

THE EVOLUTIONARY HISTORY AND DIVERSITY OF AUSTRALIAN MAMMALS

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Palaeodiversity and relationships of all groups of Australian mammals are reviewed. The fossil record spanning this time is of variable quality. 'Dark Ages' about which nothing is known in terms of Australian mammal evolution include the late Triassic to late Jurassic, late Cretaceous to late Palaeocene and middle Eocene to middle Oligocene. Very little is known about the early Cretaceous and late Miocene. The late Oligocene to middle Miocene record documents the highest levels of biodiversity known for the continent, comparable to that which characterises the lowland rainforests of Borneo and Brazil. Order Monotremata spans at least the last 110 million years and includes four families. The enigmatic *Ausktribosphenos* from 115 million-year-old sediments in Victoria may represent an archaic monotreme, specialised peramurid or previously undocumented order of mammals but is unlikely to represent a placental as suggested in the initial description. Order Microbiotheria is represented in the early Eocene (~55 mya) by two genera similar in morphology to early Eocene taxa from Argentina. Order Peramelemorphia spans the early Eocene to Holocene and includes at least five families. Order Dasyuromorphia spans at least the late Oligocene to Holocene and includes at least three families. Other dasyuromorphian-like marsupials are indeterminate in terms of family-level affinities. Order Notoryctemorphia spans the early Miocene to Holocene with one family. Order Yalkaparidontia spans the late Oligocene to middle Miocene with one genus. Order Diprotodontia spans the late Oligocene to Holocene, represented throughout by three major groups: Phalangerida (eight families), Vombatomorpha (seven families) and Macropodoidea (at least three families). A possible placental condylarth (*Tingamarra*) has been recorded from the early Eocene. An archaeonycteridid bat (*Australonycteris*) is known from the early Eocene. Among bats, the late Oligocene to middle Miocene is dominated by rhinolophoids, many of which have European, Asian and African affinities. Mystacinids, megadermatids, hipposiderids and molossids are well-represented in the Oligocene to Miocene deposits. Vespertilionids are uncommon in the Oligocene to Miocene but become more diverse in the Pliocene to Holocene. Emballonurids and rhinolophids appear for the first time in the Plio-Pleistocene. Pteropodids are unknown prior to the Holocene. Murids span the early Pliocene to Holocene. In the oldest assemblage at Riversleigh, one undescribed lineage resembles archaic forms otherwise only known from the fossil records of Africa and Eurasia.

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MODERN understanding about the evolutionary history of Australia's mammals has derived from four main arenas of research: palaeontology, comparative anatomy, cytology, and molecular biology. While palaeontological and anatomical studies have been pursued since the early part of the 19th Century, neither cytology nor molecular biology made major contributions to understanding about the relationships of Australian mammals until the late 1970s (e.g., Kirsch 1977). Since then, molecular systematic studies in particular have played an increasingly significant role in testing and refining understanding about relationships at all levels from intraspecific to interordinal (e.g., Richardson *et al.* 1986; Westerman *et al.* 1990; Springer *et al.* 1994; Messer *et al.* 1998). In a burst of activity starting in 1983, fossil representatives of most families of living Australian terrestrial, arboreal and volant mammals have now been found, thereby providing minimal ages of family-level differentiation and much new information about the interrelationships of otherwise disparate groups.

It is hoped that what follows is a brief but succinct overview of current understanding about the fossil record and relationships of all families of Australian terrestrial, arboreal and volant mammals. As would be expected in an increasingly active field of research, much of this understanding is in the process of being tested and some has yet to be published. For this reason and because of page-length restrictions, the monophyly of most taxa in the cladograms has not been able to be rationalised here. Published and/or ongoing studies that do rationalise these hypotheses are indicated in the individually authored subsections that follow.

Higher-level systematic nomenclature used here, unless otherwise indicated, follows Aplin and Archer (1987). Concepts of biocorrelation and gaps in the record of Australian Tertiary mammal-bearing sediments follow Archer *et al.* (1997c). Abbreviations used here are as follows: my, million years; myo, million years old; mya or Ma, million years ago; Ka, thousand years ago; LF, Local Fauna (= a contemporaneous assemblage of creatures recovered from a single or closely associated series of fossil localities); lfs, local faunas; Fm, Formation (= a body of rock strata, commonly of similar rock type). Dental homology in marsupials follows Luckett (1993) for P3-M4 and Flower (1867) for II-P2.

In the palaeodiversity figures below, we have amalgamated all taxa known from particular intervals of time as follows: early Cretaceous (taxa spanning only the late early Cretaceous from 115 to 100 my); early Paleocene (only the interval 63 to 61 my and only in Argentina); early Eocene (only one interval at approximately 55 my); latest Oligocene (only the latest late Oligocene from 26 to 23.3 my); early Miocene (all of it from 23.3 to 16.3 my); middle Miocene (all of it from 16.3 to 10.4 my); late Miocene (all of it from 10.4 to 5 my); early Pliocene (all of it from 5 to 3.3 my); late Pliocene (all of it from 3.3 to 2 my); Pleistocene (all of it from 2 my to 10,000 yrs); Holocene (all of the last 10,000 yrs). Allocation of particular faunal assemblages from Riversleigh to these time periods follows Archer *et al.* (1997c) and Creaser (1997). Hence, seven morphologically distinct dasyuromorphians indicated by Wroe and Muirhead (this work) for the early Miocene represents minimum species diversity for this group spanning this total interval of time. In these figures, taxa known from one or more of these intervals are shown as occurring throughout these intervals, despite the fact that in some cases they may only be known from a single fossil locality. This has been adopted because of current uncertainty about the *precise* ages (rather than 'early Miocene' etc.) of each of the hundreds of assemblages known. However, because mammal species commonly last 3 to 8 million years, these generalisations are probably not unreasonable.

SYNOPSIS AND LIMITATIONS OF THE FOSSIL RECORD OF AUSTRALIAN MAMMALS

In 1983, in a 432 page treatise over-viewing mammalian palaeofaunas of the world, Don Savage and Don Russell fairly summarised the highlights of the Australian Cainozoic record in five pages (accompanied by an upside down map of Australia!). At that time there were about 75 Tertiary species described. Subsequent growth in Australian palaeomammalogy led to many new discoveries which have more than trebled that level of understanding. Key events in the history of Australian mammals are summarised in Table 1. Correlation and age of significant Tertiary fossil mammal assemblages in Australia are summarised in Figure 1.

'Dark age 1' for Australian mammals between 220 to 115 mya; none are known despite being present in other areas of the world as early as 220 mya.

Ausktribosphenos nyktos, ~115 mya (e. Cret.), ?monotreme, peramurid or an unknown group (but almost certainly not a placent), Flat Rocks, Vic.

Steropodon galmani, *Kollikodon ritchiei*, ~110 to 100 mya (e. Cret.), monotypic members of the monotreme families Steropodontidae and Kollikodontidae, Lightning Ridge, NSW.

'Dark age 2' for Australian mammals from 100 to 55 mya.

Monotrematum sudamericanum, 63 to 61 mya (e. Paleoc.), ornithorhynchid monotreme, Argentina (Patagonia), SAM (with oldest undoubted SAM marsupials and placentals).

Marsupials probably reached Australia from SA, via Ant., sometime between 65 and 55 mya.

Thylacotinga bartholomaii, microbiotheriids, other marsupials with SAM affinities, a ?dasyuromorphian, a perameloid, *Tingamarra porterorum* (possible placent) and *Australonycteris clarkeae* (archaeonycteridid bat), ~55 mya (e. Eoc.), Murgon, SE Qld.

'Dark age 3' for Australian mammals extends from 55 to 26 mya.

After final separation from Ant. between 45 and 38 mya, apart from a 'spotty' archipelago linking SE Asia to Australia throughout Australia's northward drift, Australia's terrestrial mammals (but not bats) were isolated for 30 my resulting in a high level of endemism.

Most living families of Australian bats arrived (or evolved here) by 25 mya (l. Olig.); curiously, there is no pre-Holocene Australian record for pteropodids (fruit bats).

Between 24 and 15 mya, much if not all of central and northern Australia supported rainforest.

Between 26 and 23 mya (l. Olig. to e. Mioc.), some family-level groups went extinct (e.g., ilariids).

Mammal diversity in forest communities of e. Mioc. age (e.g., at Riversleigh, northwestern Qld) was very high, comparable to that found today in Borneo or Brazil and 44% greater in family-level diversity than the contemporary Wet Tropics rainforests of northeastern Queensland.

Endemic Australian bats (mystacinids) colonised New Zealand; others (a new Riversleigh group) may have colonised South America to become noctilionoids.

Australia crashed into SE Asia about 15 mya (m. Mioc.) after which time the New Guinea Highlands rapidly rose creating a rainshadow over northern Australia.

From 16 to 15 mya (m. Mioc.), Australia's forest mammals began a decline in diversity and distribution; family-level extinctions occurred between e. and m. Mioc. time (e.g., miralinids and wynyardiids).

Between 15 and 5 mya (m. to l. Mioc.), most of Australia began to dry and the central Australian forests declined.

'Dim age' for Australian mammals (very few sites known) from 12 to 5 mya.

New Guinea was probably colonised by dasyurids, bandicoots, zygomaturine diprotodontids and macropodine macropodids between 10 and 8 mya (l. Mioc.); however, phalangerids, dactylopsiline petaurids and acrobatids *could* have colonised New Guinea by 23 mya.

Murid rodents entered Australia from SE Asia via relatively dry corridors into northern Australia sometime between 8 and 5 mya (l. Mioc.).

By 5 mya (e. Plio.), many modern non-forest genera of marsupials had arisen and grass-eating marsupials (species of *Macropus* and modern types of vombatids) had appeared.

No plant assemblage in Australia can be described as arid, nor do grasslands develop, until sometime between 4 and 2 mya (e. Plio. to e. Pleist.).

Sometime between 4 and 1 mya (e. Plio. to Pleist.) Cuscuses probably became extinct in Australia and then later reinvaded from New Guinea.

By 2 mya (e. Pleist.), the first 'arid'-adapted marsupials appear (e.g., *Macropus (Megaleia) sp.*).

Sometime between 120,000 and 50,000 ya, Humans arrived in Australia; two or more types *may* have overlapped until 10,000 ya.

Probably by 50,000-40,000 ya, extinctions of most of Australia's 'megafaunal' mammals occurred resulting in the complete loss of diprotodontids, thylacoleonids and palorchestids as well as many genera and species in other families; the cause is controversial.

Approximately 4,000 ya, Dingoes were introduced to Australia possibly resulting in the extinction of mainland Thylacines (*Thylacinus cynocephalus*).

Contact with and colonisation by Europeans initiated the second major, ongoing extinction phase of Australian mammals.

Table 1. Summary of key events relating to the prehistory of Australian mammals. Abbreviations: mya, million years ago; e., early; m., middle; l., late; Cret., Cretaceous; Paleoc., Paleocene; Eoc., Eocene; Olig., Oligocene; Mioc., Miocene; Plio., Pliocene; Pleist., Pleistocene; NSW, New South Wales; Qld, Queensland; Vic., Victoria; SA, South Australia; Ant., Antarctica; WA, Western Australia; NT, Northern Territory; Tas., Tasmania; SAM, South America; N, northern; NE, northeastern; E, eastern; SE, southeastern; S, southern; SW, southwestern; W, western; NW, northwestern; PNG, Papua New Guinea.

Although it is likely that monotremes have a history in Australia that will eventually prove to be Jurassic in age, the base of the known Australian fossil mammal record starts in the late early Cretaceous (about 115 mya). Thus Australia's first profound 'Dark Age' extends from 220 (age of the oldest known mammals on other continents) to 115 mya; no Australian mammals from this interval are known. Early Cretaceous mammals in Australia come from two regions: Lightning Ridge, New South Wales (~110 to 100 myo, from the Griman Creek Fm); and Flat Rocks, Victoria (~115 myo, from the Wonthaggi Fm). Mammals recovered from Lightning Ridge represent two distinct families of monotremes (Musser 1998). The only mammal described from Flat Rocks is *Ausktribosphenos nyktos*, a creature of uncertain relationships although originally described as a placental (Rich *et al.* 1997; Archer *et al.* below). Although the late Cretaceous to middle Eocene rocks of most other continents have produced mammals in abundance, in Australia the relatively sparse rocks of this age have so far produced only dinosaurs and other non-synapsid vertebrates. Australia's second profound 'Dark Age' of mammalian evolution extends from 100 to 55 mya with no species known from this interval.

Illites in soft sediments exposed at Tingamarra, on the outskirts of the town of Murgon, southeastern Queensland, have been dated as >55.6 (earliest Eocene in age) on the basis of potassium/argon ratios (Godthelp *et al.* 1992). This age has been challenged by Woodburne and Case (1996) who suggest that the Tingamarra assemblage may be as young as late Oligocene in age (i.e., 25 myo). From these sediments have come many different kinds of mammals as well as osteichthyan fish, myobatrachid frogs (Tyler and Godthelp 1993), madtsoiid snakes (Scanlon 1993), trionyhid turtles (Gaffney and Bartholomai 1979), mekosuchine crocodiles (Salisbury and Willis 1996) and passerine (Boles *et al.* 1994) as well as more archaic groups of birds including graculavids which are otherwise known only from late Cretaceous and Paleocene deposits in North America and probably Asia (Boles 1999). Where it has been possible to assess the biocorrelative significance of these non-mammalian vertebrates, they are broadly supportive of an early Eocene (or marginally older) age. Although the Tingamarra passerine is, by 20 million years, the oldest in the world, a significant pre-Oligocene Southern Hemispheric record was predicted by some palaeornithologists

(Boles 1995). Biocorrelative studies of the Murgon mammals, which include a ?placental (Godthelp *et al.* 1992), archaeonycteridid bat (Hand *et al.* 1994) and many marsupials including several with affinities to Casamayoran (early Eocene) as well as Tiupampian (Paleocene) South American groups (e.g., Archer *et al.* 1993; Godthelp *et al.* 1999), provide additional support for the early Eocene illite date. The archaeonycteridid bat in particular is closely related to earliest Eocene bats from North America and Europe. This interval in Australia was characterised by relatively warm, humid 'greenhouse' climatic conditions (McGowran and Li 1997).

The complete lack of knowledge about Australian terrestrial mammals from middle Eocene to middle Oligocene time, an interval of about 30 million years, is maddening. During this third profoundly 'dark age', Australia severed its last tenuous connections to the rest of Gondwana (Antarctica plus South America), sometime between about 46 and 35 mya, as it accelerated its northward drift towards the equator. From middle Eocene to late Oligocene time, Australia was characterised by relatively cool, dry 'icehouse' climatic conditions.

The latest Oligocene (about 25 to 23.3 mya) marks the beginning of a *relatively* well-documented phase in Australian mammal evolution. Fossil assemblages from two regions in particular, northeastern South Australia (the Tirari Desert in the Lake Eyre Basin, and the Lake Frome area in the Lake Frome Embayment) and Riversleigh (northwestern Queensland; described by Archer *et al.* 1997c as 'System A' local faunas) have provided an increasingly rich late Oligocene record. The Geilston Bay LF of Tasmania is probably early Miocene in age but the faunal assemblage is small and the taxa relatively poorly preserved. Eyre Basin Tertiary sediments have been dated with reasonable confidence using palaeomagnetostatigraphy (Woodburne *et al.* 1994). Riversleigh Tertiary sediments, previously dated by biocorrelations involving central Australian (marsupial) and European (bat) taxa, are now the subject of a uranium/lead dating program.

The early Miocene (about 23.3 to 16.3 mya) record documents Australia's most diverse mammalian faunas. These are best-known from Riversleigh (the 'System B' local faunas of Archer *et al.* 1997c) and the Tirari Desert (the Kutjamarpu LF). Less well-known assemblages occur in the Northern Territory (Kangaroo Well LF) and

Tasmania (Wynyard LF). As a measure of early Miocene diversity, a single assemblage at Riversleigh (Upper Site), interpreted to represent a closed forest community (Archer *et al.* 1997b), contains 64 species of mammal and 44% more family-level diversity than occurs today in the whole of the Wet Tropics rainforests of northeastern Queensland. The Leaf Locality may represent a riparian closed-forest community but the Riversleigh deposits of this age appear to indicate regional widespread, complex rainforest. If relatively drier communities bounded these forests, they left no trace in the known fossil record. Further, Martin (1998) has argued on the basis of palaeobotanical data that there is no evidence for arid conditions in Australia prior to the end of the Tertiary, in late Pliocene times.

Although early and middle Miocene mammal diversity was relatively high compared to diversity in Australia's contemporary forests, because of the geographically restricted nature of the palaeontological sampling areas, actual continental diversity at these times was almost certainly much higher than currently documented.

The middle to late Miocene (about 16.3 to 10 mya) marks the start of significant declines in rainfall following a pronounced climatic oscillation between 16 and 15 mya (McGowran and Li 1994). Middle Miocene mammal communities are only known from Riversleigh (those described as 'System C' assemblages (Archer *et al.* 1997c) and Bullock Creek in the Northern Territory (Murray and Megirian 1992). These are commonly characterised by less family, generic and species-level diversity than those of the early Miocene. What is known about mammals in most lineages demonstrates a rapid increase in average size over those of the early and middle Miocene.

The late Miocene is represented by very few Australian assemblages. Of these, the best-known are the Alcoota and Ongeva Local Faunas of the Northern Territory (Murray and Megirian 1992). These contain many medium to larger-size mammals but very few of the smaller kinds, leaving a gap in understanding about the evolutionary transition of smaller mammals from middle Miocene to Pliocene time. A single assemblage at Riversleigh, the Encore LF, may represent the early late Miocene with taxa that appear to be antecedent to Alcoota forms. This Riversleigh assemblage is also the oldest-known to include a wombat with ever-growing teeth (a species of *Warendja*-like vombatid), a suggestion of the presence of terrestrial plants with relatively

abrasive cell walls. The Beaumaris LF from Victoria is another late Miocene site but one with very few taxa represented. Drying conditions throughout much of the continent may account in part for the relatively poor late Miocene fossil record. This also appears to be the time during which many of the modern groups of marsupials (e.g., dasyuroids, peramelids, peroryctids and macropodids), bats (vespertilionids) and perhaps rodents (murids) underwent explosive radiations to produce the high diversity of species lineages present today.

Pliocene assemblages are widespread and known from all states except Tasmania and the Northern Territory. By this time, Australian mammal communities had significantly changed with representatives of many modern genera appearing for the first time including the first-known Australian rodents. Size increases continued in most lineages, most noticeably among herbivorous marsupials such as several diprotodontids which had become the size of cattle. The first, albeit rare occurrences in inland communities of grazing mammals in the early Pliocene suggests that grasses were increasing in abundance. Other early Pliocene communities, however, indicate the persistence of refugial rainforest in continentally peripheral areas such as Hamilton, Victoria. There are indications, mainly from palaeobotany, that the early Pliocene was a time of brief amelioration of a general drying and cooling trend with brief expansions of rainforest into mesic regions.

Pleistocene diversity has been under continuous investigation since fossil mammals were first found in Australia. At least 26 of the living genera are represented by Pleistocene species, although some of these may represent anagenetic lineages (e.g., *Macropus titan* to *M. giganteus*, and *Sarcophilus laniarius* to *S. harrisii*). Because of human impact and/or climatic change, most of the Pleistocene megafauna (Murray 1991), about 50 species, had vanished by about 40,000 years ago. A few megafaunal species underwent post-Pleistocene dwarfing in proportion to their absolute size such that some of the largest living kangaroos (e.g., species of *Macropus*) are 30% smaller than their Pleistocene ancestors. Dating of some Pleistocene megafaunal assemblages is controversial (Baynes 1997 and A. Baynes, pers. comm., 1997).

Holocene increases in species-level diversity for groups such as phalangerids, pseudocheirids, dasyurids, peroryctids, peramelids, potoroids, murids, vespertilionids and probably pteropodids

AUSTRALIAN MAMMALOLOGY

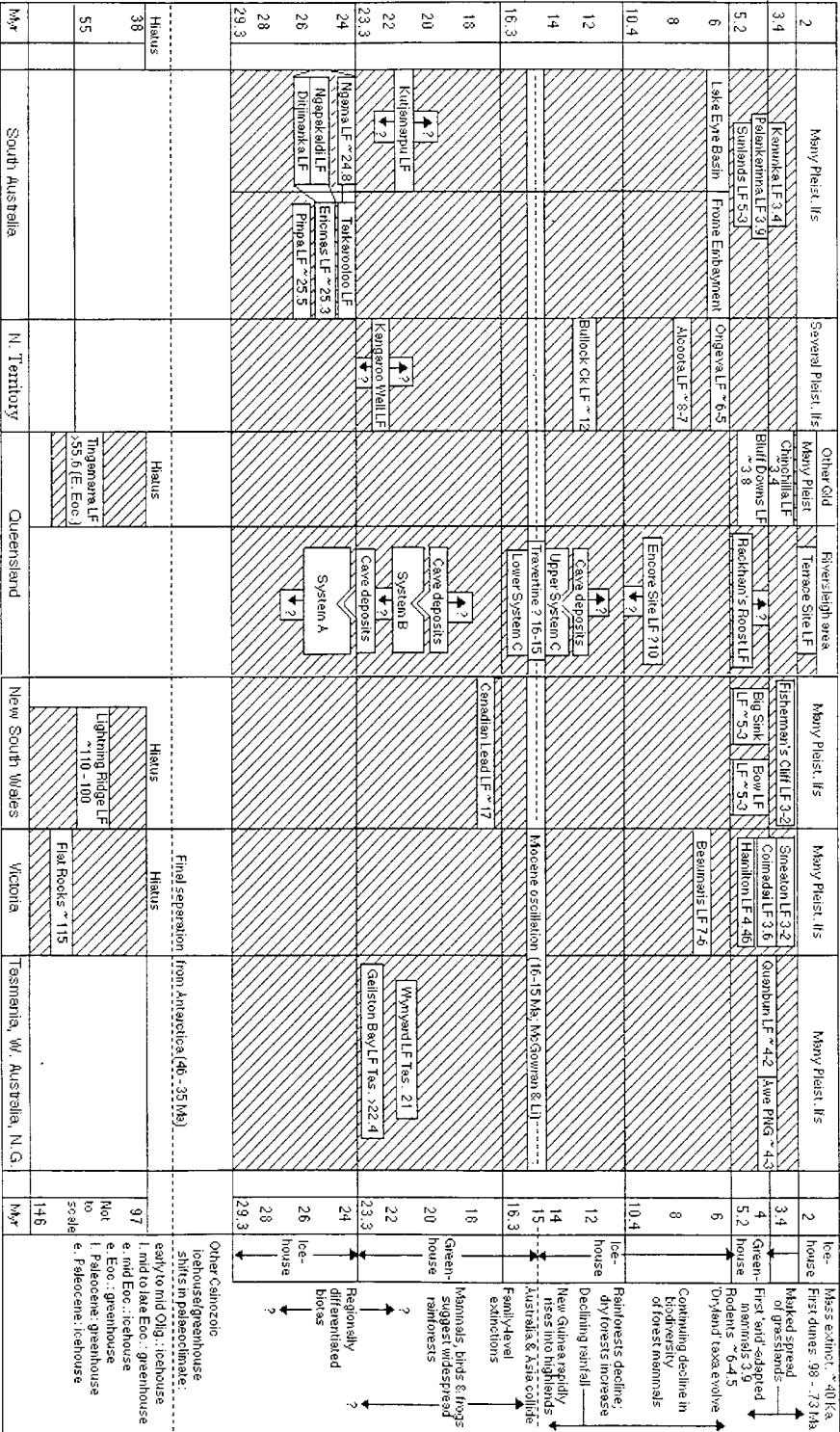


Fig. 1. Correlation chart for Australian fossil mammal communities (local faunas) noted and/or contributing to understanding summarised in this paper.

indicated in the palaeodiversity figures below is almost certainly a reflection of the limitations of the Plio-Pleistocene fossil record. This is particularly the case for smaller mammals which are less likely to be collected.

RELATIONSHIPS OF AUSTRALIAN MAMMALS

The phylogenetic relationships of Australian mammals have been extensively examined at three levels: infrafamilial, interfamilial and interordinal. Three factors restrict ability to interpret their interordinal relationships with confidence. First, yalkaparodontians, yingabalanarids and the possible placental condylarth *Tingamarra porterorum* are only known from an inadequate fossil record. As a result, there are disagreements about their ordinal and interordinal relationships (see Archer *et al.* this work). Second, two of the orders (Chiroptera and Rodentia) have more extensive non-Australian representation and almost certainly arrived in Australia as diversified groups with closer phylogenetic relationships to non-Australian mammals. Third, character systems examined for representatives of many of the other orders have in some cases produced widely differing indications of phylogenetic relationship. For example, while most mammalogists regard monotremes to not only be outside of the clade containing marsupials and placentals but even outside of therian mammals, DNA-hybridisation suggests that monotremes may be the sister group of marsupials (e.g., Janke *et al.* 1997, Kirsch and Mayer 1998). Similarly, there is considerable disagreement about the interordinal relationships of peramelemorphians, dasyuromorphians, notoryctemorphians and diprotodontians based on divergent indications of albumin serology (e.g., V. Sarich, pers. comm. in Archer 1982a), whole serum serology (Kirsch 1977), 12S ribosomal RNA (Springer *et al.* 1994), protamines (Retief *et al.* 1995), DNA-hybridisation (Kirsch *et*

al. 1997), and morphology (Szalay 1982, 1994). Although there is general consensus, following studies of tarsal anatomy by Szalay (1982), that microbiotherians share a special relationship with Australian marsupials, there are arguments about the precise nature of their placement within Australidelphia, some concluding a special relationship with dasyuromorphians and peramelemorphians (albumin serology; V. Sarich, pers. comm. in Archer 1982a), others a sister taxon relationship with dasyuromorphians (Szalay 1994), dasyuromorphians and notoryctids (Retief *et al.* 1995), diprotodontians (Kirsch *et al.* 1997), and still others with the whole of the Australian marsupial radiation (e.g., Szalay 1982), or the Australian radiation plus the early Tertiary South American genus *Andinodelphys* (Marshall *et al.* 1990). Resolution of the interordinal relationships of Australian marsupials has been further complicated following the suggestion that peramelemorphians may lie outside of a clade inclusive of all other Australian marsupials and *Dromiciops*, or even outside of all extant marsupials (Springer *et al.* 1994; Retief *et al.* 1995).

Intraordinal and infrafamilial relationships are briefly explored in the individual contributions that follow. For some of these groups such as dasyuroids, perameloids and macropodoids, interfamilial phylogenetic relationships remain uncertain. In part this reflects the fact that although many modern families are present and distinct in 26 to 23 million-year-old sediments, the fossil record between 55 and 26 million years of age, the interval when most of these families probably differentiated from each other, is so far utterly silent. Further, confident resolution of many higher-level systematic problems may be beyond the current capacity of molecular systematic techniques. With continued research, both of these limitations must be overcome.

DIVERSITY AND RELATIONSHIPS OF LIVING AND EXTINCT MONOTREMES

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TWO early Cretaceous monotremes have been described from the Griman Creek Formation, Lightning Ridge, New South Wales. The platypus-like *Steropodon galmani* (family Steropodontidae) was Australia's first known Mesozoic mammal (Archer *et al.* 1985). A second taxon, *Kollikodon ritchiei* (family Kollikodontidae), characterised by unique bunodont teeth, may have specialised in eating crustaceans (Flannery *et al.* 1995). An edentulous maxillary fragment from Lightning Ridge has been described as possibly that of a monotreme (Rich *et al.* 1989). Edentulous lower jaw fragments of a monotreme-like mammal from Lightning Ridge have also been recovered.

The oldest undoubted ornithorhynchid is *Monotrematum sudamericanum*, from late early Paleocene sediments in Patagonia, Argentina (Pascual *et al.* 1992). This species demonstrates that at least ornithorhynchids had a Gondwanan distribution (Pascual *et al.* 1992). Two species referable to the genus *Obdurodon* have been recovered from the late Oligocene central Australian Etadunna and Namba Formations: *Obdurodon insignis* (Woodburne and Tedford 1975; Archer *et al.* 1978) and the undescribed *Ob. sp. A. Ob. dicksoni*, a third *Obdurodon* species, has been recovered from the Riversleigh World Heritage fossil deposits in northwestern Queensland (Archer *et al.* 1992, 1993; Musser and Archer 1998). The only known Pliocene ornithorhynchid material consists of a limb fragment from the Bow Local Fauna, near Merriwa, NSW referred to the genus *Ornithorhynchus* (Rich *et al.* 1991b). Pleistocene ornithorhynchid material appears to represent the living *Ornithorhynchus anatinus* (e.g., Archer *et al.* 1978; Marshall 1992).

Echidnas of the genus *Megalibgwilia*, characterised by a beak shape intermediate between that of the living *Tachyglossus* and *Zaglossus*, are known from Pleistocene swamp and cave deposits from Tasmania, New South Wales and South Australia. This recently erected genus supersedes the assignment of several long-beaked types (e.g., *ramsayi*) to the genus *Zaglossus* (Griffiths *et al.* 1991). A middle Miocene echidna, *Echidna (Proechidna) robusta* Dun, 1895 from Gulgong, New South Wales, is probably a species of *Megalibgwilia* (Griffiths *et al.* 1991). A humerus found with the partial cranium of this

specimen, originally described as ornithorhynchid (*Ornithorhynchus maximus* Dun, 1895), is tachyglossid and probably belongs to the individual represented by the cranium (Mahoney and Ride 1975). The huge '*Zaglossus*' *hacketti* from Western Australia may represent a distinct genus (J. Mahoney cited in Griffiths *et al.* 1991). *Zaglossus* material from the Pleistocene of New Guinea probably represents the living *Z. bruijnii* (Murray 1991). The living Short-beaked Echidna (*Tachyglossus aculeatus*) is known from many Pleistocene to Holocene deposits in southern Australia (Murray 1978, 1991).

The cladogram (Fig. 1) reflects the uncertain phylogenetic relationships of tachyglossids as well as the unresolved position of the very derived *K. ritchiei*. Some genetic studies infer that tachyglossids separated from ornithorhynchids near the end of the Cretaceous or early in the Tertiary (e.g., Westerman and Edwards 1992; Messer *et al.* 1998 but see Retief *et al.* 1993). Given the early Cretaceous age of the platypus-like *S. galmani*, such findings suggest that tachyglossids may have been derived from a platypus-like ancestor thus making the platypus lineage paraphyletic. However, Messer *et al.* (1998) suggest that these dates may be underestimates of divergence times because evolution of at least the milk protein α -lactalbumin appears to be slower in monotremes than in living therians.

Much of the monotreme fossil material is fragmentary and vast temporal gaps separate taxa. However, some tentative conclusions about historical diversity can be drawn. The presence of *S. galmani* in the early Cretaceous is testimony to the antiquity of platypus-like monotremes (Archer *et al.* 1985), while the presence of the contemporaneous, specialised *K. ritchiei* argues for far greater intraordinal diversity than previously anticipated (Flannery *et al.* 1995).

However, from the early Tertiary to the present, only ornithorhynchids and tachyglossids are represented. Ornithorhynchids may have been more diverse during the early to middle Tertiary (four species are known) while tachyglossids appear to have radiated during the Plio-Pleistocene, with at least five Pleistocene species recognised (Murray 1978; Griffiths *et al.* 1991).

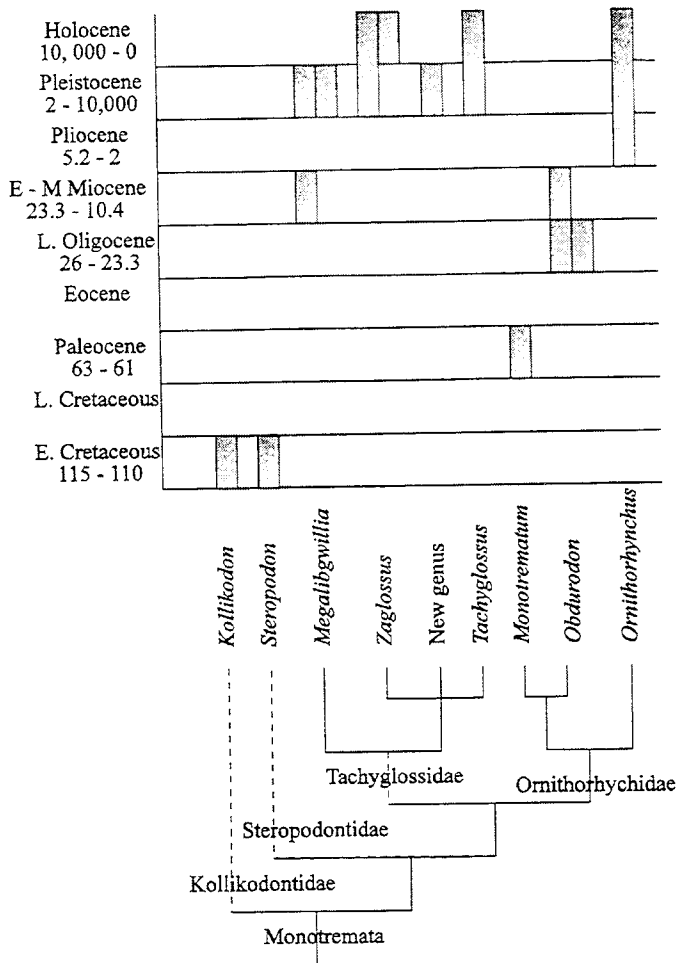


Fig. 1. Monotreme diversity through time: a cladogram of probable relationships (see text) within Monotremata. Uncertain relationships are indicated by dashed lines. Each block represents a distinct species. Blocks that extend without breaks through more than one time period indicate apparently long-surviving species.

Phylogenetic affinities of monotremes to other groups remain contentious. Dental structure, diagnosed as therian based on the triangular molar blades of *S. galmani* (Archer *et al.* 1985; Kielan-Jaworowska *et al.* 1987), may be autapomorphic with independent acquisition of therian-like triangular blade systems (Archer *et al.* 1992, 1993). Basicranial anatomy appears to link monotremes most closely with multituberculates (e.g., Wible and Hopson 1993; Meng and Wyss 1995). Several key Mesozoic taxa known from postcranial material exhibit advanced shoulder girdle morphology (e.g., Hu *et al.* 1997), placing the plesiomorphic shoulder girdle of monotremes between archaic morganucodontids or tricono-

dontids and the more derived multituberculates (Hu *et al.* 1997), and suggesting an early to late Jurassic origin for the monotreme shoulder girdle (Musser 1998). Genetic evidence is equivocal: Messer *et al.* (1998) support a middle Jurassic divergence of monotremes from therian mammals, although Westerman and Edwards (1992) place this split at the earliest Cretaceous. A close relationship between monotremes and marsupials to the exclusion of placental mammals has recently been suggested (Janke *et al.* 1997; Kirsch and Mayer 1998 in revisions of Gregory's [1947] Marsupionta hypothesis), although results from other molecular techniques argue against this

**EVOLUTION OF AUSTRALIA'S MARSUPICARNIVORES: DASYURIDAE,
 THYLACINIDAE, MYRMECOBIIDAE, DASYUROMORPHIA INCERTAE SEDIS AND
 MARSUPIALIA INCERTAE SEDIS**

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RECENT fossil discoveries have shed new light on the subject of Australian marsupicarnivore evolution (Fig. 1). The new material includes the first of Palaeogene age, as well as the first pre-Pliocene crania referable to the Dasyuridae and Thylacinidae. A new species (Godthelp *et al.* 1999), from the early Eocene Tingamarra Local Fauna, southeastern Queensland, is the oldest potential ancestor for the families of Dasyuromorphia. However, this species could be either an ameridelphian or australidelphian marsupial, and its position relative to dasyuromorphians is unclear. At the other end of the time scale, Recent, Pleistocene and Pliocene faunas are dominated by dasyurids (with at least 63 extant species), while Thylacinidae is represented by a single species (*Thylacinus cynocephalus*). The family Myrmecobiidae has no fossil record.

Fossil evidence suggests that the high diversity of dasyurids is a late middle Miocene to Pliocene phenomenon. Since the last substantial revision (Archer 1982b), seven new species of thylacinid have been described, all from late Oligocene to late Miocene deposits (Wroe 1996; Muirhead 1997; Murray 1997; Muirhead and Wroe 1998). Descriptions of four more new taxa are in progress. The rapidly expanding tally of Miocene marsupial carnivore taxa challenges the hypothesis of Flannery (1997), that Australia has not supported a diverse large mammalian carnivore fauna over the last 20 my (Wroe 1996, 1999a). In several highly localised local faunas of Miocene age from Riversleigh the number of large marsupial carnivores (*Dasyurus maculatus* size or greater) equals or exceeds that known for the vast

majority of South American localities from the same epoch (Wroe and Myers 1998). Only two new late Oligocene to late Miocene dasyurid species are known. Wroe (1996, 1997) reassigned a number of pre-Pliocene 'dasyurid' taxa (e.g., *Ankotarinja*, *Keeuna*, *Wakamatha*) to *Dasyuromorphia incertae sedis* on the grounds that their placement within Dasyuridae was based on symplesiomorphies. A new Riversleigh species (Wroe 1999b), of early to middle Miocene age, is the oldest taxon confidently placed within Dasyuridae. It is basal to a monophyletic clade inclusive of the three extant dasyurid subfamilies (Sminthopsinae, Phascogalinae, Dasyurinae), none of which includes fossil taxa older than earliest Pliocene. Wroe (1998, 1999b) considers the possibility that the common origin of extant dasyurid subfamilies may have been as recent as the late Miocene. Alternatively, on the basis of molecular data, Krajewski *et al.* (1997b) postulate that the basal polytomy within Dasyurinae occurred about 15 million years ago. If this is correct then the common ancestor of modern dasyurids is more likely early Miocene in age. Many aspects of the most recent morphology-based review of dasyurid phylogeny (Archer 1982a) have been supported by subsequent molecule-based studies, but significant amendments have also been suggested (Krajewski *et al.* 1997a, 1997b). Notable among these has been the subsumption of Archer's Phascosoricinae within Dasyurinae (Krajewski *et al.* 1994). A fundamental question that remains unanswered, using either morphological or molecular techniques, is the phylogenetic position of Myrmecobiidae.

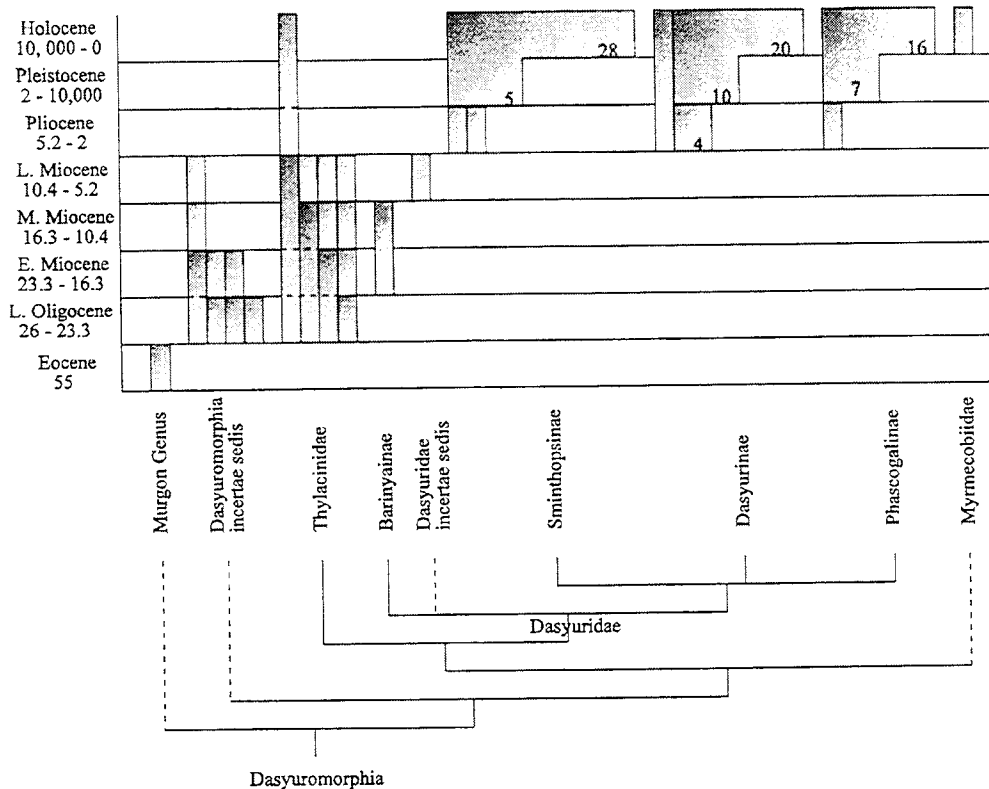


Fig. 1. Australian marsupiacarnivore diversity through time and a cladogram of probable relationships within the group. Uncertain relationships are indicated by dashed lines. Although the Murgon taxon is presented in this context, its ordinal relationships are not necessarily with Dasyuromorphia. Each block represents a distinct species, species diversity is indicated by a number. Blocks that extend without breaks through more than one time period indicate evidently long-surviving species.

BANDICOOT DIVERSITY AND EVOLUTION (PERAMELEMORPHIA, MARSUPIALIA): THE FOSSIL EVIDENCE

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MODERN bandicoots (Order Peramelemorphia) comprise three families: Peramelidae, Peroryctidae and Thylacomyidae. Living peramelids (ordinary bandicoots) include eight species in three genera. Living peroryctids (forest bandicoots) include ten species in four genera. Living thylacomyids (bilbies) include two species (one recently extinct) in one genus. Only four fossil bandicoots have been described to date: the early Pliocene *Ischnodon australis* (Stirton 1955), the early Pliocene *Perameles allinghamensis* (Archer 1976) and *Perameles bowensis* (Muirhead et al. 1997), and the early to middle Miocene *Yarala burchfieldi* (Muirhead and Filan 1995). While *Ischnodon australis*, *P. allinghamensis* and *P. bowensis* have all been placed in

peramelemorphian families dominated by Recent taxa (i.e., Thylacomyidae for *I. australis* and Peramelidae for *P. allinghamensis* and *P. bowensis*), the older *Y. burchfieldi* cannot be placed within any currently recognised peramelemorphian family (Muirhead and Filan 1995). This Tertiary taxon is regarded as representing a new family that is the plesiomorphic sister group of a peramelid/peroryctid/thylacomyid clade (Muirhead 1993, 1994; Fig. 1). No pre-Pleistocene peroryctids are known. Many other fossil peramelemorphians are known but undescribed including taxa from the early Eocene Tingamarra Local Fauna, late Oligocene and early Miocene

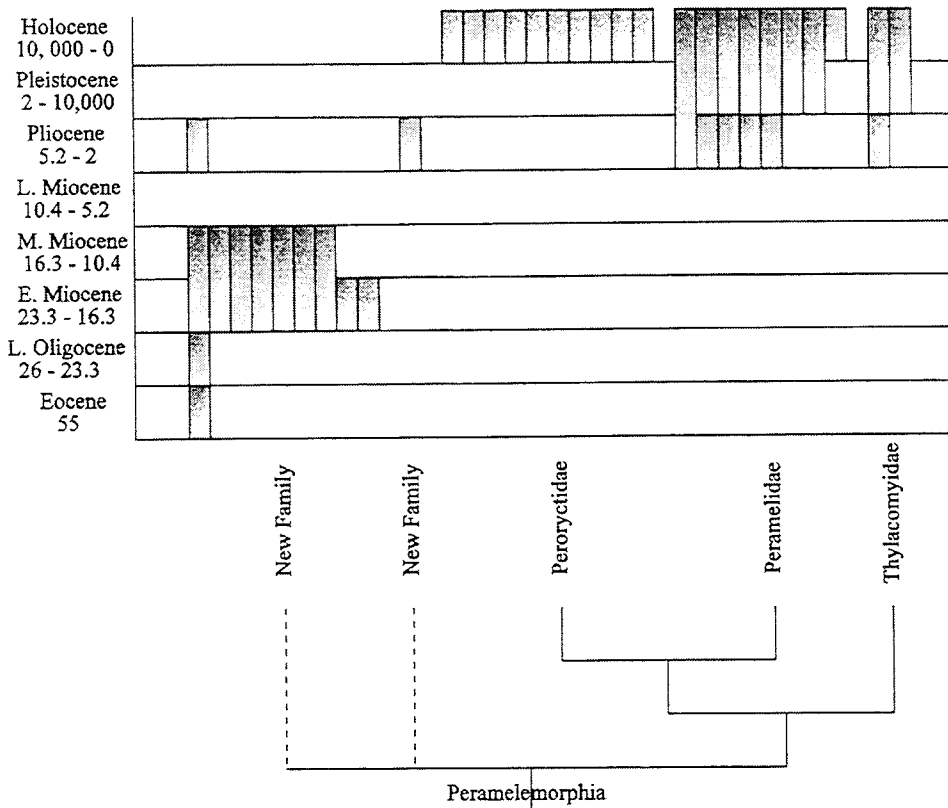


Fig. 1. Bandicoot diversity through time and a cladogram of probable relationships within the group. Uncertain relationships are indicated by dashed lines. Although the Eocene (Murgon) taxon is placed here among the most diverse of the two new families, its familial affinities are uncertain. Each block represents a distinct species. Blocks that extend without breaks through more than one time period indicate apparently long-surviving species.

assemblages of central Australia and late Oligocene to early Pliocene assemblages from Riversleigh in northwestern Queensland and early Pliocene taxa from Bluff Downs in northeastern Queensland (Rich *et al.* 1991b; Archer *et al.* 1993; Mackness *et al.* 1993; Muirhead 1994; Woodburne and Case 1996). Like *Y. burchfieldi*, none of the Oligo-Miocene Riversleigh taxa can be placed within the peroryctid/peramelid/thylacomyid clade (Muirhead 1994). Woodburne and Case (1996) similarly support a relatively late radiation of living peramelemorphians based on undescribed taxa from late Oligocene and early Miocene deposits of central Australia. In deposits younger than middle Miocene, there is no evidence of the archaic taxa typical of Oligo-Miocene deposits, with the possible exception of one species of an otherwise Miocene genus in the early Pliocene Hamilton Local Fauna

(Muirhead 1994; Dawson *et al.* 1999). All other Pliocene to Recent taxa within the peroryctid/peramelid/thylacomyid clade. This distribution suggests a post middle Miocene-pre Pliocene bottleneck for peramelemorphians, followed by a massive radiation of the 'modern' peramelid/peroryctid/thylacomyid clade – a scenario consistent with late Miocene vicariance events between New Guinea and the Australian mainland (Aplin *et al.* 1993). The fossil evidence, however, is in stark contrast to the Oligocene divergence of the living taxa proposed by biochemical analyses (e.g., 32 myo, Baverstock *et al.* 1990a; 24 myo, Baverstock *et al.* 1990b; 25 myo, Kirsch *et al.* 1997). The wide diversity of the Tertiary taxa and the presence of peramelemorphians in early Eocene deposits from Murgon (Archer *et al.* 1993; Godthelp *et al.* 1992) supports a considerably older derivation for the Peramelemorphia, evidence that provides support for the hypothesis of Kirsch *et al.* (1997) which suggests

on the basis of DNA-DNA hybridisation studies other Australian marsupials. that paramelemorphians are distinct from all

THE EVOLUTIONARY HISTORY OF NOTORYCTIDS, YINGABALANARIDS, YALKAPARIDONTIDS AND OTHER ENIGMATIC GROUPS OF AUSTRALIAN MAMMALS

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THERE are several highly autapomorphic Australian mammals whose relationships to other groups remain unclear. These include: notoryctids, yingabalanarids, yalkaparidontids, *Tingamarra porterorum*, *Thylacotinga bartholomaii*, microbiotheriids, *Auskribosphenos nyktos* and other inadequately represented or unassessed taxa (Fig. 1).

Living notoryctids, or marsupial moles, include one or two species (depending on authority) in the genus *Notoryctes*. Aplin and Archer (1987), recognising the distinction of notoryctids as well as long-standing disagreements about their phylogenetic relationships, elevated them to ordinal status as notoryctemorphians, a view generally accepted. For example, Westerman (1991), on the basis of DNA-DNA hybridisation studies, supports the view that they should be a distinct order. At least one distinct genus of notoryctids is present in the early Miocene sediments of Riversleigh (Gott 1988; Archer *et al.* 1994, 1997). In terms of postcranial and dental remains, it is unmistakably notoryctid but it is much more plesiomorphic than the living taxa with a pre-zalambdodont molar morphology that clarifies the otherwise enigmatic structure of the upper molars of species of *Notoryctes*. There is no reason known to us why the Miocene taxon could not be ancestral to the species of *Notoryctes*.

Yingabalanara richardsoni (Archer *et al.* 1990), known so far from two isolated lower molars found in early Miocene sediments of the Riversleigh World Heritage area, was conservatively placed in its own family, Yingabalanaridae. The bizarre molar morphology of this animal has made it impossible to determine

with confidence its inter-ordinal affinities. Discovery of the second molar (currently under study by one us, Y.W.) may help to narrow the range of possibilities considered by Archer *et al.* (1990) which included marsupials, noctilionoid bats, primates, symmetrodonts, zalambdodonts and tribotheres.

Yalkaparidon coheni and *Y. jonesi* (Archer *et al.* 1988), from the late Oligocene to middle Miocene sediments of the Riversleigh World Heritage area, are among the most specialised of any known Australian mammals. They combine unique and completely zalambdodont molars with an enormous, curved, hyselodont first incisor which extends below the whole of the cheektooth row. A skull of the former suggests marsupial affinities but beyond this nothing is certain. Szalay (1994) regards them to be aberrant diprotodontians presumably on the basis of the incisor formula which is I1-3/1. Archer *et al.* (1988) referred this genus to its own order, the Yalkaparidontia, based on its suite of very distinctive autapomorphic features and lack of undoubted synapomorphies with other orders of marsupials.

Tingamarra porterorum (Godthelp *et al.* 1992) was originally described, on the basis of a single lower molar, as a possible condylarth placentar from the early Eocene Tingamarra Local Fauna from Murgon, southeastern Queensland. While a second, larger but otherwise similar taxon has since been recovered from the same deposit, it does not clarify the relationships of this puzzling mammal. It remains a less parsimonious possibility that this is a very distinctive group of marsupials that has converged on placentar tooth morphology.

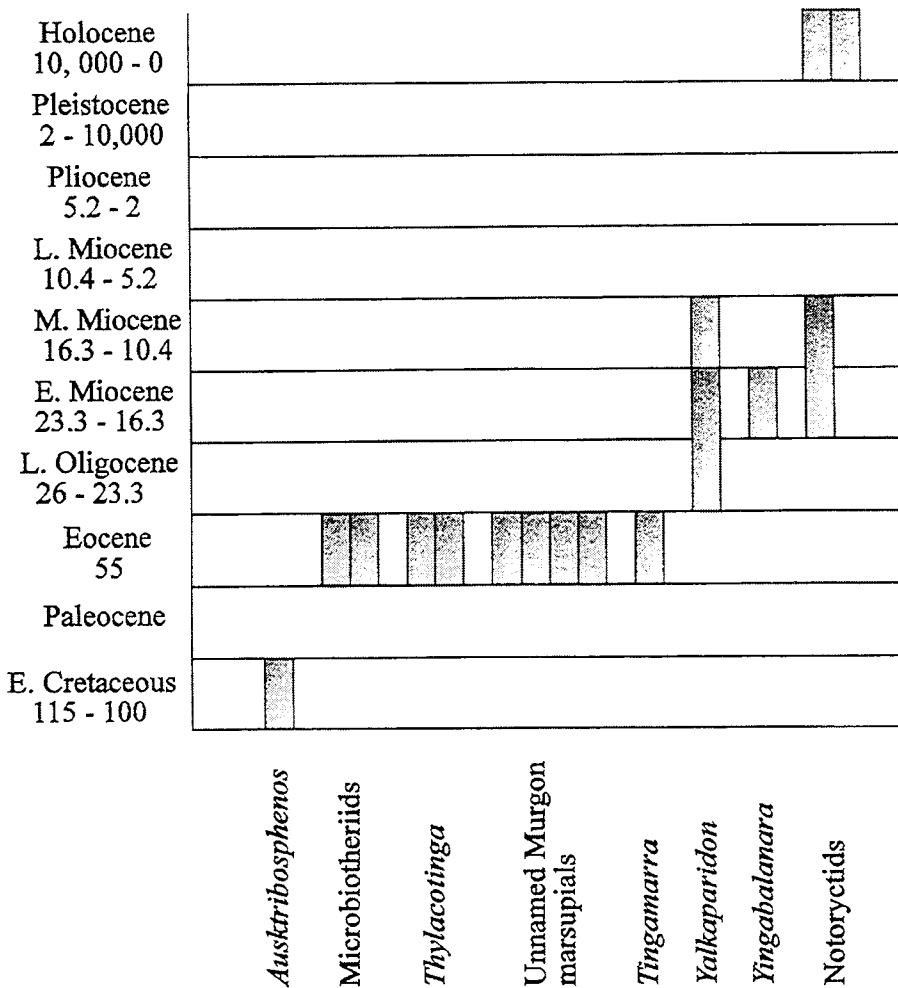


Fig. 1. Diversity through time of notoryctids, yingabalanarids, yalkaparidontids and other enigmatic groups of Australian mammals. Most of these are distinct from each other at the ordinal level. The interordinal relationships of all except (arguably) the microbiotheriids and notoryctids are unclear. Each block represents a distinct species. Blocks that extend without breaks through more than one time period indicate apparently long-surviving species.

Thylacotinga bartholomaii (Archer *et al.* 1993) was described, on the basis of isolated teeth from the early Eocene Tingamarra Local Fauna, as a semi-bunodont marsupial with uncertain ordinal affinities. Although the morphology of this animal is distinctive, bunodont molar morphology in general has been developed independently in several families of

didelphimorphian, polydolopimorphian and diprotodontian marsupials. Similarities to possibly early Paleocene marsupials from Peru are most striking and the subject of ongoing research.

Since microbiotheriids were first hypothesised by Szalay (1982), on the basis of tarsal bone morphology, to have been the sister group (or ancestral) to Australian marsupials,

many other soft-tissue studies have corroborated this broad hypothesis. The details of the relationship are, however, controversial with other authors alternatively suggesting that microbiotheriids are the sister group to a combined dasyuroid/perameloid clade or the sister group of a combined dasyuroid/diprotodontian clade. Discovery of at least two microbiotheriid-like marsupials in the early Eocene Tingamarra Local Fauna may be seen as further support for this intercontinental connection.

Other enigmatic early Eocene taxa in the Tingamarra Local Fauna are less well represented. These range from bunodont to dilambdodont marsupials, most of which are known only from isolated teeth. Some resemble early Eocene groups known from Argentina such as caroloameghiniids. Continuing work on this deposit will almost certainly enable their relationships to be better assessed and these assessments published.

Ausktribosphenos nyktos (Rich *et al.* 1997) was described, on the basis of a dentary with four teeth, from early Cretaceous (~115 million-year-old) sediments at Flat Rocks, Victoria. Its authors suggest that it is most parsimoniously interpreted as a placental mammal. If so, it would be as old as any previously known in the world (e.g., *Prokennalestes* from Mongolia) and would challenge conventional understanding about the time of arrival of placentals into Australia. This interpretation has prompted spirited debate. Examination of the specimen by one of us (M.A.) suggests that *A. nyktos* may represent either an archaic monotreme, autapomorphic peramurid or a unique ordinal-level group that has converged on therian mammals. Some features of *A. nyktos* cited by Rich *et al.* (1997) as indicative of placental affinities (e.g., molar number, decrease in size posteriorly of molars, possession of wide talonids and possibly the presence of a submolariform last premolar) are also characteristic of monotremes. Peramurid affinities are suggested by the trigonid-like nature of the posterior premolar as in other

peramurids including *Peramus* and the putative peramurid *Vincelestes*. Kielan-Jaworowska *et al.* (1998) have suggested that *A. nyktos* may have been derived from early symmetrodont stock based on certain primitive features of the mandible (including the probable presence of attached postdentary bones), the dentition being convergent on a tribosphenic pattern (as may be the case in monotremes: Archer *et al.* 1992). Discovery of additional materials will help to clarify the relationships of this very curious and oldest-known Australian mammal.

A somewhat mammal-like taxon from Lightning Ridge, New South Wales was described, on the basis of an edentulous maxillary fragment, by Rich *et al.* (1989). Alveoli indicate that the teeth were multi-rooted. Although this may well represent a mammal if not a monotreme (Musser, above), it might also represent a derived but non-mammalian synapsid. Until better material is found, this specimen will remain a tantalising mystery.

Several mammalian taxa described as fossils from Australia are even more problematical. Undoubted elephants were described by Richard Owen as *Mastodon australis* (Owen 1844) and *Notelephas australis* (Owen 1882). While it is possible (perhaps even probable) that these fossils were not collected in Australia, collection data indicate otherwise which leaves these records as provocative mysteries.

Other enigmatic mammal fossils include: *Cuscus proculus* DeVis, 1889 probably from the early Pliocene Chinchilla Local Fauna; *Archizonurus securus* DeVis, 1889 probably from the Chinchilla LF; and *Chronozoon australe* DeVis, 1883 from the Chinchilla LF. It is possible that *C. australe* represents a sirenian but the relationships of the other two DeVis taxa which are each represented by a single incomplete postcranial element, are unclear. Details of these descriptions are compiled in Mahoney and Ride (1975).

DIVERSITY AND RELATIONSHIPS OF LIVING AND EXTINCT KOALAS (PHASCOLARCTIDAE, MARSUPIALIA)

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PHASCOLARCTIDAE is an ancient, once diverse marsupial family represented by a single extant species, the Koala *Phascolarctos cinereus*. The family is believed to occupy a key position near the base of the diprotodontian ordinal tree (Archer 1976; Archer and Hand 1987; Myers *et al.* this work). Recent classifications have separated phascolarctids from all other vombatiforms (Myers *et al.* this work, fig. 1). Woodburne (1984) erected the superfamily Phascolarctoidea and Aplin and Archer (1987) the infraorder Phascolarctomorpha, each containing the single family Phascolarctidae. Of living groups, koalas are undoubtedly most closely related to vombatids, a relationship supported by both molecular and morphological data.

Six genera and at least 18 species of koalas are currently recognised (Fig. 1). Superficially there appears to have been an alarming decline in koala diversity. However, at any one time since the late Oligocene koala diversity has normally been low with a maximum of only two species contemporaneous in any given faunal assemblage. In terms of abundance, evidence from the fossil record suggests that koala populations are larger now than at any point in their history, a fact which has been linked to the spread of open sclerophyll forest during the mid-late Miocene. Archer and Hand (1987) hypothesised that a co-evolutionary relationship developed between koalas and eucalypts during the early Miocene, the age of the oldest known association between phascolarctids (e.g. *Litokoala kutjamarpensis*) and eucalypts (Stirton *et al.* 1967). Low-diversity rainforest populations of koalas in Australia's mid- to late Tertiary deposits may have resulted from competition with rapidly diversifying pseudocheirids and phalangerids.

Dental morphology within the family has remained relatively conservative over the last 25 million years, but large size differences between

fossil koalas are apparent. During the Oligo-Miocene, species of *Madakoala* and *Perikoala* and the plesiomorphic Riversleigh koala were similar in size to the modern species, whereas species of *Nimiokoala* and *Litokoala* were half to two-thirds the size of *P. cinereus*. Conversely, in response to Australia's changing climate and vegetation, Plio-Pleistocene koalas increased markedly in size, culminating in the giant Pleistocene *Cundokoala yorkensis* Pledge, 1992 which was twice the size of the modern species. The establishment of *Cundokoala* as a genus distinct from *Phascolarctos* has been questioned (Black and Archer 1997a) and may not be justified on the basis of morphological differences. Consequently, *C. yorkensis* has been regarded here (Fig. 1) as a giant species of *Phascolarctos*. Similarly, features used to distinguish *Phascolarctos maris* Pledge, 1987b from *P. stirtoni* Bartholomai, 1968 may prove to fall within the boundaries of expected intraspecific variation of the latter. However, until this issue is resolved (Black, in prep.), they are treated as distinct species.

Current understanding of phascolarctid relationships based on dental morphology (Black and Archer 1997a) are presented in Figure 1. Species of *Phascolarctos* are the most derived phascolarctids and are most closely related to species of *Litokoala*. A new genus and species of koala from Riversleigh, northwestern Queensland (Black, unpubl.) is the most plesiomorphic koala. Previous analyses (Woodburne *et al.* 1987a; Black and Archer 1997a) tentatively include species of *Koobor* as plesiomorphic phascolarctids yet raise doubts about their position within the family. Pledge (1987a) suggested *Koobor* is more closely aligned with ilariids than phascolarctids but Myers and Archer (1997) found little support for this inclusion. Clarification of *Koobor*'s position within Phascolarctomorpha requires discovery of more complete material.

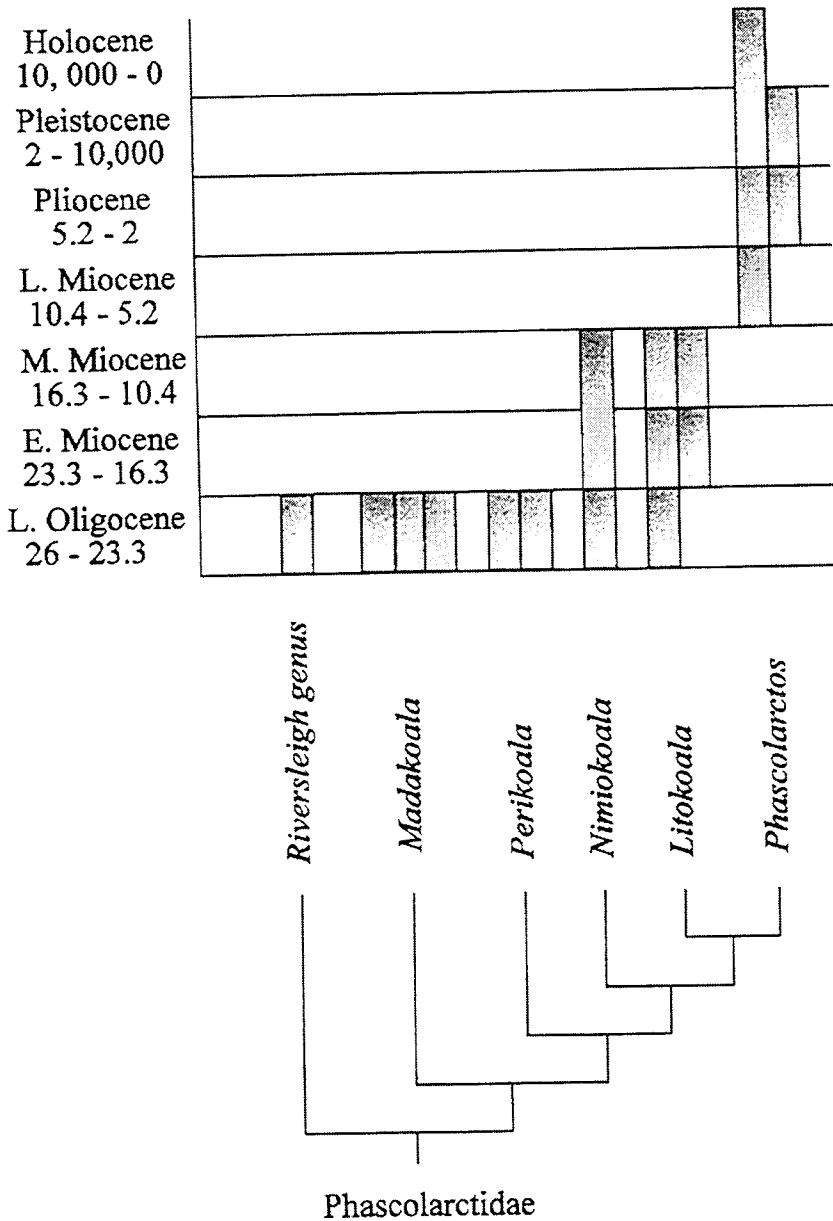


Fig. 1. Koala diversity through time and a cladogram of relationships within the group. Each block represents a distinct species. Blocks that extend without breaks through more than one time period indicate apparently long-surviving species.

DIVERSITY AND EVOLUTIONARY RELATIONSHIPS OF ILARIIDS, WYNYARDIIDS, VOMBATIDS AND RELATED GROUPS OF MARSUPIALS

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PRIOR to their discovery at Riversleigh, ilariids, with koala-like selenodont molar morphology, were known only from late Oligocene (25.5 mya) central Australian deposits: *Ilaria illumidens*, from the Pinpa Local Fauna, Lake Pinpa; and *I. lawsoni*, from the Ditjimanka Local Fauna, Lake Palankarinna (Tedford and Woodburne 1987; Woodburne *et al.* 1994). *Kuterintja ngama* (Pledge 1987), represented by one upper molar from the Ngama Local Fauna, Mammalon Hill, Lake Palankarinna, was slightly younger at approximately 24.8 mya. The geographic range of the latter species was significantly extended with discovery of indistinguishable cranio-dental material from White Hunter Site at Riversleigh, enabling tentative correlation of the central and northern Australian sites (Myers and Archer 1997).

No early to late Miocene sites at Riversleigh (Systems B and C; Creaser 1997) have produced ilariids, despite extensive investigation of sediments this age. While ilariid diversity may have been higher during the early stages of the late Oligocene, it apparently declined towards the latter stages resulting in family-level extinction by the beginning of the Miocene.

Ilariids are considered to be the primitive sister group of the Wynyardiidae and Diprotodontoidea (e.g., Munson 1992). Pledge (1987) considered *K. ngama* to be ancestral to the Pliocene species *Koobor jimbarratti* which would then be regarded as an ilariid rather than a phascolarctid. Myers and Archer (1997) considered the shared dental features of *Koobor* spp. and *Kuterintja ngama* to be symplesiomorphic. *Koobor* was found to be a primitive sister group of wynyardiids plus ilariids. Discovery of lower cheekteeth should resolve *Koobor*'s position within Vombatiformes. In the meantime, we have left the position of *Koobor* as part of an unresolved polychotomy

involving phascolarctids and vombatomorphians (Fig. 1).

The genotypic wynyardiid is a unique specimen, *Wynyardia bassiana*, comprising part of the skeleton and skull but lacking any teeth. Consequently, other species are only referred to this family on the basis, initially, of similar postcranial morphology, and subsequently dental similarity. There are thus at least six species in three genera, found in one or more of four localities: Tasmania (*Wynyardia*, Spencer 1901), early Miocene, about 20-21 my); Frome Basin, South Australia (*Muramura* sp. nov., Pinpa LF; *Namilamadeta snideri* (Rich and Archer 1979), Tarkarooloo LF); Lake Palankarinna, South Australia (*Muramura williamsi* (Pledge 1987), zone A Minkina LF; *Namilamadeta* sp. indet., zone D Ngama LF), and Riversleigh (2-3 *Namilamadeta* spp. nov., Systems A and B), and ranging in age from late Oligocene to early Miocene.

The skeletons of *Muramura* spp. allowed comparison with *Wynyardia* (Tedford *et al.* 1977), and their teeth with *Namilamadeta* (Rich and Archer 1979; Pledge 1987). Skulls are known for all three genera, but basicranial evidence for interrelationships is still to be assessed. Dentally, *Muramura* appears to be more plesiomorphic than *Namilamadeta*, and the skull, too, is more primitive. The considerably smaller skull of *Wynyardia* shows more resemblance to *Namilamadeta* from some Riversleigh sites, but still differs from all species. In general terms, the skulls of wynyardiids show remarkable gross similarities to those of the plesiomorphic wombat *Warendja wakefieldi* (Pledge 1992). Postcranially, *Wynyardia* and *Muramura* species are similar where they can be compared, and show notable similarities with wombats, although they are more plesiomorphic.

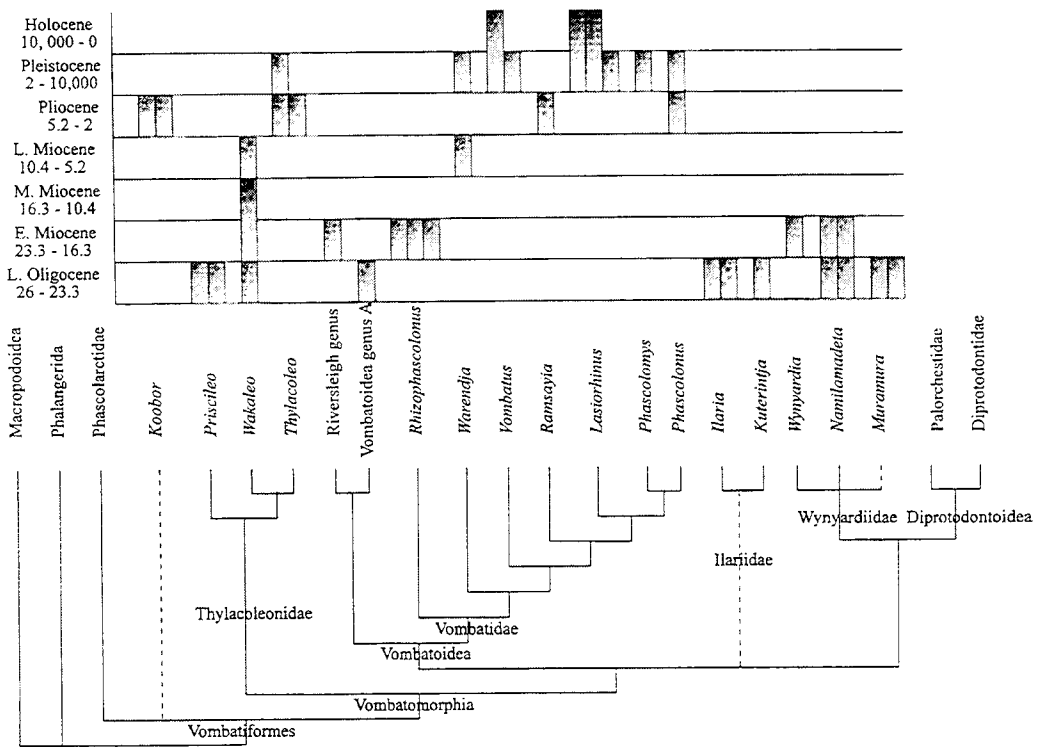


Fig. 1. Diversity through time and a cladogram of probable interfamilial and intergeneric relationships of ilariids, wynyardiids, vombatids, thylacoleonids and related groups of marsupials. Uncertain relationships are indicated by dashed lines. Each block represents a distinct species. Blocks that extend without breaks through more than one time period indicate apparently long-surviving species.

Phylogenetic relationships among vombatoids remain unresolved. Work in progress (Krikmann 1993; M. Archer and A. Krikmann) suggests there were three families. The first, from early Miocene Riversleigh deposits and the late Oligocene Pinpa Local Fauna (Tedford *et al.* 1977, as 'Vombatoidea Genus A'), is represented by primitive, low-crowned, browsing wombats with complex molar morphology and rooted teeth. The second includes *Rhizophascolonus crowcrofti* and at least two other wombat species with rooted but high-crowned teeth from the early to middle Miocene of Riversleigh and the central Australian Kutjamarpu Local Fauna. The third, Vombatidae, includes a

number of grazing wombat species with unrooted teeth, the earliest of which is a new species of *Warendja* from the late Miocene Encore Local Fauna of Riversleigh. However, the greatest diversity of vombatids did not occur until the early Pliocene (*Phascolonus* and *Ramsayia*) and Pleistocene (*Warendja*, *Phascolomys*, *Vombatus*, *Lasiorhinus*), with the increase paralleling the drying out and opening up of the continent and consequent proliferation of grasslands. There are three extant vombatids, species of *Vombatus* and *Lasiorhinus*, one of which (*Lasiorhinus krefftii*) is seriously endangered.

DIVERSITY AND RELATIONSHIPS OF DIPROTODONTOID MARSUPIALS

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TWO families of diprotodontoids are currently recognised: Palorchestidae (2 genera, 7 species); and Diprotodontidae containing Zygomaturinae (13 genera, 25 species) and Diprotodontinae (8 genera, 12 species). A third diprotodontid subfamily, the Nototheriinae (Stirton *et al.* 1967), is no longer considered valid (Archer 1977). A yet-to-be-described Pleistocene genus with two

species that have both zygomaturine and diprotodontine features may constitute a third diprotodontid subfamily. The time at which Palorchestidae and Diprotodontidae diverged from a common ancestor is currently not known, but both families were distinct by the late Oligocene (Fig. 1).

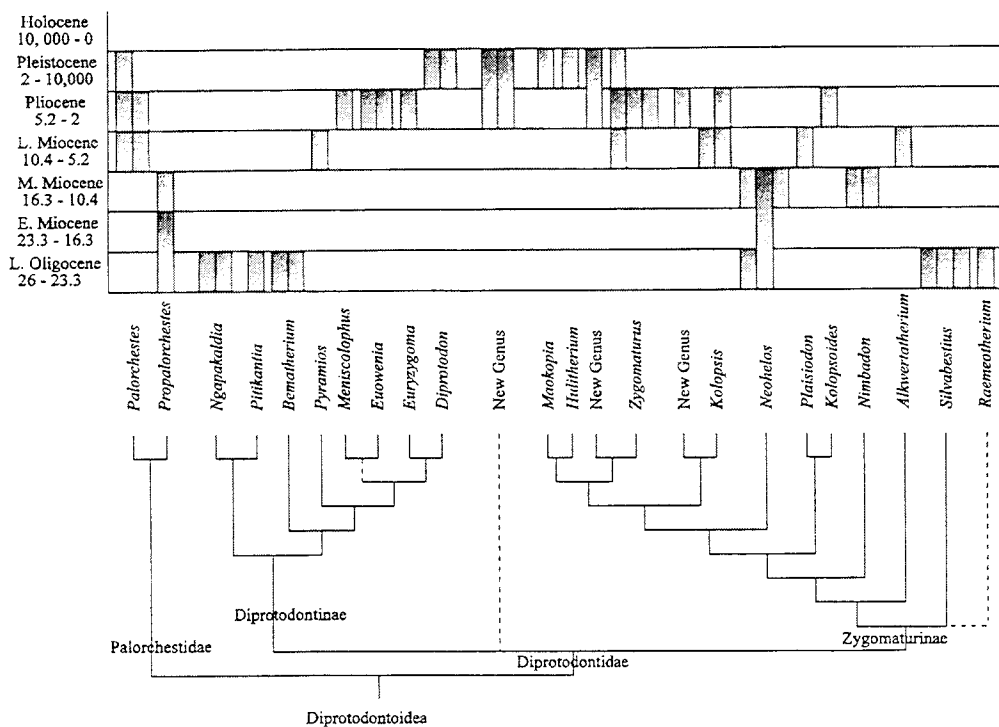


Fig. 1. Diprotodontoid diversity through time and a cladogram of probable interfamilial and intergeneric relationships. Uncertain relationships are indicated by dashed lines. Each block represents a distinct species. Blocks that extend without breaks through more than one time period indicate apparently long-surviving species.

Zygomaturine diprotodontoids exhibit a higher diversity in Tertiary fossil assemblages than either diprotodontines or palorchestids possibly indicating an ability to exploit a greater range of environments (Black 1997b). Palorchestids are rare components of fossil assemblages which may indicate a solitary habit. Normally, no more than one species is present in faunal assemblages spanning the last 25 million years. Similarly,

diprotodontines, although prolific in the late Oligocene and early Miocene, are rare throughout the rest of the Miocene but then diversify again in the Plio-Pleistocene. Drying of the Australian continent resulted in development of gigantic, highly specialised forms characterised by features useful for processing coarser food (e.g. diastemal crests and elaboration of blades in the dentition). In contrast, the New Guinea diprotodontoid

radiation consists of 'dwarf' zygomatrine species variously interpreted as either relict populations from Miocene Australia (Flannery 1988) or a mid-to-late Pliocene colonisation by a few derived Australian genera (Murray 1992). The reasons for the eventual extinction of the entire diprotodontoid radiation by the end of the Pleistocene has yet to be determined but it was probably a combination of factors including interaction with early humans, modification of the Australian environment by fire (which favoured the development of grasslands) and natural cycles of climatic change.

Interpretation of the phylogenetic relationships of diprotodontoids is hampered by the fact that many taxa are known only from isolated elements and there is a general paucity of late Miocene and early Pliocene material. Analysis of variation in several groups has revealed sexual dimorphism and ontogenetic variation which has not been taken into account in some taxonomic assignments. There has also been an underestimation of diversity in the late Tertiary with assignment often made to taxonomic 'waste bins' like 'notothere'. The current understanding of phylogenetic relationships is shown in Figure 1. Monophyly of the group has been questioned

(Archer 1984; Aplin and Archer 1987; Murray 1990a), there being few synapomorphies recognised. Within Diprotodontidae, zygomatrines appear to have been derived from a primitive diprotodontine-like form in which the parastyle on P3 was reduced, a theory first proposed by Stirton *et al.* (1967) and later confirmed by the discovery and analysis of dentitions of *Silvabestius michaelbirti* from Riversleigh (Black and Archer 1997b). This species is believed to be antecedent to the entire zygomatrine radiation (Black and Archer 1997b). Previous authors (e.g. Aplin and Archer 1987; Marshall *et al.* 1990) include *Ngapakaldia* and *Pitikantia* within Palorchestidae on the basis of similarities in the basicranium, features since recognised (e.g. Archer 1984; Murray 1986, 1990a) as plesiomorphic for Vombatomorpha. Murray's (1990b) description of *Propalorchestes* dentitions demonstrates that it is the plesiomorphic sister group of *Palorchestes*, exhibiting subselenodont molars transitional between selenodont wynyardiids and the fully bilophodont molars of *Palorchestes*. Consequently, *Ngapakaldia* and *Pitikantia* are currently recognised as primitive diprotodontines (Murray 1990; Black 1997).

DIVERSITY AND EVOLUTIONARY RELATIONSHIPS OF MARSUPIAL LIONS

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THE marsupial lion family Thylacoleonidae has a fossil history that spans the late Oligocene through to late Pleistocene. There are three genera and a total of nine species (Myers *et al.* this work, fig. 1). The oldest member of the family is the late Oligocene cat-sized *Priscileo pitikantensis* from central Australia (Rauscher 1987). A second, smaller species, *P. roskellyae*, has been described on the basis of the dentition and a nearly complete skull from early Miocene sediments of the Riversleigh World Heritage area (Gillespie 1997). The dog- to leopard-sized species of *Wakaleo* include *W. oldfieldi* from the early Miocene Kutjamarpu Local Fauna of South Australia and faunal assemblages at Riversleigh, *W. vanderleuri* (also known from a complete skull) from the middle Miocene Bullock Creek Local Fauna of the Northern Territory, and *W. alcootaensis* from the late Miocene Alcoota Local Fauna of the Northern Territory (Clemens and Plane 1974; Archer and Rich 1982; Murray *et al.* 1987). A fourth species

representing a smaller, more plesiomorphic form is currently being described (Gillespie in press) from late Oligocene sediments at Riversleigh (Archer *et al.* 1997c). The dog- to lion-sized species of *Thylacoleo* (Wroe *et al.* submitted) include *T. crassidentatus* and *T. hilli*, both from widespread early Pliocene deposits, and *T. carnifex* which is very widespread in Pleistocene deposits (Archer and Dawson 1982).

Lineages of both *Wakaleo* and *Thylacoleo* demonstrate morphocline changes through time that link otherwise distinct species. These changes generally include an increase in size, an increase in the proportional length of P3/3, and loss or reduction of the posterior molars (Murray and Megirian 1990; Archer and Dawson 1982). Although Tertiary marsupial lions are not common as fossils (a fact presumably reflecting their ecological role as carnivores), what is known suggests that up to two different-sized species

coexisted in single ecosystems. For example, in the late Oligocene to early Miocene deposits of Riversleigh, a small species of *Priscileo* coexisted with a much larger species of *Wakaleo*. Similarly, in the Bow Local Fauna of New South Wales, the small *Thylacoleo hilli* coexisted with the much larger *T. crassidentatus* (Archer and Dawson 1982).

Hypothetical intrafamilial relationships for thylacoleonids are shown as part of Figure 1 in Myers *et al.* (this work). Understanding of these relationships has changed with discovery of new

Riversleigh taxa. Previously the structural differences between species of *Wakaleo* and *Thylacoleo*, especially loss of P¹ and P² in *Wakaleo*, did not support an ancestor/descendant relationship between the two genera (Clemens and Plane 1976). However, the presence of these teeth in a new species of *Wakaleo* from Riversleigh makes it possible to argue that this lineage was ancestral to the species of *Thylacoleo*. In addition, species of *Priscileo* exhibit no features that prevent them from being ancestral to species of *Wakaleo* and *Thylacoleo*.

DIVERSITY AND EVOLUTION OF PHALANGERID, EKTOPODONTID, MIRALINID AND PILKIPILDRID MARSUPIALS

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THE superfamily Phalangoidea contains at least three families: Phalangeridae, the extinct Miralinidae and Ektopodontidae. Pilkipildridae may also belong here, but there is significant doubt about its relationships (e.g., Archer *et al.* 1987; Brammall and Archer this work).

Phalangerids are found throughout much of Meganesia. There are six genera: the bear cuscus *Ailurops*; cuscuses *Phalanger*, *Strigocuscus* and *Spilococus*; brush-tailed possums *Trichosurus*; and scaly-tailed possums *Wyulda*. Four phalangerid species have been described from the fossil record: *Trichosurus dicksoni* and *Strigocuscus reidi* from Miocene assemblages in the Riversleigh World Heritage area of northwestern Queensland (Flannery and Archer 1987) and *Trichosurus hamiltonensis* and *Strigocuscus notialis* from the early Pliocene Hamilton Local Fauna of Victoria (Flannery *et al.* 1987b). A species of *Wyulda* has also been reported but not named from the Miocene sediments of Riversleigh (Archer *et al.* 1994).

Miralinids include species of *Miralina* from Oligo-Miocene sediments in central Australia (Woodburne *et al.* 1987b) and an undescribed genus and species from the early Miocene of Riversleigh.

Four genera of ektopodontids have been described: *Ektopodon* and *Chunia* from Oligo-Miocene assemblages in central Australia (Woodburne and Clemens 1986a; Woodburne *et al.* 1994); and *Darcius* from the early Pliocene Hamilton Local Fauna of Victoria (Rich 1986).

Another undescribed genus is known from Riversleigh. An unnamed and as yet generically unassessed ektopodontid is present in the early Pleistocene Portland Local Fauna of Victoria.

Two genera of pilkipildrids have been described: *Djilgaringa* from Riversleigh and central Australia; and *Pilkipildra* from central Australia (Archer *et al.* 1987). Additional potentially distinct pilkipildrid material from Riversleigh is currently under study by M.O. Woodburne.

Relationships between phalangerids, miralinids, ektopodontids and pilkipildrids are unclear (Fig. 1). Historically, the very strange teeth of ektopodontids made it difficult to place them phylogenetically. With discovery of the more 'conventional' molars of species of *Chunia* and the less specialised dentitions of miralinids, it became apparent that ektopodontids were at least distantly related to phalangerids (Tedford *et al.* 1977; Woodburne and Clemens 1986a; Woodburne *et al.* 1987b). Miralinids and ektopodontids are now thought to be sister groups, and together form the sister group of phalangerids (Aplin and Archer 1987; Woodburne *et al.* 1987b). Pilkipildrids are considered *incertae sedis* by Archer *et al.* (1987). They suggested that this family is either the sister group of petauroids, the sister group of phalangeroids or part of an unresolved trichotomy.

Relationships within Ektopodontidae and Phalangeridae are still contentious. *Chunia* is

considered to be the most plesiomorphic ektopodontid, and *Ektopodon* and *Darcus* are derived sister groups (Woodburne and Clemens 1986b). The new genus from Riversleigh may put these relationships in doubt. Phalangerids were originally separated into four genera: *Ailurops*, *Phalanger*, *Trichosurus* and *Wyulda*. *Phalanger* has since been considered paraphyletic and split into three genera: *Phalanger*, *Strigocuscus* and

Spilococus (Flannery *et al.* 1987a). *Strigocuscus* was placed as the sister genus of *Trichosurus* plus *Wyulda* based on morphological characters (*ibid.*). Molecular studies, however, placed some members of *Strigocuscus* back within *Phalanger* (Colgan *et al.* 1993). The uncertain position of *Strigocuscus gymnotis* within Phalangeridae could affect generic allocation of fossil species originally placed in this genus (*viz.*, *S. reidi* and *S. notialis*).

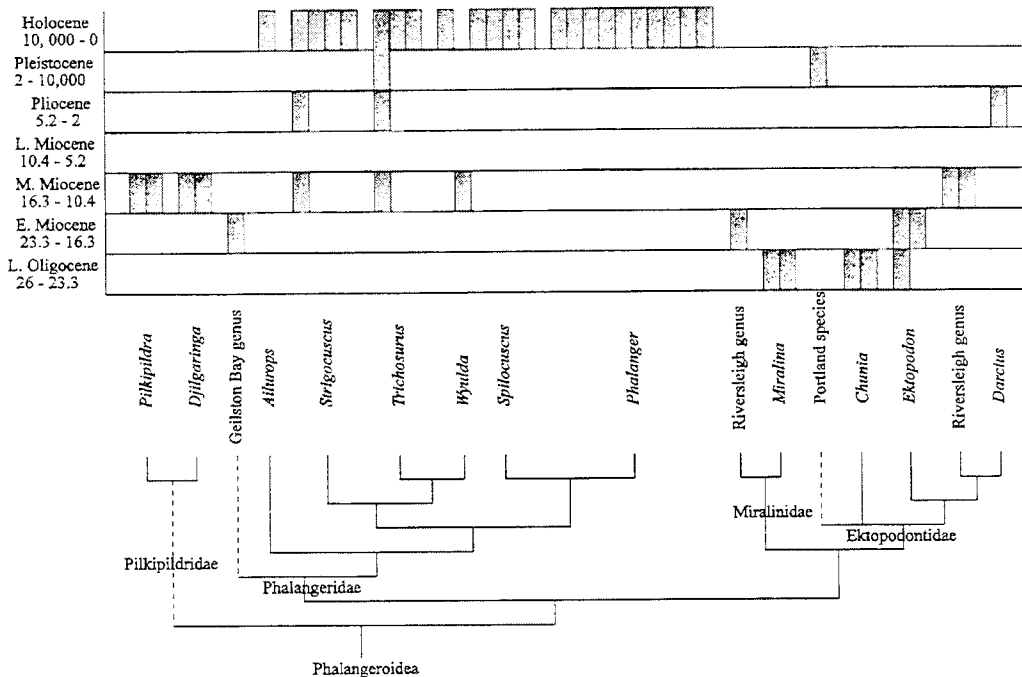


Fig. 1. Diversity through time and a cladogram of probable interfamilial and intergeneric relationships of phalangerid, ektopodontid, miralinid and pilkipildrid marsupials. Uncertain relationships are indicated by dashed lines. Each block represents a distinct species. Blocks that extend without breaks through more than one time period indicate apparently long-surviving species.

LIVING AND EXTINCT PETAURIDS, ACROBATIDS, TARSIPEDIDS AND BURRAMYIDS (MARSUPIALIA): RELATIONSHIPS AND DIVERSITY THROUGH TIME

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THE smallest contemporary possums of Australia and New Guinea are placed in four families: the Petauridae (*Petaurus*, *Gymnobelideus*, *Dactylopsila*); Acrobatidae (*Acrobates*, *Distoechurus*); Tarsipedidae (*Tarsipes*); and Burramyidae (*Cercartetus*, *Burramys*) (Aplin and Archer 1987; Strahan 1995). All living representatives (except *Burramys parvus*) are

arboreal although some live in heath (tarsipedids and some species of *Cercartetus*). All are scansorial. The species of two genera (*Petaurus*, *Acrobates*) are also gliders. All of these families have a Tertiary as well as Quaternary record except tarsipedids which as yet have no pre-Pleistocene record (Fig. 1).

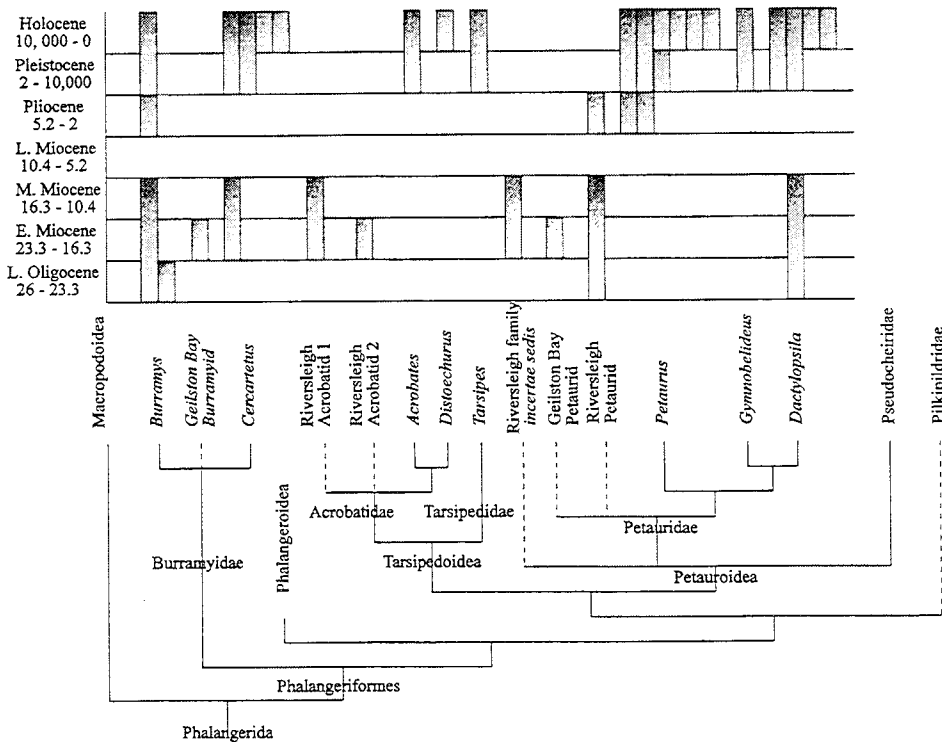


Fig. 1. Diversity through time and a cladogram of probable interfamilial and intergeneric relationships of acrobatids, tarsipedids and burramyids. Uncertain relationships are indicated by dashed lines. Each block represents a distinct species. Blocks that extend without breaks through more than one time period indicate apparently long-surviving species

Fossil burramyids ('pygmy possums') include a plethora of relatively specialised species of *Burramys* with plagiulacoid premolars, all so far only known from lowland rainforest

assemblages of late Oligocene (taxa in the Ngama and diverse Riversleigh assemblages; Pledge 1987c; Brammall and Archer 1997) to early Pliocene age (Turnbull *et al.* 1987b) in

northwestern Queensland, the Tirari Desert and western Victoria. An unnamed burramyid was reported from the early Miocene Geilston Bay Local Fauna (Tedford *et al.* 1975). At least one (unnamed) Tertiary fossil species of *Cercartetus* is known from Miocene sediments at Riversleigh. Records of large species ‘...similar in some ways to the living *Cercartetus*...’ (e.g., Woodburne *et al.* 1985, p355) from late Oligocene deposits of the Tirari Desert and Frome Embayment actually refer to pilkipildrid possums (Crosby *et al.* this work).

There are at least two undescribed acrobatids (‘feather-tail possums’) from early and middle Miocene deposits of Riversleigh that represent this highly specialised group. The living arboreal *Distoechurus pennatus* is a rainforest inhabitant in contrast to the glider *Acrobates pygmaeus* which inhabits wet and dry sclerophyll forests.

The fossil record of petaurids is more diverse.

Dactylopsila (‘striped possums’), modern species of which are strictly rainforest inhabitants, have been found in late Oligocene to middle Miocene deposits at Riversleigh. The oldest representatives of the genus *Petaurus* are from the early Pliocene Hamilton Local Fauna in Victoria. Although the postcranial anatomy of the Pliocene taxa is unknown, all modern species of this genus are gliders. Another generically distinctive group of petaurids, from late Oligocene to middle Miocene deposits at Riversleigh, appears to be closely related to an early Pliocene taxon from the Rackham’s Roost Local Fauna of Riversleigh. At least one petauroid is interpreted to be among the unnamed taxa from the early Miocene Geilston Bay Local Fauna of Tasmania (Tedford and Kemp 1998). A highly distinctive petaurid-like group, known from the early to middle Miocene of Riversleigh, appears to represent a plesiomorphic sister group to Petauridae.

LIVING AND EXTINCT PSEUDOCHEIRIDS (MARSUPIALIA, PSEUDOCHEIRIDAE): PHYLOGENETIC RELATIONSHIPS AND CHANGES IN DIVERSITY THROUGH TIME

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THE family Pseudocheiridae is comprised of ten genera of ringtail possums and greater gliders. Six genera (*Hemibelideus*, *Petauroides*, *Pseudochirops*, *Petroseudes*, *Pseudocheirus* and *Pseudochirulus*) contain extant as well as extinct species; four genera (*Paljara*, *Pildra*, *Marlu* and *Pseudokoala*) contain only extinct species. The highest species-level diversity for this family occurs today in rainforest environments of northern Australia and New Guinea. The only living species found in relatively drier areas of Australia, such as open forests and woodlands, are the Common Ringtail (*Pseudocheirus peregrinus*), Greater Glider (*Petauroides volans*) and Rock Ringtail (*Petroseudes dahli*).

Pseudocheirid species diversity was greater in the late Oligocene to early Miocene than at present (Fig. 1) with, for example, up to nine species

present in a single local fauna at Riversleigh (Archer 1992; Archer *et al.* 1994).

The oldest-known pseudocheirids are late Oligocene in age from the Tirari Desert and Frome Basin of South Australia and the Riversleigh World Heritage area of northwestern Queensland. These are referable to the genera *Pildra*, *Marlu* and *Paljara* (Woodburne *et al.* 1987c; Archer 1992; Archer *et al.* 1997a). The species of *Paljara* include the most plesiomorphic known pseudocheirids which appear to retain, for example, well-developed paraconids on the first lower molar. Current research on undescribed Riversleigh specimens referable to *Paljara* indicates that more than one species and possibly up to three species are represented by the material. The species of *Pildra* are the next most plesiomorphic and are highly diverse in the

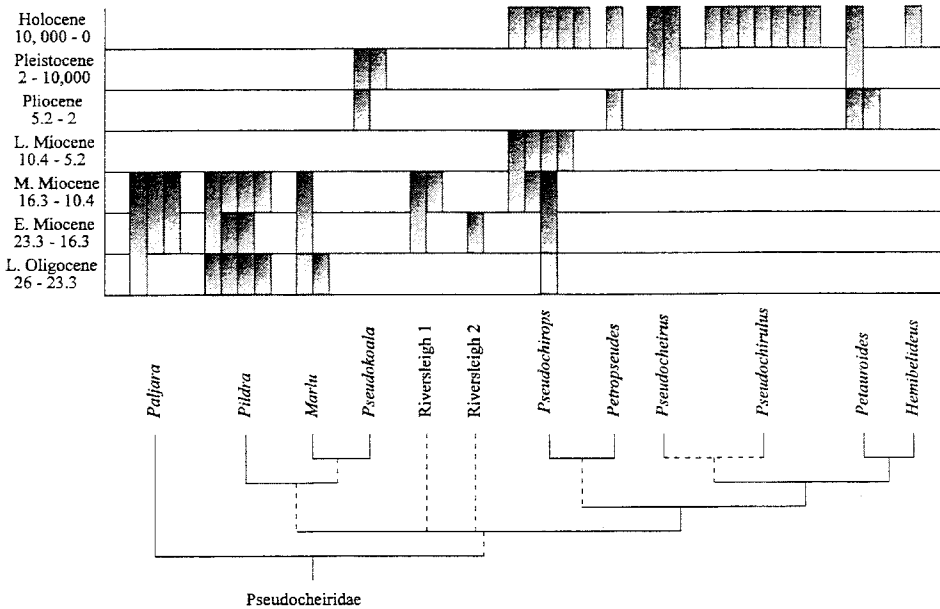


Fig. 1. Pseudocheirid diversity through time and a cladogram of probable intergeneric relationships. Uncertain relationships are indicated by dashed lines. Each block represents a distinct species. Blocks that extend without breaks through more than one time period indicate apparently long-surviving species.

Oligocene to Miocene sediments of South Australia and Queensland. Species of *Marlu* are less diverse being known from possibly only two species in the Tirari Desert deposits, one of which may also be represented at Riversleigh.

Species of *Pseudokoala* are known from the early Pliocene Hamilton LF and from various Pleistocene deposits in South Australia and New South Wales. Archer *et al.* (1997a) suggest that the Miocene or early Pliocene genus *Corracheirus* Pledge, 1992 is a junior synonym of *Pseudokoala* and that all species of this genus occupied rainforest. *Pseudokoala cathysantamaria* from the early Pleistocene Portland Local Fauna of Victoria was a giant megafaunal ringtail that weighed possibly ten kilograms.

Of the extant ringtail genera, *Pseudocheirops* has the oldest record with a minimum of three as yet unnamed species occurring in Oligo-Miocene deposits at Riversleigh. Another as yet unnamed extinct species possibly referable to *Pseudocheirops* occurs in the late Miocene Alcoota LF (Archer and Bartholomai 1978). *Petropseudes*, which some authors regard to be a junior synonym of *Pseudocheirops*, has a fossil record that extends

back to the early Pliocene at Riversleigh. From the same early Pliocene Riversleigh deposit also comes the oldest record of the living species, *P. dahli*. *Petauroides* may be represented by the early Pliocene species *P. stirtoni* and *marshalli* (Turnbull and Lundelius 1970; Turnbull *et al.* 1987a; Archer 1984). There are no pre-Pleistocene records for *Pseudocheirus*, *Pseudochirulus* or *Hemibelideus*.

Considered overall, a massive radiation of archaic ringtails clearly characterised the late Oligocene to middle Miocene. The only 'modern' group represented among these is *Pseudocheirops*. We suspect that our sustained failure to find Tertiary records for *Pseudochirulus* and *Pseudocheirus* indicate that they were a late Miocene to Pliocene and perhaps Pleistocene radiation in New Guinea and Australia respectively.

Intergeneric phylogenetic relationships of pseudocheirids are either unresolved or controversial (Fig. 1). Woodburne *et al.* (1987c) have proposed that *Pildra* and the common ancestor of *Marlu* and *Pseudokoala* are sister taxa. However, Springer (1993), on the basis of dental synapomorphies, suggests in contrast that species of *Marlu*, *Pseudokoala* and extant pseudocheirids may form a clade to the exclusion of species of *Pildra* and *Paljara*. Relationships of extinct to extant ringtails

have not been clarified, in part because of the incomplete fossil record. Many different fields of research (molecular and morphological) provide evidence to suggest that, among extant genera, *Hemibelideus* and *Petauroides* are sister taxa, *Pseudochirops* and *Petropseudes* are sister taxa (Archer 1984; Baverstock 1984; Baverstock *et al.* 1987, 1990c; Kirsch *et al.* 1997; McKay 1984; McQuade 1984; Springer 1993; Springer *et al.* 1992), and *Pseudochirulus* forms a monophyletic group (Archer 1984; Baverstock *et al.* 1990; Flannery 1994; Springer 1993; Springer *et al.* 1992). The phylogenetic position of *Pseudocheirus* and the trichotomy between *Hemibelideus-Petauroides*, *Pseudochirops-Petropseudes* and *Pseudochirulus* remain unresolved because of disagreements about the most appropriate methods of phylogenetic analysis.

Petauroids (pseudocheirids plus petaurids) appear to be most closely related to tarsipedoids (acrobatids and tarsipedids) (Aplin and Archer 1987; Baverstock 1984; Baverstock *et al.* 1987; Kirsch *et al.* 1997).

The relationships of petauroids to burramyoids and phalangeroids have not been clarified; see Springer and Kirsch (1991) and Springer and Woodburne (1989) for conflicting phylogenetic conclusions.

Archer (1984) and Woodburne *et al.* (1987c) have suggested the possibility that pseudocheirids are the outgroup to all other phalangeridans because of their retention of many plesiomorphic dental features (e.g., complete diprotodontian dental formula, paraconid on the first lower molar and a well-developed styler shelf on the upper molars).

EVOLUTION AND DIVERSITY OF KANGAROOS (MACROPODOIDEA, MARSUPIALIA)

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NUMEROUS attempts have been made to unravel the complexities of kangaroo phylogeny. Character systems utilised in such analyses include: morphological (e.g., Bensley 1903; Raven and Gregory 1946; Tate 1948; Archer 1984; Flannery 1989); cytological (e.g., Sharman 1989); immunological (e.g., Kirsch 1977; Baverstock *et al.* 1989, 1990b); and molecular biology (e.g., Westerman *et al.* 1990; Kirsch and Foeste 1995). Earlier attempts, particularly those reliant on morphological characters, were hampered by the lack of an adequate fossil record extending much further back than the Pliocene. That situation has improved with discovery of older Tertiary kangaroos in a variety of deposits in the Northern Territory (late Miocene deposits at Alcoota and Bullock Creek), South Australia (deposits in the Lake Eyre and Frome Basins) and Queensland (Riversleigh). Riversleigh is particularly important because it includes sites ranging from late Oligocene to Holocene in age, and which yield very well preserved kangaroo fossil remains, including complete skulls and some articulated skeletons for many taxa.

Flannery's (1989) analysis of macropodoid phylogeny is the first comprehensive attempt to incorporate data obtained from Oligo-Miocene taxa. Notable among these are lophodont

representatives of two previously unknown groups: Balbarinae and Bulungamayinae, both described by Flannery *et al.* (1983). They assigned Balbarinae to Macropodidae and Bulungamayinae to Potoroidae. Case (1984) disagrees with placement of Bulungamayinae within Potoroidae, maintaining that lophodony represents a macropodid synapomorphy. Flannery's (1989) phylogenetic analysis supports placement of Bulungamayinae as a monophyletic group within Potoroidae, but indicates Balbarinae as a likely paraphyletic macropodid group, directly ancestral to both Macropodinae and Sthenurinae.

Cooke (1997a) indicates that lophodony has arisen independently in these two subfamilies, representing another example of the rampant evolutionary convergence that plagues kangaroo phylogenetics. Cooke (1997a, in press) argues that characters such as a laterally broad M₁ trigonid, absence of ornamentation of the posterior face of the hypolophid of lower molars, elongate permanent premolars and parietal-aiisphenoid contact on the lateral wall of the cranium, represent synapomorphies uniting bulungamayines and macropodids. A phylogenetic analysis by Cooke (1997b) incorporates cranial and dental characters present

in remains discovered at Riversleigh subsequent to Flannery's (1989) analysis. It indicates that Balbarinae represent a monophyletic group, basal to all other macropodoids (and therefore should be elevated to familial status as Balbaridae). This analysis supports the monophyly of Hypsiprymodontidae (Ride 1993) but indicates that bulungamayines are members of a large, pectinately branching clade that includes as bulungamayines some taxa previously regarded to be potoroines (*Bettongia moyesi*, *Wakiewakie*

lawsoni and *Purtia mosaicus*), sthenurines and macropodines. Bulungamayines appear in this analysis to be a paraphyletic stem group, occupying much the same position as Flannery (1989) argued for balbarines.

Recent studies of cranial remains of the propleopine *Ekaltadeta ima* by Wroe *et al.* (1998) indicate potential synapomorphies uniting Balbarinae and Propleopinae which casts some doubt on the monophyly of Hypsiprymodontidae (*sensu* Ride 1993; see Fig. 1).

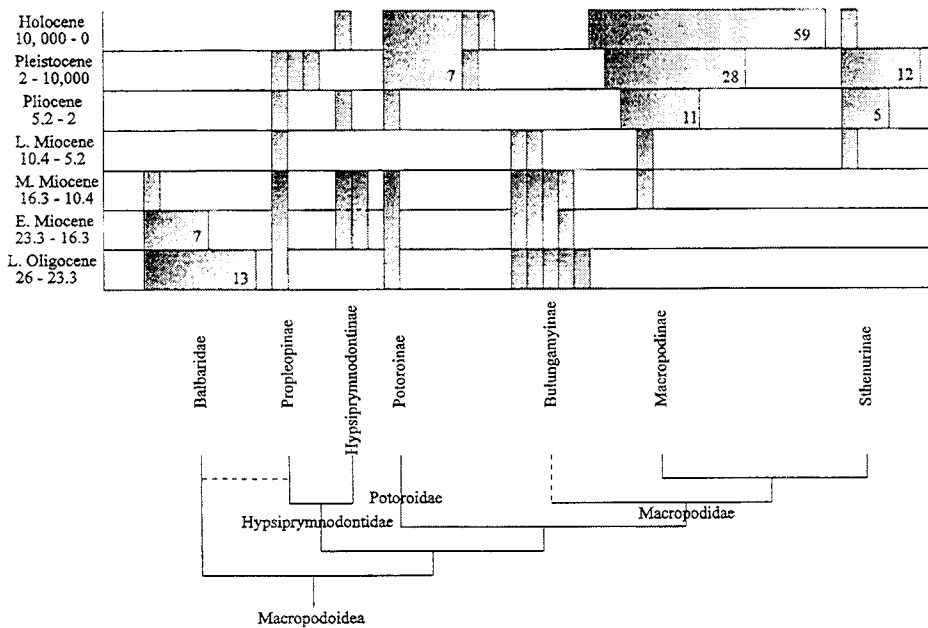


Fig. 1. Kangaroo diversity through time and a cladogram of probable interfamilial and subfamilial relationships. Uncertain relationships are indicated by dashed lines. Particularly uncertain is the position of Propleopinae. Each block represents a distinct species unless species diversity is indicated by a number. Blocks that extend without breaks through more than one time period indicate apparently long-surviving species. Unindicated are many Pleistocene occurrences of living macropodids among the undifferentiated Pleistocene cohort.

More recent phylogenetic analysis of macropodoids by Kear (1998), utilising postcranial morphology, supports the monophyly of balbarines and their status as a basal macropodoid group. However, it also suggests that Bulungamayinae may be polyphyletic.

Uncertainties indicated in Figure 1 are a measure of the lack of resolution about key aspects of macropodoid phylogeny. However, continuing discovery of new fossil material from Riversleigh and elsewhere supplies new data which, together with that contributed from other fields, enable existing hypotheses to be continuously tested. Evidence from postcranial

fossil remains of the kind routinely found at Riversleigh will be of particular importance in this regard.

Current research by Kear (1998) on postcranial morphology of Riversleigh macropodoids suggests that the transition from more quadrupedal gaits to bipedal hopping occurred during the late Oligocene to early Miocene. Assessment of postcranial remains of a late Oligocene Riversleigh balbarine (*Nambaroo*) indicates that the forelimb to hindlimb ratio was comparable to that of *Hypsiprymnodon moschatus* (a habitual quadruped; Johnson and Strahan 1982). Other features also suggest that this animal

did not hop. These include reduced quadratus femoris and adductor magnus muscle scars on the femur, shortened tibia/fibula contact and a short, broad foot. Morphology of the forelimb also hints at quadrupedalism and, combined with a high degree of lateral flexibility in the pedal digits and a well developed first toe, may be indicative of albeit limited climbing ability.

Middle to late Miocene macropodoids such as the Riversleigh bulungamayines *Ganguroo bilamina* Cooke, 1997a, and a species of *Wanburoo* sp. (Cooke 1999) suggest a more bipedally adapted morphology, particularly in the pes, with a shift of digits II and III ventromedially below digit IV (accompanied by a loss of digit I), and shortening of the navicular facet on the astragalus. Pedal development in *Wanburoo* sp. also suggests limited capacity of the upper ankle joint for fore-aft motion (possibly in response to a transfer of support of the body weight to digit IV), thus making the pes functionally monodactyl.

The origin of kangaroos remains a vexed question. Most recent authors (Aplin and Archer 1987; Flannery 1987; Springer and Woodburne

1989; Marshall *et al.* 1990; Ride 1993) have favoured a sister-group relationship between macropodoids and phalangeroids. Recent cladistic analyses of kangaroos (e.g., Flannery 1987, 1989; Cooke 1997b) have used phalangerids as an outgroup, although Wroe *et al.* (1998) suggest that Burramyidae is possibly more appropriate for this role, thereby renewing interest in a potential relationship first suggested by Broom (1896).

What is clear is that the origin of kangaroos must be sought further back in time than the late Oligocene. The oldest known kangaroos, from Oligo-Miocene deposits at Riversleigh and central Australia, demonstrate an already considerable degree of diversity, particularly within Balbarinae and Bulungamayinae. The record indicates a marked and steady decline in diversity of some macropodoids (notably balbarines) during the Oligocene and Miocene. In contrast, there was clearly an explosive radiation in macropodines and sthenurines from late Miocene to Quaternary time, probably a measure of the late Cainozoic development and spread of grasslands.

AUSTRALIAN FOSSIL BAT DIVERSITY AND EVOLUTION

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THE Australian fossil bat record is one of the world's oldest and best. *Australonycteris clarkae*, recovered from 55 million-year-old sediments near Murgon, southeastern Queensland, is one of the world's oldest bats (Hand *et al.* 1994). Since its description, additional fossil material from Murgon (including postcranial remains) clearly indicates *Australonycteris* is a member of the family Archaeonycterididae, an archaic bat group otherwise known only from early to middle Eocene sediments in Europe and North America. How bats first reached Australia is not yet known; dispersal could have been through either South America or southeastern Asia.

There is a gap in the Australian fossil record for bats (as for all non-marine mammals) between 55 and 26 million years ago. By the early to middle Tertiary all modern bat families had evolved, with the weight of evidence now suggesting that many modern bat families evolved in the Southern Hemisphere in the early Eocene (Sigé 1991; Simmons 1996). The next oldest Australian bat record is a single tooth from the 26 million-year-old Ditjimanka LF of the Lake Eyre Basin which was described by Archer (1978) as a

possible rhinolophid but which is now understood to be a mystacinid (see below).

Hipposiderids and megadermatids dominate the 25 to 4 million-year-old Riversleigh freshwater limestone deposits, representing more than half of Australia's Tertiary bats, with emballonurids, molossids, vespertilionids and mystacinids comprising the rest (Fig. 1).

In general, Australian Oligo-Miocene bats include ancestors or close relatives of extant Australian taxa (e.g., *Macroderma* and *Brachhipposideros* spp.), relatives of extinct and extant non-Australian taxa (e.g., *Xenorhinos* and *Riversleigha* spp.), and taxa representing archaic cosmopolitan groups with no living descendants (e.g., *Petramops* and *Hydromops* spp.). Australian Pliocene bats are typically closely related to, or represent early populations of, extant Australian bats (e.g., *Taphozous* spp., *Macroderma gigas*, *Micronomus* sp.).

A minimum of 22 hipposiderid species occur in Riversleigh's Oligo-Miocene deposits, with some taxa represented by many hundreds of individuals. Hipposiderids have not yet been

recorded from Australian Tertiary deposits outside the Riversleigh region. In some Riversleigh deposits (e.g. Upper and Bitesantennary Sites), as many as eight hipposiderid species (representing four genera) appear to be syntopic. The predominance of hipposiderids (in both diversity

and abundance) in Riversleigh's limestone deposits is perhaps not surprising since almost all living hipposiderids are cave-dwellers and most extinct taxa have been recovered from cave or karstic deposits.

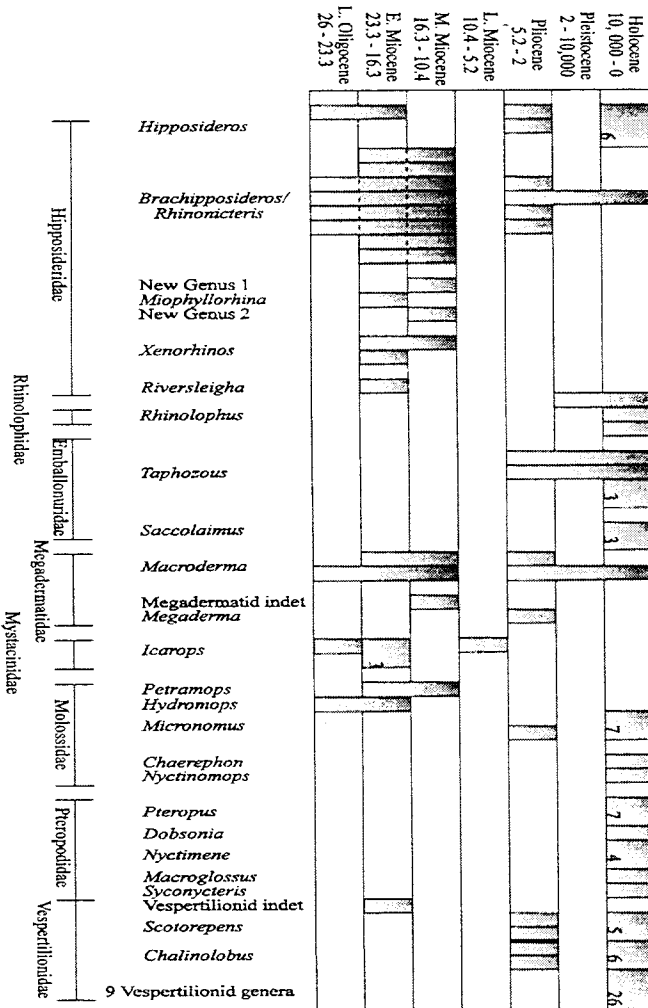


Fig. 1. Australian bat diversity through time. Each block represents a distinct species unless species diversity is indicated by a number. Blocks that extend without breaks through more than one time period indicate apparently long-surviving species.

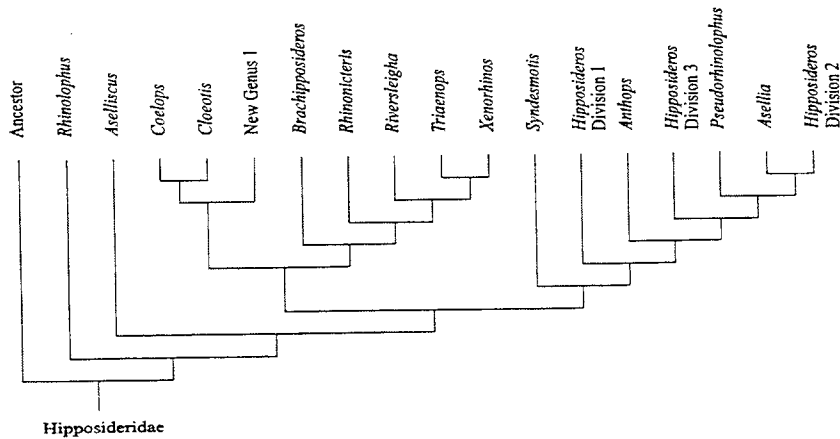


Fig. 2. Cladogram of possible relationships among hipposiderids (after Hand and Kirsch 1998).

However, high diversity also appears to have occurred in European middle Tertiary karstic and lacustrine deposits (commonly five species, Remy *et al.* 1987), suggesting a once more diverse hipposiderid radiation worldwide. Six genera of hipposiderids are now described from Riversleigh (*Brachipposideros*, *Hipposideros*, *Rhinonicters*, *Riversleigha*, *Xenorhinos* and *Miophyllorhina*; Sigé *et al.* 1982; Hand 1993, 1997a,b,c, 1998a,b). The latter four genera are known only from Australia. *Brachipposideros* and *Hipposideros* have much broader distributions: the former in Oligo-Miocene sediments of western Europe and northern Africa (Sigé *et al.* 1994), and the latter represented by at least 55 modern species throughout the Old World tropics. Only three extinct species of *Hipposideros* have been described worldwide, two of these being from Riversleigh: the early Miocene *Hipposideros bernardsigei* (Hand 1997a) and the Pliocene *H. winsburyorum* (Hand and Godthelp 1999). Five species of the *Brachipposideros*-*Rhinonicters* clade are represented in Riversleigh's Tertiary sediments and the oldest representatives of the living northern Australian *R. aurantius* (Sigé *et al.* 1982; Hand 1997b). Another three species of this clade are yet to be described from the Pliocene Rackham's Roost deposit, and at least six others from Oligo-Miocene sediments.

Skulls have been described for all hipposiderid genera represented at Riversleigh with the exception of *Miophyllorhina*. Additional, generically distinct hipposiderid taxa have yet to be described.

Although some Australian fossil hipposiderids are members of highly specialised, derived lineages (e.g., *H. bernardsigei*), many seem to belong to a group of relatively plesiomorphic lineages (e.g., *Rhinonicters*, *Xenorhinos*, *Brachipposideros*) which represent early (though nonetheless specialised) offshoots of the hipposiderid radiation. Because of the diversity of plesiomorphic hipposiderids (fossil and living) in the Australian Region (Fig. 2), Hand and Kirsch (1998) speculate that the primary radiation of the family probably occurred here.

Eight Australian fossil megadermatids have been described: seven from Riversleigh Tertiary sediments and one from Wellington Caves, New South Wales (Hand 1985, 1995, 1996; Hand *et al.* 1988). Most appear related or referable to the endemic Australian genus *Macroderma* but several appear to represent quite different lineages. Of these, *Megaderma richardsi* (Hand 1995), from the Pliocene Rackham's Roost Site, is the first Australian record of this otherwise Afro-Eurasian genus which elsewhere has a record that extends from the late Oligocene to Holocene. The earliest fossil representatives of the living *Macroderma gigas* also occur in the Rackham's Roost deposit (Hand 1996). A second, large Pliocene species (*Macroderma koppa*) is known from Wellington Caves (Hand *et al.* 1988). The record for *Macroderma* extends from the late Oligocene to Recent with a maximum of two species occurring syntopically during that period.

Australian Tertiary molossid bats are known from Riversleigh and also from Bluff Downs, northeastern Queensland. These bats were present in Australia from at least the late Oligocene. Several species occur in Riversleigh's Oligo-Miocene deposits. Two species have been described: *Petramops creaseri*, a plesiomorphic taxon from the middle Miocene (Hand 1990), and a species of the otherwise Eurasian subgenus *Mormopterus* (*Hydromops*) from the late Oligocene and early Miocene (Hand *et al.* 1997). Riversleigh's *Petramops* and *Hydromops* species do not appear to be closely related to each other, nor do they appear to be ancestral to any living Australian molossid. They represent part of an older, archaic bat fauna that was widespread, and had close relatives in Eurasia and North America. The modern Australian subgenus *Mormopterus* (*Micronomus*) is represented in Riversleigh's Pliocene Rackham's Roost Site, and the Pliocene Bluff Downs deposit on Allingham Creek near Charters Towers (Hand *et al.* 1999).

The first pre-Pleistocene record for New Zealand's only endemic mammal family, the Mystacinidae, has been found in Australia. Several species of the new genus *Icarops* are known from early and middle Miocene Riversleigh deposits and another species from middle Miocene limestone sediments at Bullock Creek, Northern Territory (Hand *et al.* 1998). The presence of plesiomorphic mystacinids in the Australian Tertiary suggests an Australian origin for the family. Geographic and phylogenetic data suggest the most likely time of dispersal from Australia to New Zealand would have been the middle to late Oligocene. The Australian Miocene mystacinids provide the only Tertiary record of a very distinctive southern bat lineage of which a single, threatened species (*Mystacina tuberculata*) survives in New Zealand.

Other non-rhinolophoid bats are rare and fragmentary in Riversleigh's Oligo-Miocene

deposits. This rarity may relate to relative scarcity of non-rhinolophoids in the Riversleigh region, or northern Australia, during the Oligo-Miocene or, more likely, preservational biases due to the roost and habitat preferences of such taxa. To date, the only Oligo-Miocene vespertilionid known from Australia is a single tooth from an early Miocene Riversleigh site. By Pliocene time, vespertilionids had increased in number in the Riversleigh region with at least four vespertilionid species represented in the Rackham's Roost deposit; the fragmentary remains are possibly referable to the modern Australian genera *Chalinolobus* and *Scotorepens*, neither of which has an older record anywhere. The only Tertiary emballonurids known from Australia are two Pliocene species of *Taphozous* from Riversleigh's Rackham's Roost deposit, one species of which may represent the living Australian *T. hilli* from northwestern Australia. This Afro-Australasian genus has Miocene records in both Africa and Europe (Butler and Hopwood 1957; Butler 1969, 1978; Legendre 1980); the now cosmopolitan family Emballonuridae may date back to the earliest Eocene of England (Hooker 1996).

Rhinolophids have been recorded only from Pleistocene deposits in eastern Australia (Archer *et al.* 1984) and, incredibly, pteropodids have no fossil record in Australia. These groups appear to be fairly recent immigrants to our shores, although both have early to middle Tertiary records elsewhere. It is possible that in Australian tropical palaeofaunas, such as those of Riversleigh, hipposiderids filled the rhinolophid niche (Hand 1998b). In the case of pteropodids, competition with marsupials for food resources may have played a role in preventing their Tertiary colonisation of Australia, or perhaps suitable food resources may not have been readily available in Australia until the recent past.

DIVERSITY, RELATIONSHIPS AND ORIGINS OF THE TERTIARY AND QUATERNARY RODENTS OF AUSTRALIA

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ENDEMIC Australian rodents make up about 25% of the modern species-level diversity of terrestrial mammals of that continent. All living taxa, which comprise at least 70 species in 15 genera, are placed in the family Muridae. Despite relatively high modern diversity, the Australian fossil record of murids is very limited and only known to

extend with certainty back to the early Pliocene (Fig. 1). Even then, no Pliocene fossil assemblage in Australia, except that from the early Pliocene Rackham's Roost deposit of the Riversleigh World Heritage area of northwestern Queensland, has more than 2% of its species-level diversity represented by murids.

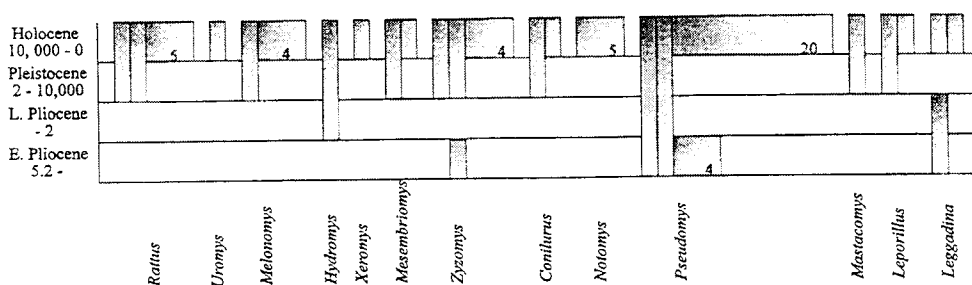


Fig. 1. Australian rodent diversity through time. Each block represents a distinct species unless species diversity is indicated by a number. Blocks that extend without breaks through more than one time period indicate apparently long-surviving species.

To date only two undoubtedly distinct, extinct fossil species have been named from Australia: *Pseudomys vandycli* Godthelp, 1989 from the early Pliocene Chinchilla LF of southeastern Queensland; and *Zyzomys rackhami* Godthelp, 1997 from Riversleigh's early Pliocene Rackham's Roost deposit. There are other undescribed Pliocene species in the genera *Leggadina*, *Pseudomys* and *Zyzomys* (part of the Rackham's Roost assemblage) and *Hydromys* (from the Floraville assemblage of northern Queensland), and other undescribed taxa from Pleistocene deposits around the continent. Several Australian living genera lack any fossil representation. Overall, this relatively poor fossil record for such a diverse modern group may reflect biases in collection strategies, which traditionally favoured discovery of larger mammals, and problems in taphonomy, with smaller, more fragile specimens being less likely to end up as fossils.

Among Pliocene rodents in Australia, the Rackham's Roost assemblage appears to be the oldest. All of its rodent taxa except one represent murines. The exception is a dendromurine-like animal, a group still living in Africa but once widespread across Eurasia including Thailand. This unexpected discovery indicates that the initial wave of immigrants into Australia was more complex than previously assumed.

The diversity of endemic murine genera in the Rackham's Roost assemblage suggests one of two things. Murids invaded Australia much earlier than Rackham's Roost time to enable evolution of these distinctive groups on this continent. Alternatively, murids may have entered Australia already differentiated (somewhere in southeastern Asia) into at least this many groups. Considering

the first hypothesis, the potential for a much earlier origin is limited by the total absence of rodents in the late Miocene Alcoota and Ongeva Local Faunas of the Northern Territory (8 and 7 my respectively; e.g. Murray and Megirian 1992), despite years of collecting at those sites. This does not rule out a time of origin between latest late Miocene and early Pliocene (7 to 5 million years ago), a time of climatic crisis in Australia and elsewhere (Archer *et al.* 1995). At present, however, there is no way to test these alternative scenarios.

What little is known about the generic representation and probable habitat requirements of the Rackham's Roost murids suggests that murids first invaded Australia from southeastern Asia via the Indonesian Archipelago. The earliest invaders probably utilised expanding corridors of relatively dry habitat developing at the time across northwestern Australia.

The apparent absence of murids from Pliocene sites in southern Australia may be attributed to two factors. In the case of the Bow LF of New South Wales, it is likely to be due to taphonomic bias against preservation of small mammals. In the case of the Hamilton LF in Victoria, it is more likely to be related to palaeohabitat. It is generally accepted that the Hamilton LF represents a rainforest assemblage (Archer *et al.* 1995), a contemporary habitat from which 'Old Endemics' are absent.

Relationships of the dendromurine-like rodent have yet to be determined but almost certainly these lie outside Australia. Nothing can be said either, with certainty, about the broader relationships of Australia's endemic murine genera. Molecular and genetic data suggest they

are each other's closest relatives thereby forming a distinct 'Australian clade' (Watts and Baverstock 1995).

Species of *Rattus* in the Plio-Pleistocene deposits at Floraville, northern Queensland, are the earliest record of the genus in Australia. This record postdates an explosion in diversity in southeastern Asia (Chaimanee and Jaeger 1999). It seems probable that the Floraville *Rattus* lineage is part of this southeastern Asian adaptive radiation. Other endemic Australian species of *Rattus* appear, in contrast, to be descendants of a second wave of immigrants that arrived from New Guinea. No representatives of this group are known from pre-Pleistocene deposits anywhere in Australia.

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