake Eyre is probably Pliocene–Pleistocene in age. The pollen spectrum is very like the modern pollen in a surface sample from Lake Frome, except that there is appreciable Cyperaceae, suggesting that the dryland vegetation was arid scrubland, but with appreciable wetlands not seen in the region today. The charcoal content is quite considerable, similar to the Pliocene assemblages of the southeast and the Western Slopes (Martin, 1998a).

Along the coast of southern Australia, open vegetation with abundant *Casuarina*, *Eucalyptus*, Asteraceae and Poaceae was present. Some rainforest taxa persisted in suitable habitats (Benbow et al., 1995).

At Lake Tay in southwest Australia (Fig. 7), an early Pliocene palynoflora from the lacustrine sequence of the now dry palaeodrainage system indicates a Casuarinaceae and *Eucalyptus* sclerophyll woodland, a lake edge community and very minor rainforest elements (Bint, 1981). At Yallalie, lacustrine late Pliocene palynofloras from a supposed meteor crater indicates a woodland heath similar to today, but with very minor rainforest elements. Both of these palynofloras infer a generally wetter climate to that of today (Dodson and Ramrath, 2001).

In summary, the trend during the late Miocene–Pliocene is to a drier climate, with the exception of the brief period of a wetter climate in the early Pliocene. The vegetation was mainly sclerophyll forest/woodland, with arid shrublands and grasslands in northwestern central Australia. There were minor pockets of rainforest, except in northeast Queensland where rainforest were still extensive. By the end of the Pliocene, the modern climate is evident, but it was still wetter than today (Martin, 1987, 1998b).

5.8. *Pleistocene*

In Australia, there was very little glaciation and it was restricted to Tasmania and the Southeastern Highlands. For all of Australia, the interglacial periods were more humid and glacial times drier. Reduced vegetation cover, particularly in arid regions, allowed greater sand dune activity and dust advection. The largest changes in circulation patterns over the glacial cycle probably occurred in the location and/or intensity of summer tropical convergence in northern Australia. Over southern Australia, changes to the temperature and humidity of the westerly circulation have been more significant than the small fluctuations in latitude of the subtropical high pressure ridge (Hesse et al., 2004). There are many studies of the late Pleistocene and Holocene for about the last 40 ka, especially in southern Australia, but they are beyond the scope of this review. This study concentrates on selected long records through the Pleistocene.

In the northwest offshore site 765, the previous trend continued: tree cover decreased and grasses and desert shrubs increased throughout the Pleistocene (Martin and McMinn, 1994) indicative of a drying climate. Other offshore cores (Fig. 7), which collected pollen mainly from Australia, show that at times of low sea levels, grasslands expanded and pteridophyte spores decreased, inferring increased aridity. Mangroves signal rising sea levels and *Eucalyptus* woodlands were typical of high sea levels (van der Kaars, 1991). A core off Cape Range Peninsula in the central part of the west coast spans the last 100 ka. At about 46 ka, open *Eucalyptus* woodlands rich in grasses changed to the drier open *Eucalyptus* and *Gyrostemon* shrublands rich in Chenopodiaceae/ Amaranthaceae shrubs, which persisted through the glacial period of 20–18 ka (van der Kaars and De Deckker, 2002). In an intriguing study of plant phytoliths at Carpenters Gap, an archaeological site, Wallis (2001) has shown that the period ca. 40,000 years BP was probably wetter than today, allowing palms to expand south of their present day distribution. Changes in the composition of the grassland occurred ca. 33,000 years BP, probably the result of a lowered rainfall. Palms were reduced at the same time, and they disappeared completely prior to the last glacial maximum (Wallis, 2001).

Pollen in the northeast offshore site 820 (Fig. 7) suggests that the Araucariaceae rainforest and Casuarinaceae sclerophyll of the Pliocene persisted, at least in the coastal vegetation. About 120 ka, there was a major change when Araucariaceae was reduced and mangroves increased greatly, following a peak in charcoal particles, which suggests that burning and disturbance may have caused the change (Kershaw et al., 1993; Moss and Kershaw, 2000). At sites on the tablelands, angiosperm rainforests at times of interglacial periods were replaced by gymnosperm forests in glacial times. However, during the last glacial period, Casuarinaceae sclerophyll forests became prominent. This deviation from the cyclic pattern has been attributed to burning also (Kershaw, 1994).

Lake Bungunnia in southeast Australia (Fig. 7) was a Plio-Pleistocene megalake which existed between 2.5 and 0.7 Ma and was formed from the tectonic damming of the Murray River. Studies have shown that it could not have existed under the present climatic regime and it would have required a discharge of more than double that of the Murray-Darling catchment today. The onset of the aeolian and saline-gypseous deposits that characterize the arid-zone facies today occurred about 500,000 years ago (Stephenson, 1986; Zhisheng et al., 1986; Rogers, 1995).

Off southern southeast Australia, the offshore core E55–6 (Fig. 7) covers a full glacial cycle. During the last interglacial period, wet sclerophyll forest and rainforest were widespread, suggesting maximum precipitation. With a decrease in rainfall, the *Eucalyptus* forests were replaced with open heath and mallee eucalypt shrubland communities. About 40–25 ka, a brief increase in rainfall, which allowed limited expansion of *Eucalyptus*, was followed by a steady decline in precipitation and an expansion of open heath and grasslands during the last glacial period (Harle, 1997). Numerous studies of sites covering about 20–40 ka show that during the last glacial period, much of southeastern Australia was grasslands/herbfields. Forests returned gradually, generally about the beginning of the Holocene (Hope, 1994; Sweller and Martin, 2001). This alternation of more open or steppe vegetation in the drier glacial periods with more wooded vegetation in the wetter interglacial periods is evident in the early–mid-Pleistocene, about 1 Ma, in southeastern Australia (Wagstaff et al., 2001).

In central Australia, the sediments of Lake Amadeus, a ground-water discharge playa, shows a sequence similar to that of Lake Bungunnia. The boundary between the lacustrine clay and the playa sequences is dated at about 0.9 Ma, earlier than the 0.5 Ma in Lake Bungunnia (Chen and Barton, 1991), suggesting that aridity was more intense and developed earlier in this central location, when compared with the southeast. However, the very restricted catchment may mean the results reflect local conditions only. Lake Lewis to the north has a larger catchment influenced by the summer monsoons and has a record more in keeping with other megalakes (English et al., 2001).

Former beach ridges around Lake Eyre allow the reconstruction of former lake levels. At the peak of the last interglacial highstand, at 125 ka, Lake Eyre covered more than three times the area of the playa today and overflow from the enhanced runoff connected up the major terminal lakes. There was another highstand between 55 and 40 ka (Callan and Benbow, 1995; Nanson et al., 1998; DeVogel et al., 2004). These large lakes represent conditions very different from those of today. Lake Eyre receives the majority of its moisture from the summer monsoon, so these major lacustrine episodes must indicate enhanced monsoonal precipitation in northern Australia (Magee et al., 1995; DeVogel et al., 2004).

The Gregory Lakes in northwest Australia is also monsoonal fed and the sedimentary record there spans 300 ka. Megalakes were formed at about 300, 200 and 100 ka, which roughly coincides with interglacial periods. Each successive megalake was smaller than its predecessor, showing a progressive decrease in monsoonal influence and increase in aridity during the late Pleistocene (Bowler et al., 2001).

In southwest Australia, aeolian and lacustrine evidence from playas "is in broad agreement with general patterns of late Quaternary palaeoenvironmental change in

Australia'' (Zheng et al., 2002, p. 90). Gypsum-dominated sediments, indicating full arid condition commenced within the last 0.5 Ma (Zheng et al., 1998).

In summary, the modern climatic patterns were established by the beginning of the Pleistocene, but it was considerably wetter than today. Throughout the Quaternary, wet/dry periods generally corresponded to the interglacial/glacial cycles. About 0.5 Ma there was a change to a drier climate which initiated the saline-gypseous deposition in the arid zone, although it was still wetter than today. Even the last interglacial period, about 120 ka, was wetter than today, the present interglacial period. Thus, the overall trend through the Pleistocene has been a decreasing precipitation. The major changes in climate in Australia appear to follow global trends.

6. Discussion

6.1. *The development of aridity*

At the beginning of the Cenozoic, practically all of Australia experienced high humidity, yet climatic gradients similar to those of today were apparent. Central Australia, the driest part today, was seasonal dry in the late Palaeocene–early Eocene and probably the driest part of the continent also. There was limited aridity in the northwest, which may have been seasonal also, and temperatures were at least warm temperate. Mean annual temperatures in central Australia were 18–19 °C and mean annual precipitation greater than 1400 mm during the late Palaeocene. Southern Australia was cool temperate.

In the early Eocene, humidity remained high and temperatures increased, but the northwest probably experienced a decrease in rainfall. Southeastern Australia became subtropical. In central Australia, mid-Eocene mean annual temperatures were more than 20 °C, with a seasonally dry period. Temperature began to decline by the mid-Eocene, and in the mid–late Eocene central Australia experienced mean annual temperature of 17–18 °C and a mean annual precipitation of at least 1500 mm.

In the earliest Oligocene, there was an abrupt decrease in temperature, but precipitation remained high and freshwater swamps became prominent, particularly in southeastern Australia. Temperatures continued to decline, due to increasing development of the Circum–Antarctic current. Northern Australia was temperate and southern Australia, cool temperate. Temperatures began to increase in the late Oligocene and a dry season became apparent in southeastern Australia and probably in Western Australia also.

Temperatures increased through the early Miocene, a time of high sea level, culminating in a warm and humid mid-Miocene. Northern Australia returned to subtropical/tropical conditions and coral reefs grew again. Southern Australia was warm but not tropical. The first major step towards a drier climate became apparent: regular flows in the palaeodrainage systems of Western Australia had stopped by the mid-Miocene. In central Australia, there must have been a well-defined dry season with high evaporation to allow dolomite deposition in the giant lake system.

In the late Miocene, there was a marked cooling, accompanying lowered sea levels. The climate became considerably drier and rainforests contracted drastically. Sclerophyll forests expanded and there was a well-marked dry season in southeastern Australia that allowed burning to become a regular part of the environment. In the earliest Pliocene, there was a brief period when it was wetter, allowing the expansion of rainforests in some river valleys. Drier climates returned, becoming drier still through the rest of the Pliocene, further reducing the rainforest element in inland regions.

At the beginning of the Pleistocene, an essentially modern climatic regime was operating, but precipitation was higher than that of today. Where records extend back far enough, wetter/drier episodes correspond to interglacial/glacial periods (respectively). There was a major change to 'fully arid conditions' about 0.5 Ma. The last interglacial, ~120 ka, was also wetter than today, the present interglacial. The last glacial period, ~20 ka ago, was particularly dry, and although precipitation has increased since then, it has not reached the levels of the former interglacial period.

The almost constantly changing climate of the Pleistocene must have had a profound effect on the biota. With each glacial/interglacial cycle, populations would have been squeezed into refugia and then when the environment became more favourable, they would have expanded their range. This almost constant shuffling must have favoured the more adaptable taxa and there would have been many local extinctions.

6.2. The development of the arid vegetation

In the beginning of the Cenozoic, most of the vegetation was rainforest, with some swamps. Central Australia supported megathermal to mesothermal (warm temperate) rainforest whereas southern Australia supported mesothermal to microthermal (cool temperate) rainforest. Gymnosperms were a prominent part of the vegetation, especially in the south.

A rich diversity of angiosperms flourished in the Eocene. Mesothermal/megathermal rainforests continued to dominate in southern Australia, but in central Australia, rainforests occupied the valleys and open sclerophyllous vegetation was found in the hinterland. Sclerophyll leaf characters are thought to have arisen as a response to low soil fertility and not to low moisture although when moisture became limiting, the sclerophyll characteristics were well adapted to the drier conditions. In the late Eocene/early Oligocene, diversity declined.

During the Oligocene, diversity of angiosperms increased, and in the early Miocene, there was considerable regional variation in vegetation of southeastern Australia. In central Australia, rainforest was reduced to pockets within woodlands. In the late Miocene, rainforest was drastically reduced in southern Australia with remnants confined to the wetter habitats of the coastal and highland regions. On the Western Slopes of the Eastern Highlands, it was replaced with *Eucalyptus* wet sclerophyll forest which was subjected to regular burning. In northwest Australia, the vegetation was Casuarinaceae sclerophyll forests with shrubs. In northeast Australia, however, rainforests persisted, together with Casuarinaceae sclerophyll forests.

In the earliest Pliocene, there was a brief expansion of rainforest in the river valleys of the Western Slopes, but it soon contracted and continued to decline through the Pliocene. Rainforest was then confined to the favourable habitats in the highlands and to northeastern Australia, roughly its present distribution Open vegetation with only a few pockets of rainforest extended across southern Australia. Asteraceae and Poaceae become more common through the Pliocene. In central Australia, Casuarinaceae sclerophyll open vegetation is found with chenopodiaceous shrublands and salt marsh and freshwater species in suitable habitats. Grasslands developed during the early Pliocene, somewhere in the central/northern interior, as inferred from offshore cores to the west and to the east of the continent. Grasslands did not develop in southern Australia until the late Pliocene/early Pleistocene.

During the Pleistocene, changes in the vegetation accompanied the glacial/interglacial cycles: more open vegetation and grasslands in the glacial periods and more wooded vegetation in the interglacial periods.

6.3. *The origins of some arid taxa*

The arid flora developed from a pre-existing flora. Beadle (1981) recognizes: (1) some taxa from the rainforests that have persisted with hardly any change. There are arid adapted species from about 30 rainforest genera: (2) *Eucalyptus*-dominated communities that were replaced by *Acacia*, although *Eucalyptus* remained dominant in semi-arid regions; (3) *Callitris* persisted in the arid zone; (4) a number of littoral zone species invaded the arid zone, mostly on saline and subsaline soils; (5) the evolution of a large number of endemic genera and species. This section examines the origins of some of the arid flora from the historical (fossil) evidence (if any).

The distinctive 'eucalypt pollen type' is found in species of *Angophora* and the bloodwood eucalypts (now *Corymbia*). Most of the other species of *Eucalyptus* have smaller, less distinctive pollen and it is difficult to distinguish their pollen from some of the other genera in Myrtaceae. In central Australia, pollen of the family is found in the late Palaeocene (Sluiter, 1991; Martin, 1998a) but the eucalypt pollen type dates from the mid-Eocene. Rare fruits of *Eucalyptus* are found in the late Eocene also (Benbow et al., 1995). The vegetation in central Australia during the Eocene was rainforest, seasonally dry forests and sclerophyll, but *Eucalyptus* was probably not common. In southeast Australia, *Eucalyptus* was rare in the Eocene–Oligocene, becoming more common in the early Miocene and rising to prominence in the late Miocene.

Acacia pollen is first recorded in the mid–late Eocene (Alley and Beecroft, 1993) and late Eocene lignites of the Eucla Basin (Milne, 1988) in what were then coastal locations. Two different pollen types are recorded and they are found in rainforest pollen assemblages, but the plants need not have been growing in the rainforest. A coastal location could have a variety of different environments. In southeastern Australia, it is first found in the early Oligocene in the Murray Basin where there would have been frequent changes to the shoreline. It did not become common until the late Oligocene–early Miocene (Macphail and Hill, 2001). Today, species of *Acacia* may be found in all kinds of vegetation from the arid zone where they are dominant, to semi-arid communities, woodlands, *Eucalyptus* forests, and there are even a few species that inhabit rainforests.

Chenopodiaceous shrublands are found in the southern part of the arid zone. The 'chenopod pollen type' is not restricted to the family Chenopodiaceae, but is also found in the Caryophyllaceae and possibly other families, but most of the pollen is thought to be from the family Chenopodiaceae. The pollen appears to date from the Oligocene (Macphail, 1999), but it is not common. Large quantities of the chenopod pollen type which may indicate chenopodiaceous shrublands are found in the Pliocene in central Australia (Benbow et al., 1995; Martin, 1998a) and younger sediments (e.g. Singh and Luly, 1991).

A number of species in the family Chenopodiaceae are halophytes and may be common in coastal locations. This probably led to the notion that some of the arid flora originated from littoral species. There would have been littoral environments around both freshwater and alkaline lakes which were present in central Australia throughout the Cenozoic. The chenopod pollen type has not been studied in relation to this topic, but the history of *Wilsonia* (Convolvulaceae), a halophyte, is known. The pollen of *Wilsonia* (and possibly *Cressa*) is first found in the late Eocene of the Murray Basin (Macphail, 1999), in a location subjected to episodic marine transgressions; an environment likely to stimulate evolution. It is found in central Australia in early Miocene and late Miocene–Pliocene sediments. For all of the known occurrences of this pollen type, the plant would have grown in saline/alkaline environments (Martin, 2000).

Two species of *Eucalyptus*, *E. spathulata* and *E. suggrandis*, have very distinctive pollen (Martin, 1997). The fossil pollen is first seen in late Oligocene sediments in the southwest of the Murray Basin on what was an archipelago. The pollen is found in a rainforest assemblage typical for the time, but it need not have been growing in the rainforest. It had a wide distribution across southern Australia in the late Miocene–Pliocene, but nearly all of the occurrences would have been coastal or near coastal at the time of deposition. Today, these two species are endemic to a small area in southwestern Australia and are well known for their salt tolerance (Martin, 1997).

These very few examples show that palaeobotany can trace the evolution of specific taxa, but it require precise identification of the fossil, and this precision is not possible for many taxa. It does show, however, that taxa in the arid zone may have originated long before the climate became arid, and may have grown in the same landscape as rainforest, though not necessarily mixed with it. When the climate became drier, some taxa were able to cope with the new conditions, but any taxon that could not adapt (presumably through speciation), were eliminated from the region.

It is readily accepted that rainforest taxa have been eliminated from the arid regions, but the fossil record reveals that taxa found in other kinds of vegetation have been eliminated also. *Dodonaea triquetra* has distinctive pollen and is found in wet and dry sclerophyll communities, where the rainfall is about 900–1700 mm/a (Martin, 1997). The fossil pollen is first found in the mid-Eocene in central Australia (Kemp, 1976; Sluiter, 1991), and subsequently from across southern Australia and as for north as the southern Great Barrier Reef (Martin, 1997). Its present distribution, along the southern half of the east coast of Australia, is thus a fraction of its former distribution.

Pollen of Poaceae, the grass family, is found in mid-Eocene sediments in central Australia (Sluiter, 1991; Alley et al., 1996), southern and southeastern Australia (Macphail and Hill, 2002) but it is rare. Grasses need an open habitat to be abundant, and there are swamp species of grasses as well as dryland species. Grass pollen is not common until the early Pliocene when an increase is found in two offshore sites, one in the northwest and the other to the east of the continent, inferring that grassland were developing on land, presumably in the interior (Martin, 1990b). The development of grasslands in the Pliocene accords with faunal evidence: grazing animals became common in the Pliocene (Archer et al., 1994).

These attempts to trace the origins of the arid flora show that many typical arid-zone taxa were in central Australia long before it became arid. There would have been a diversity of habitats in rainforests, open sclerophyll vegetation and the shorelines of lakes, through almost all of the Cenozoic, that could accommodate taxa with greatly disparate ecological tolerances. Climatic change to a drier climate sifted out those that could not tolerate the new conditions, leaving only the few that could thrive under the drier climates.

7. Conclusions

In the Palaeocene, all of Australia was warm and wet, and the vegetation was almost entirely rainforest. There was probably limited aridity in the northwest and central Australia was seasonal. Gymnosperms were predominant in the vegetation of southeastern Australia but angiosperms were dominant in central Australia.

The early Eocene was warmer than the Palaeocene and humid also. Angiosperms became more diverse and were dominant. There was an increase in megathermal taxa in southeastern Australia.

There was an overall decrease in temperature in the mid–late Eocene. The vegetation was predominantly rainforest, but there was some open vegetation and sclerophyllous taxa in central Australia. Sclerophylly developed as a response to infertile soils, long before the climate became dry. *Nothofagus* became the dominant pollen type, especially in southeastern Australia, and Lauraceae the dominant leaf type.

In the latest Eocene–early Oligocene, there was an abrupt cooling, the result of opening of the seaway between Australia and Antarctica and strengthening of the Circum-Antarctic current. Angiosperm diversity declined and *Nothofagus* pollen became more prominent.

During the Oligocene, temperatures increased and the diversity of angiosperms increased. The Oligocene was a time of particularly high rainfall, especially in southeast Australia where swamps were common.

In the early Miocene, temperatures increased and the vegetation became more variable in southeastern Australia. The warm, humid climates of the Miocene have not been matched since that time. Rainforest was restricted to small pockets in central Australia.

The mid-Miocene also marks the first step towards aridity with the cessation of regular flows in palaeodrainage systems over much of Western Australia and in central Australia. The alkaline lakes of inland basins in central Australia deposited dolomite; hence, the climate there was warm, with a well-marked dry season with high evaporation.

During the late Miocene, the climate became colder and drier. Rainforest was severely reduced and Myrtaceae pollen, most of which was *Eucalyptus*, became prominent. Regular burning became part of the environment.

There was a brief warming and increase in rainfall in the early Pliocene which allowed an expansion of rainforest in river valleys of the Western Slopes and southeastern Australia.

In the late Pliocene, the climate gradually became drier and rainforest taxa contracted further to the better-watered coastal and highland regions. Grasslands became prominent in inland regions and by the end of the Pliocene, the modern climatic regime was operating, but it was substantially wetter than today.

During the Pleistocene, the climate and vegetation reflect the drier glacial periods and the wetter interglacial periods. At about 0.5 Ma, there was a shift to a drier climate, though this shift may have occurred earlier in parts of central Australia. The last interglacial period (~120 ka) was wetter than the present interglacial. The last glacial period (~20–18 ka) was particularly harsh and although conditions have ameliorated considerably, rainfall has not returned to the levels of the previous interglacial period.

The rapidly changing Pleistocene climate, in terms of thousands of years, must have had a profound effect on plant and animal distributions. Any taxon that could not readily adapt to these changes would have been eliminate from all but the few equitable refuges.

The development of aridity has thus been gradual, over some 15 million years. There have been wetter periods during this time, but the overall pattern has been a continual decrease in precipitation. Such a history prompts the question: what of the future for Australia?

References

Allan, R.J., 1990. Climate. In: Tyler, M.J., Twidale, C.R., Davies, M., Wells, C.B. (Eds.), Natural History of the North East Deserts. Royal Society of South Australia, Adelaide, pp. 81–84.

Alley, N.F., 1998. Cainozoic stratigraphy, palaeoenvironment and geological evolution of the Lake Eyre Basin. Palaeogeography, Palaeoclimatology, Palaeoecology 144, 239–263.

Alley, N.F., Beecroft, A., 1993. Foraminiferal and palynological evidence from the Pidinga Formation and its bearing on Eocene sea level events and palaeochannel activity, eastern Eucla Basin, South Australia. Memoirs of the Association of Australasian Palaeontologists 15, 375–393.

Alley, N.F., Krieg, G.W., Callan, R.A., 1996. Early Tertiary Eyre Formation, lower Nelly Creek, southern Lake Eyre Basin. Australia: palynological dating of macrofloras and silcrete, and palaeoclimatic interpretations. Australian Journal of Earth Sciences 43, 71–84.

Apthorpe, M.C., 1988. Cainozoic depositional history of the North West Shelf. In: Purcell, P.G., Purcell, R.R. (Eds.), The North West Shelf Australia: Proceedings of the Petroleum Exploration Society of Australia Symposium. Petroleum Exploration Society of Australia, Perth, pp. 55–84.

Archer, M., Hand, S.J., Godhelp, H., 1994. Patterns in the history or Australia's mammals and inferences about palaeohabitats. In: Hill, R.S. (Ed.), History of the Australian Vegetation: Cretaceous to Recent. Cambridge University Press, Cambridge, England, pp. 80–103.

Ashton, D.H., Attiwell, P.M., 1994. Tall open forests. In: Groves, R.H. (Ed.), Australian Vegetation, second ed. Cambridge University Press, Cambridge, pp. 157–196.

Barnes, R.W., Hill, R.S., 1999. Macrofossils of *Callicoma* and *Codia* (Cunoniaceae). Australian Journal of Systematic Botany 12, 647–670.

Beadle, N.C.W., 1966. Soil phosphate and its role in molding segments of the Australian flora and vegetation, with special reference to xeromorphy and sclerophylly. Ecology 47, 992–1007.

Beadle, N.C.W., 1981. The vegetation of the arid zone. In: Keast, A. (Ed.), Ecological Biogeography of Australia, vol. 1. Dr. W. Junk, The Hague, pp. 695–716.

Benbow, M.C., Alley, N.F., Callan, R.A., Greenwood, D.R., 1995. Geological history and palaeoclimate. In: Dexel, J.F., Preiss, W.V. (Eds.), The Geology of South Australia, the Phanerozoic, vol. 2. Geological Survey of South Australia Bulletin 54, Adelaide, pp. 208–217.

Bint, A.N., 1981. An early Pliocene assemblage from Lake Tay, south-western Australia, and its phytogeographic implications. Australian Journal of Botany 29, 277–291.

Bowler, J.M., Wyrwoll, K.-H., Lu, Y., 2001. Variations of the northwest Australian summer monsoon over the last 300,000 years: the paleohydrological record of the Gregory (Mulan) Lakes System. Quaternary International 83–85, 63–80.

Busby, J.R., Brown, M.J., 1994. Southern rainforests. In: Groves, R.H. (Ed.), Australian Vegetation, second ed. Cambridge University Press, Cambridge, pp. 131–155.

Callan, R.A., Benbow, M.C., 1995. The deserts—playas, dunefields and watercourses. In: Dexel, J.F., Preiss, W.V. (Eds.), The Geology of South Australia, the Phanerozoic, vol. 2. Geological Survey of South Australia Bulletin 54, Adelaide, pp. 244–251.

Carpenter, R.J., Pole, M., 1995. Eocene plant fossils from the Lefroy and Cowan Paleodrainages, Western Australia. Australian Systematic Botany 8, 1107–1154.

Carpenter, R.J., Hill, R.S., Jordan, G.J., 1994. Cenozoic vegetation in Tasmania: the macrofossil record. In: Hill, R.S. (Ed.), History of the Australian Vegetation: Cretaceous to Recent. Cambridge University Press, Cambridge, pp. 276–298.

Chen, X.Y., Barton, C.E., 1991. Onset of aridity and dune-building in central Australia: sedimentological and magnetostratigraphic evidence from Lake Amadeus. Palaeogeography, Palaeoclimatology, Palaeoecology 84, 55–73.

Christophel, D.C., 1994. The early Tertiary macrofloras of continental Australia. In: Hill, R.S. (Ed.), History of the Australian Vegetation: Cretaceous to Recent. Cambridge University Press, Cambridge, pp. 262–275.

Christophel, D.C., Scriven, L.J., Greenwood, D.R., 1992. An Eocene megafossil flora from Nelly Creek, South Australia. Transactions of the Royal Society of South Australia 116, 65–76.

Dettmann, M.E., Clifford, H.T., 2003. Miocene palynofloras from subsurface sediments in the Bundaberg district. Memoirs of the Queensland Museum 49, 261–267.

De Vogel, S.B., Magee, J.M., Manley, W.F., Miller, G.H., 2004. A GIS-based reconstruction of late Quaternary paleohydrology: Lake Eyre, arid central Australia. Palaeogeography, Palaeoclimatology, Palaeoecology 204, 1–13.

Dodson, J.R., Ramrath, A., 2001. An upper Pliocene lacustrine environmental record from south-Western Australia—preliminary results. Palaeogeography, Palaeoclimatology, Palaeoecology 167, 309–320.

English, P., Spooner, N.A., Chappel, J., Questiaux, D.G., Hill, N.G., 2001. Lake Lewis basin, central Australia: environmental evolution and OSL chronology. Quaternary International 83–85, 81–101.

Feary, D.A., Davies, P.J., Pigram, C.J., Symonds, P.A., 1991. Climatic evolution and control on carbonate deposition in northeastern Australia. Palaeogeography, Palaeoclimatology, Palaeoecology (Global and Planetary Change Section) 89, 341–361.

Gallagher, S.J., Smith, A.J., Jonasson, K., Wallace, M.W., Holdgate, G.R., Daniels, J., Taylor, D., 2001. The Miocene palaeoenvironment and palaeoceanographic evolution of the Gippsland Basin, southeast Australia: a record of Southern Ocean change. Palaeogeography, Palaeoclimatology, Palaeoecology 172, 53–80.

Gallagher, S.J., Greenwood, D.R., Taylor, D., Smith, A.J., Wallace, M.W., Holdgate, G.R., 2003. The Pliocene climatic and environmental evolution of southeastern Australia: evidence from the marine and terrestrial realm. Palaeogeography, Palaeoclimatology, Palaeoecology 193, 349–382.

Gill, A.M., 1994. Patterns and processes in open-forests of *Eucalyptus* in southern Australia. In: Groves, R.H. (Ed.), Australian Vegetation, second ed. Cambridge University Press, Cambridge, pp. 197–226.

Greenwood, D.R., 1994. Palaeobotanical evidence for Tertiary climates. In: Hill, R.S. (Ed.), History of the Australian Vegetation: Cretaceous to Recent. Cambridge University Press, Cambridge, pp. 44–59.

Greenwood, D.R., 1996. Eocene monsoon forests in Central Australia? Australian Systematic Botany 9, 95–112.

Greenwood, D.R., Haines, P.W., Steart, D.C., 2001. New species of *Banksieaeformis* and a *Banksia* 'cone' (Proteaceae) from the Tertiary of Central Australia. Australian Systematic Botany 14, 871–890.

Greenwood, D.R., Moss, P.T., Rowett, A.I., Vadala, A.J., Keefe, R.L., 2003. Plant communities and climatic change in southeastern Australia during the early Paleogene. In: Wing, S.L., Gingerich, P.D., Schmitz, B., Thomas, E. (Eds.), Causes and Consequences of Globally Warm Climates in the Early Paleogene. Geological Society of America Special Paper 369, Boulder, USA, pp. 365–579.

Groves, R.H., 1999. Present vegetation types. In: Orchard, A.E. (Ed.), Flora of Australia, vol. 1, second ed. ABRS/CSIRO, Australia, pp. 369–401.

Haq, B.U., Hardenbold, J., Vail, P., 1987. Chronology of fluctuating sea levels since the Triassic. Science 235, 1156–1166.

Harle, K.J., 1997. Late Quaternary vegetation and climate change in southeastern Australia: palynological evidence from marine core E55–6. Palaeogeography, Palaeoclimatology, Palaeoecology 131, 465–483.

Harris, W.K., 1965a. Basal Tertiary microfloras from the Princetown area, Victoria, Australia. Palaeontographica Abteil B 115, 75–106.

Harris, W.K., 1965b. Tertiary microfossils from Brisbane, Queensland. Geological Survey of Queensland Report No. 10, pp. 1–7.

Hekel, H., 1972. Pollen and spore assemblages from Queensland Tertiary sediments. Geological Survey of Queensland Publication 355, Palaeontological Papers 30, pp. 1–34.

Hesse, P.P., Magee, J.W., van der Karrs, S., 2004. Late Quaternary climates of the Australian arid zone: a review. Quaternary International 118–119, 87–102.

Hill, R.S., 1998. Fossil evidence for the onset of xeromorphy and scleromorphy in Australian Proteaceae. Australian Systematic Botany 11, 391–400.

Hill, R.S., 2004. Origins of the southeastern Australian vegetation. Philosophical Transactions of the Royal Society of London 359, 1537–1549.

Hill, R.S., Christophel, D.C., 2001. Two new species of *Dacrydium* (Podocarpaceae) based on vegetative fossils from Middle Eocene sediments at Nelly Creek, South Australia. Australian Systematic Botany 14, 193–205.

Hill, R.S., Merrifield, H.E., 1993. An early Tertiary macroflora from West Dale, southwestern Australia. Alcheringa 17, 285–326.

Hill, R.S., Truswell, E.M., McLoughlin, S., Dettmann, M.E., 1999. Evolution of the Australian flora: fossil evidence. In: Orchard, A.E. (Ed.), Flora of Australia, vol. 1, second ed. ABRS/CSIRO, Australia, pp. 251–320.

Hobbs, J.E., Lindesay, J.A., Bridgman, H.A., 1998. Climates of the Southern Continents. Wiley, Chichester, England (295pp).

Holmes, W.B.K., Holmes, F.M., Martin, H.A., 1983. Fossil *Eucalyptus* remains from the Middle Miocene Chalk Mountain Formation, Warrumbungle Mountains, New South Wales. Proceedings of the Linnean Society of New South Wale 106, 299–310.

Hope, G.S., 1994. Quaternary vegetation. In: Hill, R.S. (Ed.), History of the Australian Vegetation: Cretaceous to Recent. Cambridge University Press, Cambridge, pp. 368–388.

Johnson, R.W., Burrows, W.H., 1994. *Acacia* open-forests, woodlands and shrublands. In: Groves, R.H. (Ed.), Australian Vegetation, second ed. Cambridge University Press, Cambridge, pp. 257–290.

Kamp, P.J.J., Waghorn, D.B., Nelson, C.S., 1990. Late Eocene–early Oligocene integrated isotope stratigraphy and biostratigraphy for paleoshelf sequences in southern Australia: paleoceanographic implications. Palaeogeography, Palaeoclimatology, Palaeoecology 80, 311–323.

Keast, A., 1959. The Australian environment. In: Keast, A., Crocker, R.L., Christian, C.S. (Eds.), Biogeography and Ecology in Australia. Dr. W. Junk, The Hague, pp. 9–35.

Kemp, E.M., 1976. Early Tertiary pollen from Napperby, central Australia. BMR Journal of Australian Geology and Geophysics 1, 109–114.

Kershaw, A.P., 1994. Pleistocene vegetation of the humid tropics of northeastern Queensland, Australia. Palaeogeography, Palaeoclimatology, Palaeoecology 109, 399–412.

Kershaw, A.P., McKenzie, G.M., McMinn, A., 1993. A Quaternary vegetation history of northeast Queensland from pollen analysis of ODP site 820. In: McKenzie, J.A., Davies, P.J., Palmer-Julson, A., (Eds.), Proceedings of the Ocean Drilling Program, Scientific Results, vol. 133, pp. 107–114.

Kershaw, A.P., Martin, H.A., McEwen Mason, J.C., 1994. The Neogene: a time of transition. In: Hill, R.S. (Ed.), History of the Australian Vegetation: Cretaceous to Recent. Cambridge University Press, Cambridge, pp. 299–327.

Kolwicki, V., 2004. Floods of Lake Eyre. 〈http://k26.comm/eyre〉.

Lange, R.T., 1978. Carpological evidence for fossil *Eucalyptus* and other Leptospermeae (Subfamily Leptospermoideae of Myrtaceae) from a Tertiary deposit in the South Australian arid zone. Australian Journal of Botany 26, 221–233.

Lawver, L.A., Gahagan, L.M., 2003. Evolution of Cenozoic seaways in the circum-Antarctic region. Palaeogeography, Palaeoclimatology, Palaeoecology 198, 11–37.

Leigh, J.H., 1994. Chenopod shrublands. In: Groves, R.H. (Ed.), Australian Vegetation, second ed. Cambridge University Press, Cambridge, pp. 345–368.

Locker, S., Martini, E., 1986. Phytoliths from the southwest Pacific Site 591. Initial Reports of the Deep Sea Drilling Program 90, 1079–1084.

Macphail, M.K., 1997. Late Neogene climates in Australia: fossil pollen- and spore-based estimates in retrospect and prospect. Australian Journal of Botany 45, 425–464.

Macphail, M.K., 1999. Palynostratigraphy of the Murray Basin, inland southeastern Australia. Palynology 23, 197–240.

Macphail, M.K., Hill, R.S., 2001. Fossil record of Acacia in Australia: Eocene to recent. In: Orchard, A.E., Wilson, A.J.G. (Eds.), Flora of Australia: Mimosaceae, Acacia pt1, vol. 11A. ABRS/CSIRO Publishing, Melbourne, pp. 13–29.

Macphail, M.K., Hill, R.S., 2002. Palaeobotany of the Poaceae. In: Mallett, K., Orchard, A.E. (Eds.), Flora of Australia, Poaceae 1: Introduction and Atlas, vol. 43. ABRS/CSIRO Publishing, Melbourne, pp. 37–70.

Macphail, M.K., Alley, N.F., Truswell, E.M., Sluiter, I.R.K., 1994. Early Tertiary vegetation: evidence from spores and pollen. In: Hill, R.S. (Ed.), History of the Australian Vegetation: Cretaceous to Recent. Cambridge University Press, Cambridge, pp. 189–261.

Magee, J.W., Bowler, J.M., Miller, G.H., Williams, D.L.G., 1995. Stratigraphy, sedimentology, chronology and palaeohydrology of Quaternary lacustrine deposits at Madigan Gulf, Lake Eyre, South Australia. Palaeogeography, Palaeoclimatology, Palaeoecology 113, 3–42.

Martin, H.A., 1987. Cainozoic history of the vegetation and climate of the Lachlan River region, New South Wales. Proceedings of the Linnean Society of New South Wales 109, 214–257.

Martin, H.A., 1990a. Tertiary climate and phytogeography in southeastern Australia. Review of Palaeobotany and Palynology 65, 47–55.

Martin, H.A., 1990b. The palynology of the Namba Formation in the Wooltana-1 bore, Callabonna Basin (Lake Frome), South Australia, and its relevance to Miocene grasslands in central Australia. Alcheringa 14, 247–255.

Martin, H.A., 1991. Tertiary stratigraphic palynology and palaeoclimate of the inland river systems in New South Wales. Geological Society of Australia Special Publication 18, 181–194.

Martin, H.A., 1992. The Tertiary of southeastern Australia: was it tropical? Palaeobotanist 39, 270–280.

Martin, H.A., 1993. The palaeovegetation of the Murray Basin, late Eocene to mid Miocene. Australian Systematic Botany 6, 491–531.

Martin, H.A., 1994. Australian Tertiary phytogeography: evidence from pollen. In: Hill, R.S. (Ed.), History of the Australian Vegetation: Cretaceous to Recent. Cambridge University Press, Cambridge, pp. 104–142.

Martin, H.A., 1997. The use of ecological tolerance for the reconstruction of Tertiary palaeoclimates. Australian Journal of Botany 45, 475–492.

Martin, H.A., 1998a. Late Cretaceous–Cainozoic palynology of the Poonarunna No. 1 Well, Central Australia. Transactions of the Royal Society of South Australia 122, 89–138.

Martin, H.A., 1998b. Tertiary climatic evolution and the development of aridity in Australia. Proceedings of the Linnean Society of New South Wales 119, 1115–1136.

Martin, H.A., 2000. Re-assignment of affinities of the fossil pollen type *Tricolpites trilobatus* Mildenhall and Pocknall to *Wilsonia* (Convolvulaceae) and a reassessment of ecological interpretations. Review of Palaeobotany and Palynology 111, 237–251.

Martin, H.A., McMinn, A., 1993. Palynology of sites 815 and 823: the Neogene vegetation history of coastal northeastern Australia. In: McKenzie, J.A., Davies, P.J., Palmer-Julson, A. (Eds.), Proceedings of the Ocean Drilling Program, Scientific Results, vol. 133, pp. 115–125.

Martin, H.A., McMinn, A., 1994. Late Cainozoic vegetation history of north-western Australia from the palynology of a deep sea core (ODP site 765). Australian Journal of Botany 42, 95–102.

Martin, H.A., Worral, L., Chalson, J., 1987. The first occurrence of the Palaeocene *Lygistepollenites balmei* Zone in the Eastern Highlands region, New South Wales. Australian Journal of Earth Sciences 34, 359–365.

Milne, L.A., 1988. Palynology of a late Eocene lignitic sequence from the western margin of the Eucla Basin, Western Australia. Association of the Australasian Palaeontologists Memoir 5, 285–310.

Moss, P.T., Kershaw, A.P., 2000. The last glacial cycle from the humid tropics of northeastern Australia: comparison of a terrestrial and a marine record. Palaeogeography, Palaeoclimatology, Palaeoecology 155, 155–176.

Mott, J.J., Groves, R.H., 1994. Natural and derived grasslands. In: Groves, R.H. (Ed.), Australian Vegetation, second ed. Cambridge University Press, Cambridge, pp. 369–392.

Nanson, G.C., Callan, R.A., Price, D.M., 1998. Hydroclimatic interpretation of Quaternary shorelines on South Australian playas. Palaeogeography, Palaeoclimatology, Palaeoecology 144, 281–305.

Nix, H.A., 1981. The environment of Terra Australis. In: Keast, A. (Ed.), Ecological Biogeography of Australia, vol. 1. Dr. W. Junk, The Hague, pp. 103–133.

Nix, H.A., 1982. Environmental determinants of biogeography and evolution in Terra Australis. In: Barker, W.R., Greenslade, P.T. (Eds.), Evolution of the Flora and Fauna of Arid Australia. Peacock Publications, Adelaide, pp. 47–66.

Ogg, J.G., 2004. Status of divisions of the International Geologic Time Scale. Lethaia 37, 183–199.

Pole, M.S., Macphail, M.K., 1996. Eocene *Nypa* from Regatta Point, Tasmania. Review of Palaeobotany and Palynology 92, 55–67.

Pole, M.S., Hill, R.S., Green, N., Macphail, M.K., 1993. The Oligocene Berwick Quarry flora—rainforest in a drying environment. Australian Systematic Botany 6, 399–427.

Prior, L.D., Johnson, L.A.S., 1981. *Eucalyptus*, the universal Australian. In: Keast, A. (Ed.), Ecological Biogeography of Australia, vol. 1. Dr. W. Junk, The Hague, pp. 499–535.

Quilty, P.G., 1994. The background: 144 million years of Australian palaeoclimate and palaeogeography. In: Hill, R.S. (Ed.), History of the Australian Vegetation: Cretaceous to Recent. Cambridge University Press, Cambridge, pp. 14–43.

Robert, C., Chamley, H., 1991. Development of early Eocene warm climates, as inferred from clay mineral variation in oceanic sediments. Palaeogeography, Palaeoclimatology, Palaeoecology 89, 315–331.

Rogers, P.A., 1995. Continental sediments of the Murray Basin. In: Dexel, J.F., Preiss, W.V. (Eds.), The Geology of South Australia, the Phanerozoic, vol. 2. Geological Survey of South Australia Bulletin 54, Adelaide, pp. 252–254.

Rowett, A., 1997. Earthwatch '96. MESA Journal 5, 27–29.

Savin, S.M., Douglas, R.G., Stehli, F.G., 1975. Tertiary marine temperatures. Geological Society of America Bulletin 86, 1499–1510.

Shackleton, N.J., Kennett, J.P., 1975. Paleotemperature history of the Cenozoic and the initiation of Antarctic glaciation: oxygen and carbon isotope analyses in DSDP sites 277, 279 and 281. In: Kennett, J.P., et al. (Eds.), Initial Reports of the Deep Sea Drilling Project 29. US Government Printer, Washington, DC, pp. 743–756.

Singh, G., Luly, J., 1991. Changes in vegetation and seasonal climate since the last full glacial at Lake Frome, South Australia. Palaeogeography, Palaeoclimatology, Palaeoecology 84, 75–86.

Sluiter, I.R.K., 1991. Early Tertiary vegetation and climates, Lake Eyre region, northeastern South Australia. In: Williams, M.A.J., De Deckker, P., Kershaw, A.P. (Eds.), The Cainozoic in Australia: a Re-appraisal of the Evidence. Geological Society of Australia Special Publication 18. The Geological Society of Australia, Sydney, pp. 99–166.

Specht, R.L., 1972. The Vegetation of South Australia. A.B. James Government Printer, Adelaide (328pp).

Specht, R.L., Specht, A., 1999. Australian Plant Communities: Dynamics of Structure, Growth and Biodiversity. Oxford University Press, Melbourne (492pp).

Stephenson, A.E., 1986. Lake Bungunnia—a Plio-Pleistocene megalake in southern Australia. Palaeogeography, Palaeoclimatology, Palaeoecology 57, 137–156.

Sweller, S., Martin, H.A., 2001. A 40,000 year vegetation history and climatic interpretations of Burraga swamp, Barrington Tops, New South Wales. Quaternary International 83–85, 233–244.

Taylor, G., 1994. Landscapes of Australia: their nature and evolution. In: Hill, R.S. (Ed.), History of the Australian Vegetation: Cretaceous to Recent. Cambridge University Press, Cambridge, pp. 60–79.

Taylor, G., Truswell, E.M., McQueen, K.G., Brown, C., 1990. Early Tertiary palaeogeography, landforms evolution and palaeoclimates of the southern Monaro, N.S.W Australia. Palaeogeography, Palaeoclimatology, Palaeoecology 78, 109–134.

Truswell, E.M., 1993. Vegetation changes in the Australian Tertiary in response to climatic and phytogeographic forcing factors. Australian Systematic Botany 6, 533–557.

Truswell, E.M., Harris, W.K., 1982. The Cainozoic palaeobotanical record in arid Australia: fossil evidence for the origins of an arid-adapted flora. In: Barker, W.R., Greenslade, P.T. (Eds.), Evolution of the Flora and Fauna of Arid Australia. Peacock Publications, Adelaide, pp. 367–376.

van der Graaff, J.W.E., Crowe, R.W.A., Bunting, J.A., Jackson, M.J., 1977. Relict early Cainozoic drainages in arid Western Australia. Zeitschrift für Geomorphologie, Neue Folge 21, 379–400.

van der Kaars, S., 1991. Palynology of eastern Indonesian marine piston-cores: a late Quaternary vegetational and climatic record for Australasia. Palaeogeography, Palaeoclimatology, Palaeoecology 85, 239–302.

van der Kaars, S., De Deckker, P., 2002. A late Quaternary pollen record from deep-sea core Fr10/95, GC17 offshore Cape Range Peninsula, northwestern Western Australia. Palaeogeography, Palaeoclimatology, Palaeoecology 120, 17–39.

Veevers, J.J., 1991. Mid-Cretaceous tectonic climax, Late Cretaceous recovery, and Cainozoic relaxation in the Australian Region. In: Williams, M.A.J., De Deckker, P., Kershaw, A.P. (Eds.), The Cainozoic in Australia: a Re-Appraisal of the Evidence. Geological Society of Australia Special Publication 18. The Geological Society of Australia, Sydney, pp. 1–14.

Wagstaff, B.E., Kershaw, A.P., O'Sullivan, P.B., Harle, K.J., Edwards, J., 2001. An early to middle Pleistocene palynological record from the volcanic crater of Pejark Marsh, Western plains of Victoria, southeastern Australia. Quaternary International 83–85, 211–232.

Wallis, L.A., 2001. Environmental history of northwest Australia based on phytolith analysis at Carpenter's Gap. Quaternary International 83–85, 103–117.

Wasson, R.J., 1982. Landform development in Australia. In: Barker, W.R., Greenslade, P.J.M. (Eds.), Evolution of the Flora and Fauna of Arid Australia. Peacock Publications, Adelaide, pp. 23–33.

Webb, L.J., Tracey, J.G., 1981. Australian rainforests: pattern and change. In: Keast, A. (Ed.), Ecological Biogeography in Australia, vol. 1. Dr. W. Junk, The Hague, pp. 605–694.

Wei, W., 1991. Evidence for an earliest Oligocene abrupt cooling in the surface waters of the Southern Ocean. Geology 19, 780–783.

Wilford, G.E., Brown, P.J., 1994. Maps of late Mesozoic–Cenozoic Gondwana break-up: some palaeogeographical implications. In: Hill, R.S. (Ed.), History of the Australian Vegetation: Cretaceous to Recent. Cambridge University Press, Cambridge, pp. 5–13.

Zachos, J., Pagani, M., Sloan, L., Thomas, E., Billups, K., 2001. Trends, rhythms, and aberrations in global climate 65 Ma to present. Science 292, 686–693.

Zheng, H., Wyrwoll, K.-H., Li, Z., Powell, C.Mc.A., 1998. Onset of aridity in southern Western Australia—a preliminary palaeomagnetic appraisal. Global and Planetary Change 18, 175–187.

Zheng, H., Powell, C.Mc.A., Zhao, H., 2002. Eolian and lacustrine evidence of late Quaternary palaeoenvironmental changes in southwestern Australia. Global and Planetary Change 35, 75–92.

Zhisheng, A., Bowler, J.M., Opdyke, N.D., Macumber, P.G., Firman, J.B., 1986. Palaeomagnetic stratigraphy of Lake Bungunnia: Plio-Pleistocene precursor of aridity in the Murray Basin, southeastern Australia. Palaeogeography, Palaeoclimatology, Palaeoecology 54, 219–239.