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Excerpt
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A brief history of Australia's mammals

OOLACUNTA

In December 1931 the mammalogist Hedley Herbert Finlayson travelled from Adelaide to Appamunna on the northwestern edge of the Simpson Desert in search of the desert rat-kangaroo *Caloprymnus campestris*. This species was something of a mystery to science. It had been described in 1843 on the basis of two specimens sent to John Gould in London from an unspecified location, but had not been recorded again until L. Reese, the owner of Appamunna Station, sent Finlayson a specimen and reported some sightings of the animal, which was known to the local Aborigines as 'oolacunta' (Figure 1.1). Finlayson wanted to learn more about oolacunta and to collect a series of specimens for the South Australian Museum. With Reese's help he recruited four knowledgeable Aboriginal men as expedition members and guides, and followed them into what they said was prime oolacunta country. This turned out to be perhaps the most extreme environment in an extraordinarily harsh region: a chain of gibber plains fringed by low sandhills, with no water, very little plant cover, and practically no shade (Plate 1).

Finlayson's party decided they would search for oolacunta on horseback, beating across country and following tracks if any could be found among the stones. If an oolacunta broke from cover it would be pursued, one rider chasing it at full gallop and the others replacing the lead rider when his horse began to tire. This plan worked, and the group soon put up their first animal. Finlayson (1935a) provides a vivid account of this first sighting:

> it was only after much straining of the eyes that the oolacunta could be distinguished – a mere speck, thirty or forty yards ahead. At that distance it seemed scarcely to touch the ground; it almost floated ahead in an eerie, effortless way that made the thundering horse behind seem, by compari-

OPPOSITE Summary of major events in the history of Australian mammals, in relation to the geological time scale, changes in climate and vegetation (shown on the vertical bar, where darker shading indicates more warm and wet conditions), and the changing location of Australia in the southern hemisphere.
Notes: Information on climate and vegetation from McGowran *et al.* (2000) and Kershaw *et al.* (2000). The date of 2.6 million years ago for the beginning of the Pleistocene follows Kershaw *et al.* (2000).

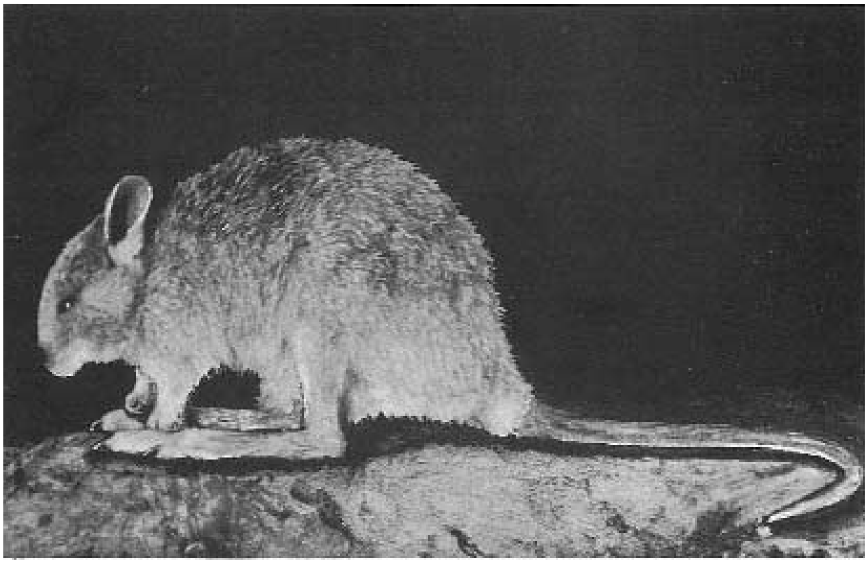

FIGURE 1.1 The desert rat-kangaroo, or oolacunta, photographed by Finlayson (1932).

> son, like a coal hulk wallowing in a heavy sea. They were great moments as it came nearer; moments filled with curiosity and excitement, but with a steady undercurrent of relief and satisfaction. It was here!

This little animal led them on an astonishing chase: they did not catch it until it had run twelve miles and tired out three horses, whereupon it died of exhaustion. The party collected seven specimens in this way, and all showed the same amazing tenacity. Another two animals, a mother and young, were caught by hand from their nest by one of the Aborigines who had hunted oolacunta before and could remember when it had been abundant. In all, seventeen animals were sighted in a week of searching (Finlayson 1932), a tally suggesting that oolacunta was locally common. Further specimens were received from the area until 1936. Reliable sightings continued until the mid-1950s, with some possible sightings as late as the 1970s, but there have been no more confirmed records and oolacunta is now thought to be extinct (Carr & Robinson 1997). What could have caused an animal like this – a survivor in one of the harshest environments in Australia, with the heart for such extraordinary feats of endurance – to disappear for ever?

THE EXTINCTION PROBLEM

The loss of oolacunta was just one of the latest in a long series of extinctions that have depleted Australia's mammal diversity in the geologically recent past. One hundred thousand years ago there were at least 340 species of land mammals in Australia; 67 of them are now extinct. These extinctions came in three waves. First, some time in the last glacial cycle (the late Pleistocene, between 130 000 and 10 000 years ago), over 50 species of mainly very large marsupials disappeared. Next, in the Holocene (between 10 000 and 200 years ago) the remaining large carnivores declined to extinction on the mainland. Finally, in the two hundred years or so since European settlement a further ten marsupial species and eight rodents have gone extinct, and almost one in four marsupial species is now threatened with extinction (Maxwell *et al.* 1996).

Mammal faunas on other continents have suffered recent extinctions, but not as badly as this. For example, there were megafauna extinctions in the late Pleistocene in South America (and in many other parts of the world) just as there were in Australia, but the South American loss was only about 10 per cent of the mammal fauna compared with 18 per cent in Australia. There was no parallel in South America to the Holocene decline of Australian large carnivores, and no South American mammals have gone extinct since the arrival on that continent of Europeans. Of the 40 mammal species worldwide known to have vanished in the last two hundred years, almost half have been Australian (MacPhee & Flemming 1999).

What is it about Australian mammals, or the Australian environment, or the nature of human impact on them, that can explain these high extinction rates? This book reviews the history of environmental change in Australia in a search for the answer to this question. Its three main sections deal with the declines of the late Pleistocene, Holocene and European periods respectively. Nonetheless, I am concerned to see this history as a whole: I will argue that the three waves of extinction were part of a single unfolding sequence of cause and effect, and that to understand the high rate of extinction and endangerment of Australian mammals in recent history we must begin by looking back at the events of the late Pleistocene and Holocene.

ORIGINS AND EVOLUTION

Australia has a unique and special mammal fauna. It is only here (along with New Guinea) that all three of the world's major lineages of living mammals – the monotremes, marsupials and placental mammals – can be found together. The monotremes occur nowhere else, and the Australo-Papuan region is the global centre of marsupial diversity. The long period of evolution of these groups in Australia and New Guinea produced a spectacular diversity of forms paralleling the great radiations of placental mammals over the rest of the globe. Many Australian mammals independently evolved remarkable similarities to their placental counterparts: gliding possums are strikingly similar to flying squirrels, for example, and marsupial moles look almost identical to the golden moles of Africa. Others evolved to gigantic size, producing rhinoceros-sized herbivores and lion-sized predators. On the other hand, some Australian mammals are unlike any species found elsewhere in the world. There is no other mammal quite like a wombat (a large herbivore that lives in a burrow), a Tasmanian devil (a small bone-crushing scavenger) or a honey possum (a specialised tube-nosed non-flying nectar feeder), not to mention outstanding oddities such as the platypus.

MYSTERY MAMMALS OF THE CRETACEOUS

The earliest fossil mammals from Australia date from the middle Cretaceous, around 105 to 120 million years ago. The small collection of fossils from this period consists of two monotremes plus several species that are not closely related to any living mammals. One of the monotremes, *Steropodon galmani* from Lightning Ridge, was probably platypus-like but was larger than the living platypus and may have weighed close to three kilograms; the other, *Teinolophos trusleri* from Flat Rock in Victoria, was a tiny relative of *Steropodon* with an estimated total length of only nine centimetres (Long *et al.* 2002). The enigmatic *Kollikodon ritchiei*, also from Lightning Ridge, was originally described as a monotreme (Flannery *et al.* 1995) but a more detailed analysis shows that it may be an entirely new type of mammal only distantly related to monotremes (Musser 2003, and personal communication). It was about the same size as *Steropodon*, making these two species among the largest mammals of their time anywhere in the world.

The other two mammals known from the Cretaceous of Australia belong to a group known as the ausktribosphenids, so far known only from the Flat Rock fossil site. These were small shrew-like creatures less than ten centimetres in total length. Just how they are related to the other mammal groups is a great puzzle. Rich *et al.* (1997) argued that they were placental mammals, a claim that challenges the accepted view of the history of the placental mammals, which are otherwise known only from the northern hemisphere until just after 65 million years ago (Rich *et al.* 1999). The controversy ignited by Rich *et al.*'s interpretation of the ausktribosphenids has not yet died down and many alternative affinities have been proposed for them, including that they were actually monotremes.

The various interpretations are summarised by Woodburne (2003), who thinks the ausktribosphenids belong in an ancient and now completely extinct lineage of eutherian mammals allied to the living placentals.

We still know very little about Australia's Cretaceous mammals, but the diversity represented by the five species described so far, which have been collected from only two fossil sites, suggests a rich fauna with a long evolutionary history reaching back probably into the Jurassic. All that remains are the living monotremes, the platypus and the echidnas. Monotremes are great survivors, being the last representatives of the ancient mammal group Prototheria (as distinct from the Theria, the group to which all other living mammals belong). The platypus lineage, which connects *Steropodon* and the living *Ornithorhynchus*, has been splashing about in freshwater streams in Australia for at least 120 million years.

From 105 to 55 million years ago no fossil Australian mammals are known. Presumably, the ausktribosphenids died out during this period. True platypuses (family Ornithorhynchidae) first appeared in the Australian fossil record about 25 million years ago, and echidnas somewhat later. The echidnas became moderately diverse, and before the late Pleistocene extinctions there were at least six species spread through Australia and New Guinea (Musser 1999).

The ancient monotremes and ausktribosphenids lived on a continent that for the most part was warmer than now and had a more uniform climate, except that the far south, which was still in contact with Antarctica, was cold and seasonal. The land was covered by forests of tall conifers from the families Araucariaceae and Podocarpaceae. These forests were evidently quite open-canopied and in most places the diversity of understorey vegetation was high (Henderson *et al.* 2000). From the late Cretaceous the climate appears to have become warmer and wetter, and there was an expansion of dense rainforests dominated by flowering plants. By the Eocene, about 50 million years ago, wet rainforest covered most of the continent. Species of *Nothofagus* (subgenus *Brassospora*) were typical of these Eocene forests, but they now occur only in New Guinea and New Caledonia in very warm, continuously wet environments. Another indicator of the Eocene climate of Australia was the very wide distribution of *Gymnostoma*, a rainforest-restricted lineage of the Casuarinaceae that now occurs only in a small area on the Atherton Tableland in the wet tropics of north Queensland (Hill 1994). *Nothofagus* and *Gymnostoma* grew even in the now-arid centre of the continent (Kershaw *et al.* 1994). It was into these vast, dense, wet and warm rainforests that the marsupials wandered when they completed their journey to Australia.

THE LONGEST JOURNEY: THE MARSUPIALS

The history of the marsupials can be traced back to a 125 million-year-old fossil from northeastern China, *Sinodelphys szalayi* (Luo *et al.* 2003). *Sinodelphys* was a small, agile, insectivore/carnivore that was well-adapted for tree climbing. While not strictly a marsupial, it is the earliest known member of the Metatheria, the major mammal group of which the marsupials are the living representatives. Metatherians appeared in western North America about 115 million years ago, probably having crossed from eastern Eurasia via a land-bridge that opened between Alaska and Siberia in the mid-Cretaceous (see the PALEOMAP project web site: www.scotese.com). These early mammal fossils from western North America include *Kokopellia juddi*, the earliest mammal actually classified (by some authorities) as a marsupial (Cifelli & Muizon 1997).

From 115 to 65 million years ago marsupials flourished in North America along with placental mammals (Cifelli & Davis 2003). They entered South America just after the end of the Cretaceous, between 65 and 60 million years ago (Muizon *et al.* 1997). At that time there was no land connection between North and South America, but a chain of volcanic islands in what was probably a shallow ocean separating the two continents may have allowed mammals to island-hop from north to south, presumably by accidental rafting on flotsam (Lillegraven 1974). South America was in contact with Antarctica, which in turn was in contact with Australia, providing the marsupials with a southern route to Australia. Fossil marsupials have been found in Antarctica, at Seymour Island on the Antarctic Peninsula near South America (Goin *et al.* 1999). These fossils are thought to be about 45 million years old, but they resemble taxa from much earlier South American faunas, except for two that are distinct from any known South American species and probably diverged after entering Antarctica. On these grounds Goin *et al.* (1999) suggest that the original members of this fauna may have colonised Antarctica about 60 million years ago.

The oldest fossil marsupials in Australia are from a site at Tingamurra near Murgon in southeastern Queensland that is dated to at least 55 million years ago (Archer *et al.* 1993; Godthelp *et al.* 1992). Most of the Tingamurra marsupials are unlike South American or Antarctic forms, suggesting that they underwent a significant period of evolution after reaching Australia, and therefore that they arrived substantially earlier than 55 million years ago. So, the evidence from both the Antarctic and Australian fossil record is that marsupials spread through Antarctica and into Australia very soon after they first entered South America (Woodburne & Case 1996).

In most cases it is not possible to trace the connections of particular lineages of marsupials across South America, Antarctica and Australia. The one exception is the family Microbiotheriidae, which has only one living species, *Dromiciops australis* or the monito del monte (little monkey of the mountains) of southern South America. The Seymour Island fauna includes one microbiotheriid and there are two more species in the Tingamurra fauna (Long *et al.* 2002). The living *Dromiciops* is restricted to *Nothofagus* forest, which was the dominant vegetation in Antarctica at the time the Seymour Island fossil beds were laid down and in eastern Australia at the time of the Tingamurra fauna. Although the microbiotheriids are now extinct in Australia, the living *Dromiciops* is more closely related to Australian than to South American marsupials (Cardillo *et al.* 2004). Probably the majority of living Australian marsupials are descended from a common ancestor with microbiotheriids.

Placental mammals also crossed from North to South America just after the end of the Cretaceous. The oldest known placental mammals in South America were rather less diverse and less divergent from their North American ancestors than were the South American marsupials of the time, suggesting that they crossed into South America later than the marsupials (Muizon *et al.* 1997). There are fossil placentals along with marsupials in Antarctica, but again their low diversity and close affinities with South American species suggest that they crossed into Antartica after the marsupials (Goin *et al.* 1999). Finally, the Tingamurra fauna of Australia includes a species, *Tingamurra porterorum*, that was described as a placental mammal by Godthelp *et al.* (1992). Apart from early bats (see below) this is the only placental identified in the Tertiary of Australia until the arrival, much later, of rodents. However, the interpretation of *T. porterorum* as a placental mammal rather than a marsupial has been challenged (Szalay 1994; Woodburne & Case 1996). Godthelp's announcement of a placental mammal in the company of the early marsupials of Australia was an event deeply felt by Australian mammalogists, because it seemed to refute the old opinion that marsupials had been successful in Australia only because of the absence of competition from (superior?) placental mammals. Given the uncertainty over what *Tingamurra* was, however, it remains very possible that placental mammals did not complete the journey along the southern route into Australia in the early Tertiary.

Why might marsupials but not placental mammals have managed to cross into Australia from Antarctica? There could be two explanations.

First, the ocean gap between the two continents may have begun to form as early as 70 million years ago (Smith *et al.* 1994), and the likelihood that a terrestrial mammal from Antarctica could find its way to Australia would have diminished steadily after that time. It seems that the marsupials got into South America before placental mammals, and also beat the placentals into Antarctica. Maybe they reached eastern Antarctica in time to make the crossing into Australia, but the placentals did not. Second, it is possible that even if marsupials and placentals reached eastern Antarctica at the same time, the marsupials were better fitted to make the journey north if that required a sea crossing. The marsupials known from Antarctica were all small, probably less than 350 grams, and they were arboreal insectivores or frugivores (Goin *et al.* 1999). Probably they were more likely to be cast out to sea on flotsam than the placentals, which were larger herbivores; such rafts might also have carried insects, and the marsupials could have stayed alive by eating them as they drifted north.

As far as we know the first marsupials to reach Australia encountered no terrestrial mammals other than a few monotremes, which were already quite specialised creatures. Their subsequent evolutionary history is a classic example of diversification to exploit the many opportunities offered by an unoccupied new land mass. Because the marsupials arrived in Australia when rainforests were expanding, their initial diversification was predominantly of forms adapted to complex forest. Unfortunately we know nothing about the early development of this rainforest fauna, because after Tingamurra there is a 30 million-year gap in the fossil record of Australian mammals (Archer *et al.* 1999). The mid-Oligocene faunas that emerged from this palaeontological dark age were remarkably rich in species. Marsupial diversity continued to increase until it reached an all-time high in the Early Miocene, when there were about 50 per cent more families in existence than in the last few million years (Archer *et al.* 1999).

At that point the climate began to turn cooler, drier and more variable. Eventually this trend produced fully arid conditions in much of inland Australia (McGowran *et al.* 2000; Quilty 1994). The major cause of this change was a re-arrangement of ocean circulation in the southern hemisphere following the final breaking apart of Gondwana. Before the break-up, cold currents flowing along the coast of Antarctica were turned northward when they struck the west coasts of South America and Australia. Their waters then circulated through the tropics before returning south, transporting tropical warmth to the Antarctic region. As Australia and South America moved away from Antarctica, a closed circum-Antarctic current formed. The waters of the southern ocean were therefore separated from those of the tropics, and the result was a drop in temperature of the southern ocean, the freezing over of Antarctica, and the establishment of cooler conditions in southern Australia. Latitudinal gradients in temperature became steeper, and climate zones became more strongly differentiated. At the same time the northward drift of Australia removed most of its central and northern parts from the influence of moisture-laden westerly winds and exposed them to drier and warmer subtropical high pressure systems (Bowler 1982; Bowman 2000).

With the drying and cooling of the climate the Eocene rainforests retreated and were replaced by more open and drier forests and woodlands, and in some places by shrublands and grasslands (Figure 1.2). These dry forests and woodlands were often dominated by Casuarinaceae (casuarinas) and they included *Acacia*, Asteraceae (daisies) and Chenopodaceae (chenopods, i.e. bluebush and saltbush) as indicators of the expansion of a shrub and herb layer under an opening forest canopy. By the end of the Pliocene the vegetation of Australia broadly resembled that of today in its composition and in the geographic distribution of structural types. One major difference was that rainforests were still rather more widespread and, in particular, there was a more extensive development of dry rainforest dominated by conifers, especially Araucariaceae. Another was that in the dry forests Casuarinaceae were often more abundant than eucalypts.

This drying trend caused the extinction of some specialised rainforest-dependent marsupial groups, and the family-level diversity of marsupials declined from the mid- to late-Miocene, never to fully recover. But the new environmental conditions also stimulated the diversification of dry-country species. In the dasyuromorph (insectivorous and carnivorous) marsupials, for example, there was a surge of diversification in the mid–late Miocene that coincided with the expansion of dry vegetation across inland and northern Australia (Figure 1.2). Most of the species produced in this late Miocene burst of evolution were small insectivores of grasslands, shrublands and open woodlands: animals such as dunnarts, planigales, and so on (see Plate 2).

The drier environments of the Pliocene and Pleistocene also provided many opportunities for large terrestrial herbivores, among which the Macropodidae (kangaroos) were the most successful. Macropodid diversity exploded and by 100 kyr ago there were at least 95 species of kangaroos and wallabies in Australia and New Guinea (Cooke & Kear 1999; Prideaux 2004). The main evolutionary trend in this diversification was increased body size and the accumulation of adaptations – in the teeth, skull and digestive system – for feeding on tough, abrasive plant material of low nutritional value. This was carried furthest in the sub-family

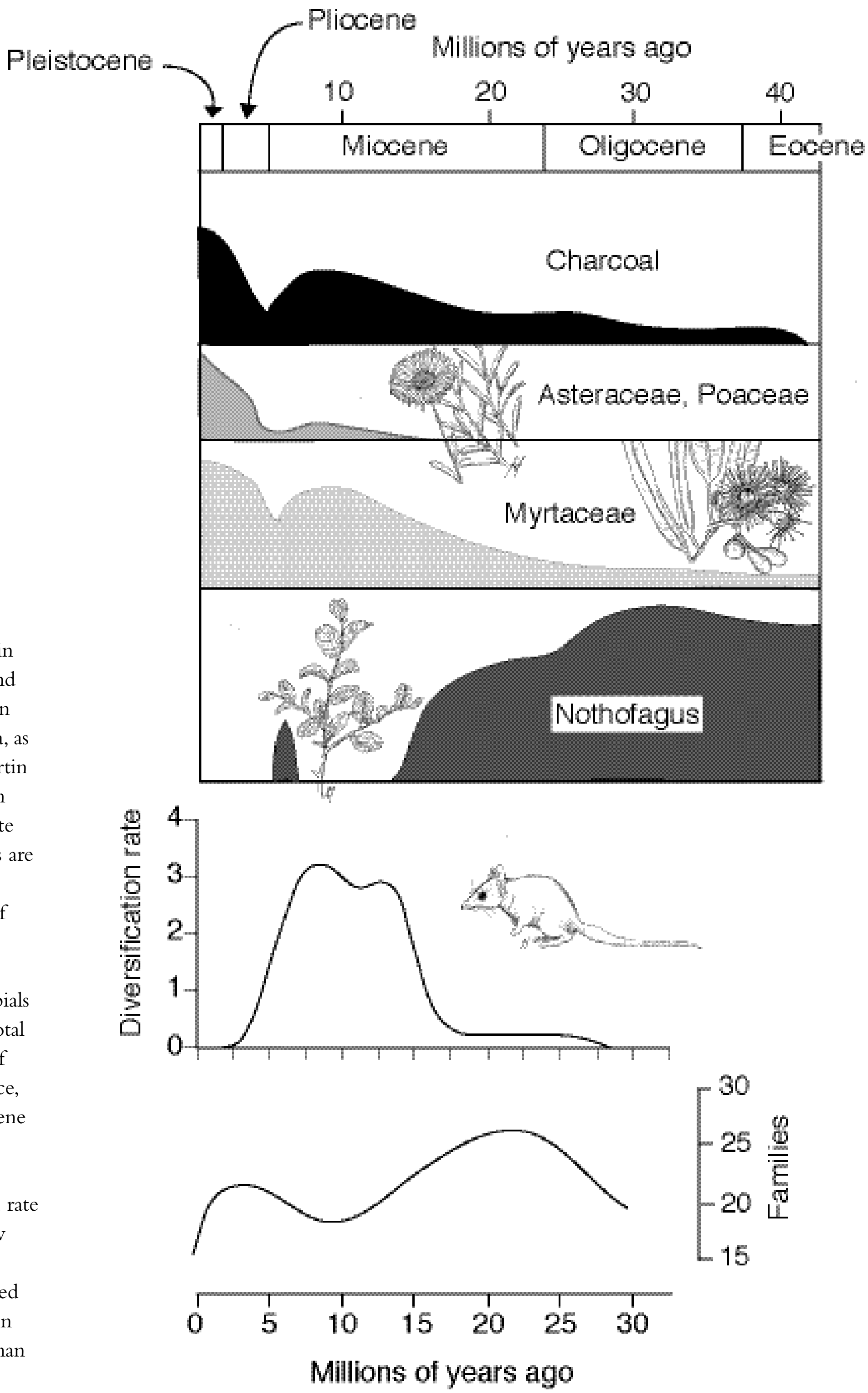

FIGURE 1.2 Changes in vegetation, climate and charcoal abundance in southeastern Australia, as reconstructed by Martin (1990) for the eastern Murray Basin. Climate and vegetation trends are compared with diversification rates of dasyuromorph (carnivorous and insectivorous) marsupials and changes in the total number of families of marsupials in existence, from the late Oligocene to the present (from Archer *et al.* 1999). *Notes:* Diversification rate is the number of new lineages arising per million years, estimated from the phylogeny in Krajewski & Westerman (2003).