

## 2. Evolution of Hind Limb Proportions in Kangaroos (Marsupialia: Macropodoidea)

Benjamin P. Kear\*  
Department of Genetics  
School of Molecular Sciences  
La Trobe University  
Melbourne, Victoria 3086  
South Australian Museum  
North Terrace  
Adelaide, South Australia 5000  
Australia

Michael S.Y. Lee  
South Australian Museum  
North Terrace  
Adelaide, South Australia 5000  
Australia

Wayne R. Gerdtz  
School of Ecology and Environment  
Melbourne Campus, Deakin University  
Burwood, Victoria 3125  
Australia

Timothy F. Flannery  
Division of Environment and Life Sciences  
Macquarie University  
Sydney 2109  
Australia

### 2.1 Introduction

Kangaroos (Macropodoidea: Marsupialia) are a characteristic group of Australo-New Guinean mammals that diversified during the geographic isolation of the Australian continent in the Cenozoic. They are first recorded in the Late Oligocene, although the clade diverged from other diprotodontians around 38 million years ago (mya; Westerman et al., 2002), with early forms perhaps resembling small arboreal ‘phalangerids’ (Flannery, 1982).

Living macropodoids vary widely in body size (<500 g in *Hypsiprymnodon* to >60 kg in larger species of *Macropus*), and show a high degree of ecological diversity. They include forms specialized for climbing (e.g., *Dendrolagus*), bur-

rowing (e.g., *Bettongia lesueur*), and occupation of closed rainforest/woodland (e.g., *Hypsiprymnodon*, *Setonix*) through to open temperate/tropical and/or arid zone grassland (e.g., *Macropus*). Despite this variability, the appendicular skeleton of macropodoids is remarkably conservative with all members of the group showing similar modifications (particularly in the long bones of the hind limb, tarsus, and pes) favoring a bipedal hopping gait. Windsor and Dagg (1971) standardized terminology for kangaroo locomotion designating ‘slow pentapedal progression’ as that involving synchronous use of the limbs and tail (present in all macropodoids and extensively used by species of *Dorcopsis*; Bourke, 1989), ‘walking’ as a gait involving asynchronous use of all limbs (confined to species of *Dendrolagus*; Windsor and Dagg, 1971), ‘quadrupedal bounding’ as movement employing synchronous use of all limbs (present in species of *Dendrolagus*, Windsor and Dagg, 1971; Flannery et al., 1996; and *H. moschatus*, Johnson and Strahan, 1982), and bipedal hopping characterized by synchronous use of the hind limbs only (used at high speeds by

---

\* Address for correspondence: kear.ben@saugov.sa.gov.au

all Recent macropodoids except *H. moschatus*; Johnson and Strahan, 1982).

The macropodoid taxa studied in this paper (Appendix) can be placed within four major family-level clades (Balbaridae, Hypsiprymnodontidae, Potoroidae and Macropodidae; see Kear and Cooke, 2001) each of which exhibits a range of characteristic locomotor strategies. The first of these, Balbaridae, is an extinct Oligo-Miocene group of basal macropodoids that is thought to have used slow quadrupedal bounding as their primary gait (Cooke and Kear, 1999). The presence of an opposable first toe, together with a high degree of lateral flexibility in the foot and robust fore limbs, is also potentially indicative of climbing ability (Cooke and Kear, 1999). The record of confidently attributed balbarid appendicular elements is scant, and most inferences about locomotor behavior are drawn from a single near complete skeleton (representing a new species of *Nambaroo* from Riversleigh, northwestern Queensland; see Cooke and Kear, 1999). However, because of the close similarities with living hypsiprymnodontids, a potential analogue for the locomotor habits of extinct balbarids is available. Modern hypsiprymnodontids are represented by the single species *Hypsiprymnodon moschatus* (Hypsiprymnodontinae); a small plesiomorphic macropodoid currently restricted to the tropical rainforest areas of northeastern Australia (Johnson and Strahan, 1982). However, the fossil occurrences of hypsiprymnodontids are geographically widespread (as far as southeastern Australia) indicating a broader distribution during the mid-late Tertiary (Flannery and Archer, 1987; Flannery et al., 1992; Wroe, 1996). Locomotor behavior in extant hypsiprymnodontids (*H. moschatus*) is characterized by consistent use of quadrupedal bounding at both high and low speeds (Johnson and Strahan, 1982). This contrasts with most other living macropodoid groups (Macropodidae, Potoroidae), which predominantly employ both slow pentapedal locomotion during feeding and full bipedal hopping at higher speeds. However, some notable exceptions include the potoroos (*Potorous*: Potoroidae: Potoroinae), which, like hypsiprymnodontids, mainly use quadrupedal bounding (not incorporating the tail) at slower speeds (see Buchmann and Guiler, 1974), and tree kangaroos (*Dendrolagus*: Macropodidae: Macropodinae), which utilize an asynchronous walk when moving along branches and/or climbing (Windsor and Dagg, 1971). Some intriguing fossil taxa are also thought to have employed distinctive locomotor strategies. For example, Plio-Plesitocene sthenurines (Macropodidae), a group that includes some of the largest kangaroos (e.g., *Procoptodon* ~2.5 m high), have been interpreted as specialized high level browsers that habitually used bipedal hopping at the expense of quadrupedal and/or pentapedal gaits (Wells and Tedford, 1995).

Considerable work has been devoted to the structure and function of the limb skeleton in marsupials (e.g., Elftman, 1929; Jenkins, 1971; Van Valkenburgh, 1987; Szalay, 1994). A number of contributions have also discussed functional aspects in fossil taxa (e.g., Finch and Freedman, 1988; Munson, 1992; Muizon, 1998; Szalay and Sargis, 2001; Argot,

2001, 2002, 2003a, b, 2004). For macropodoids, research has focused largely on functional analysis of particular species or clades (e.g., Flannery, 1982; Bishop, 1997; Ride et al., 1997; Kear et al., 2001a, b), but as yet few studies have investigated broad-scale evolutionary trends in the group as a whole.

The purpose of this study is to examine the relationship between locomotor strategy and proportional changes in the proximal limb bones and metatarsals of a range of modern and extinct macropodoids using morphometric analyses. In addition, trends in hind limb evolution through time are investigated, firstly using only observations on extant taxa and inferring ancestral conditions on dated molecular phylogenies, and secondly by adding information from the fossil record. The results suggest that incorporating fossils can drastically change inferences about past diversity and evolutionary trends.

## 2.2 Materials and Methods

One hundred and eighty-six specimens belonging to 44 species of macropodoids (Appendix) were included together with a phalangerid (*Trichosurus vulpecula*), phascolarctid (*Phascolarctos cinereus*), and vombatid (*Vombatus ursinus*), which served as outgroups. Material was derived from collections of the South Australian Museum, Museum Victoria, Australian Museum, Queensland Museum, and University of New South Wales. Measurements for some fossil taxa were also derived from the literature; these include *Sthenurus tindalei* (Wells and Tedford, 1995), *Procoptodon goliah* (Tedford, 1967), *Protymnodon tumbuna* (Menzies and Ballard, 1994), and *Macropus mundjabus* (Flannery, 1980). All skeletal remains examined were from adults and only articulated or definitively associated fossil elements were used.

A set of three measurements for the maximum lengths of the long bones were taken for each specimen using digital calipers (where <150 mm) to the nearest 0.01 mm, or steel tape (where >150 mm) to the nearest 0.1 mm. Mean and standard deviation values for each species are reported in the Appendix.

- (1) *Femur length* (FL) was the distance from the distal apex of the greater trochanter to the distal point of the femoral condyles.
- (2) *Tibia length* (TL) was the distance between the proximal and distal articular surfaces of the tibia.
- (3) *Metatarsal IV length* (MtL) was the distance between the proximal and distal articular surfaces of metatarsal IV.

Measurements were combined into two functional indices derived from the literature (see Howell, 1944; Hildebrand, 1985, 1988; Finch and Freedman, 1988; Garland and Janis, 1993; Christiansen, 2002). These represent indicators of primary locomotor habits.

- (1) *Femoro-tibial index* (T/F = [TL/FL] × 100) is the tibia length divided by the femur length. It gives a measure of proportional change in the proximal limb elements.

(2) *Femoro-metatarsal index* ( $Mt/F = [MtL/FL] \times 100$ ) is the longest metatarsal (metatarsal IV in macropodoids) length divided by the femur length. This gives an indication of proportional change in the metapodials relative to the propodial part of the limb.

To test for potential correlations between limb bone lengths and inferred primary locomotor strategy, measurements were log-transformed and regression lines fitted to the data using standard least-squares. Tibia and metatarsal lengths were arbitrarily treated as the dependent variables. Regression analyses were carried out using *Prism 4.0a*, which also provided 95% confidence intervals (CI) for the slopes.

The relationships between limb bone length, locomotion, and phylogeny was examined using the functional index (T/F, Mt/F) values, which were averaged for each species (Appendix) and optimized onto dated phylogenies based on molecular and fossil information. The most common molecule sequenced for macropodoids is a ~2.5 kB region of mtDNA spanning 12S, valine tRNA, and 16S rRNA. Eighteen of the living species measured above have been sequenced for this gene. The other widely sequenced molecule, protamine P1, was not used, as it was available for fewer taxa and produced poorly resolved trees (see Westerman et al., 2002). Alignments followed Westerman et al. (2002). The arrangement for these 18 taxa found in the larger taxon set of Westerman et al. (2002) was used to infer branch lengths (analyses of the 18 taxa alone yielded a very similar topology). Branch lengths were inferred using PAUP (Swofford, 2000) and the optimal model selected by hierarchical likelihood ratio tests (Posada and Crandall, 1998), the GTRig model. As the chi-squared test detected no significant rate heterogeneity ( $P > 0.05$ ), the molecular clock constraint was enforced to generate an ultrametric tree. This was calibrated to absolute time using the first calibration point used by Westerman et al. (2002); this is one of the most robust and precise calibration points for macropodoids. *Purtia* has traditionally been considered a primitive member of the potoroine (*Bettongia* + *Aepyprymus*) clade and occurs in late Oligocene deposits around 24 my old (see Case, 1984; Woodburne et al., 1993). Accordingly, we set the potoroine-macropodine split at 25 mya. The other fossil Westerman et al. (2002) used to date this divergence, the putative basal macropodine *Nambaroo*, has been reinterpreted as a basal macropodoid (Kear and Cooke, 2001) and thus can no longer be used to date this split. However, the ~23 my old (early Miocene) *Ganguroo* is a true basal macropodid, further supporting the interpretation that this split occurred at least 24 mya but not much earlier. Based on these two calibration fossils, the branch lengths of the ultrametric tree were scaled with *Mesquite* (Maddison and Maddison, 2003) so that the depth of the potoroine-macropodine split was 25; branch lengths throughout this rescaled tree thus represented millions of years. This tree is hereafter termed the 'extant tree'.

Fossil lineages were then added to the 'extant tree', to generate the 'full tree'. *Purtia* and *Ganguroo* were assumed

to insert low on the potoroine and macropodine stem lineages (diverging at 24 mya), due to their plesiomorphic characteristics. Within sthenurines, the split between *Sthenurus tindalei* and *S. stirlingi* was set at 1.4 mya, the split between *S. andersoni* and the previous two species at 3.5 mya, and the split between *Procoptodon* and *Sthenurus* at 4.2 mya (see Prideaux, 2004). In the absence of more precise information, other fossil taxa are assumed to have diverged mid-way along the branch connecting relevant extant taxa. For example, *Nambaroo* is a sister taxon to all other macropodoids (*sensu* Balbaridae; Cooke and Kear, 1999; Kear and Cooke, 2001), and is assumed to have diverged mid-way along the stem leading from the outgroups to macropodoids. The three species of *Protemnodon* diverged along the stem leading to derived macropodines (Dawson, 2004), *Macropus mundjabus* diverged along the stem leading to *M. giganteus* (Flannery, 1980), and the sthenurine clade diverged along the stem leading to the *Wallabia-Macropus* clade (e.g., Szalay, 1994).

For each of the two trees (extant and full) and for each of the two traits (T/F and Mt/F), the values for each species (terminal branches) were used to infer ancestral conditions along internal branches (extinct ancestral lineages) with square-change parsimony (Huey and Bennett, 1987) in *Mesquite* (Maddison and Maddison, 2003). The other available option in *Mesquite*, linear parsimony, appears less reliable (Webster and Purvis, 2001) and was not employed. The trends through time were then examined by plotting the inferred values of lineages passing through each time slice. This was done for the extant and full trees to investigate the effects of adding fossil taxa on inferences of past diversity. The fossil taxa contribute the only direct observations for the past, and could also potentially change the inferred values for other (internal) branches, which are not directly observed.

## 2.3 Results

### 2.3.1 Regression Analyses of Hind Limb Bone Lengths

Both tibia (Figure 2.1A) and metatarsal IV lengths (Figure 2.1B) were found to scale differently with femur length in bipedal saltating, and in obligate quadrupedal diprotodontians (see Table 2.1). When tibia length is plotted against femur length, the regression slope is  $>1$  in bipedal saltators, and not significantly different from 1 in quadrupeds. This implies strong positive allometry in tibia length in hopping forms, and corroborates the conclusions of others including Windsor and Dagg (1971), who noted that tibia length in particular increased in proportion to that of the femur in larger-bodied macropodoids. Furthermore, for the size ranges considered here, the hopping forms had consistently longer tibiae (relative to femur length) than did the quadrupeds. When metatarsal IV length is plotted against femur length, the regression slopes for both bipedal and quadrupedal taxa do not differ



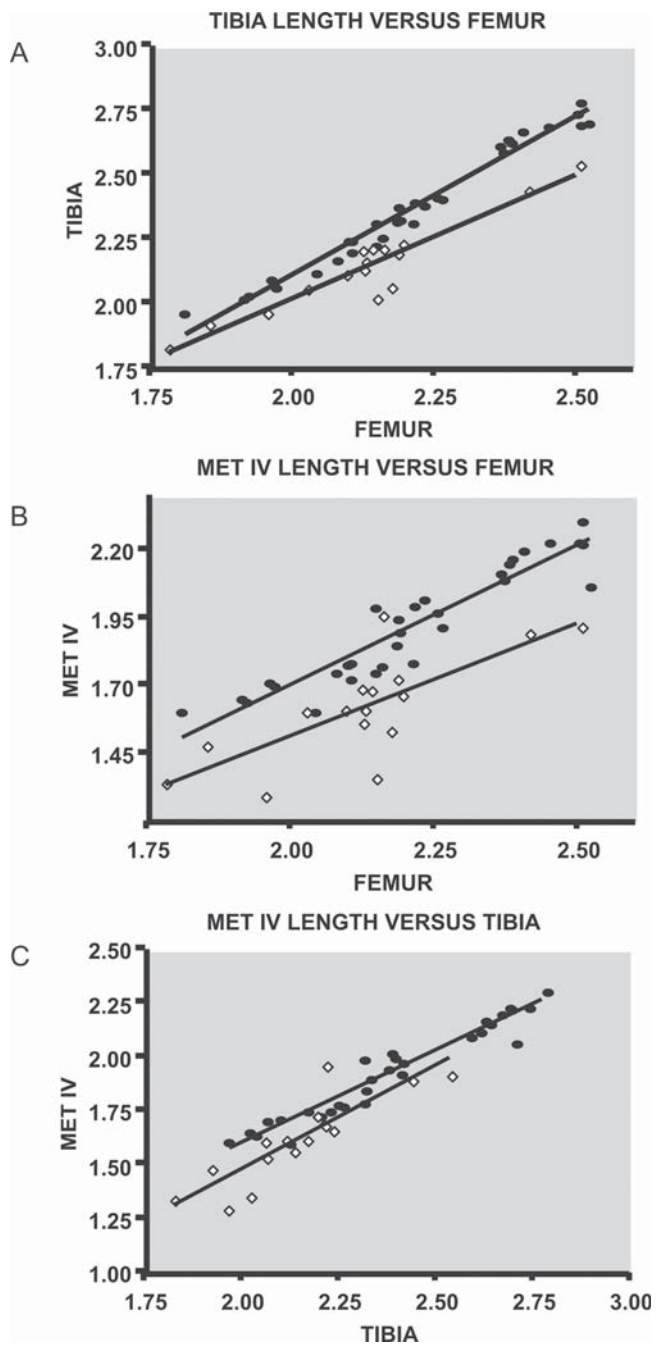


FIGURE 2.1. Regression plots of, A, log tibia versus log femur, B, log metatarsal IV versus log femur, and C, log metatarsal IV versus log tibia lengths, showing close fit of standard regression lines to the data for consistently bipedally saltating ( $\bullet$ ), and consistently quadrupedal ( $\diamond$ ) macropodoid taxa.

from 1, suggesting that metatarsal IV scales approximately isometrically in both groups. However, as before, for the size ranges considered here, the hopping forms had consistently longer metatarsals (relative to femur length) than did the quadrupeds. These results suggest that high tibia or metatarsal IV lengths correlate with locomotor mode.

## 2.3.2 Comparison of Index Values In Macropodoids

### 2.3.2.1 Femoro-Tibial Index

Amongst mammals, high T/F values (around 100–200) are traditionally correlated with adaptations towards bipedal saltating gaits (Finch and Freedman, 1988). This trend is evident in the present sample, which indicates that kangaroos of all body sizes consistently have T/F values  $>100$  (see Appendix). The ougroup taxa generally fall below this range (e.g., *Vombatus ursinus*, 74.8; *Phascolarctos cinereus*, 77.8), although the primarily arboreal phalangerid *Trichosurus vulpecula* (101.3) does exhibit tibia/femur proportions similar to some ‘short-legged’ kangaroo taxa (most notably tree kangaroos; e.g., *Dendrolagus bennettianus*, 101.8). This is significant given that phalangerids are thought to be closely related to macropodoids (Aplin and Archer, 1987; Kear and Cooke, 2001), and indeed utilize a high speed quadrupedal bound similar to that of some more plesiomorphic kangaroos when moving about on the ground (Goldfinch and Molnar, 1978).

Within Macropodoidea, the lowest values occur in tree kangaroos (ranging from 101.1 in *Dendrolagus matschei* to 109.1 in *D. goodfellowi*) in which the tibia and femur show little differentiation in relative length. Similar T/F proportions also occur in some species of the consistently pentapedal (see Windsor and Dagg, 1971) *Dorcopsis* (*D. atrata*, 109.8), and in the New Guinean Plio-Pleistocene species of *Protemnodon* (105.8 in *P. hopei*, 107.8 in *P. tumbuna*). Murray (1991) suggested that *Protemnodon* might have been a ‘low-g geared’ macropodid, favouring slower speed locomotor modes, and requiring considerable energy expenditure and distance to achieve high-speed saltation. The only other macropodoid to exhibit markedly low T/F values is *Setonix brachyurus* (108.2). Windsor and Dagg (1971) noted that this species also utilizes a quadrupedal bounding gait similar to that of *Dendrolagus*.

The plesiomorphic *Hypsiprymnodon moschatus* (110.6) has T/F values close to those of *Potorous tridactylus* (117.6) and the Riversleigh *Nambaroo* (Balbaridae) species (113.9). Both *H. moschatus* and species of *Potorous* are known to be habitual quadrupedal bounders (Buchmann and Guiler, 1974; Johnson and Strahan, 1982), and a similar locomotor strategy has been suggested for balbarids (Cooke and Kear, 1999).

T/F values are also comparable in Recent bipedal saltating potorines (123.9 for *Aepyprymnus rufescens*, 126.9 for species of *Bettongia*) and the enigmatic Oligo-Miocene taxon *Purtia* (121.2). Whether this relationship reflects similar locomotor habits or ecology is unclear. Notably, however, *Purtia* has been considered an early potoroid (Case, 1984), although Kear and Cooke (2001) have alternatively suggested affinity with the extinct macropodid subfamily Bulungamayinae.

Some species of the small forest-dwelling *Dorcopsis* (*Dorcopsis* sp., 121.7; *D. luctosa* 119.1) and *Thylogale* (120.3

TABLE 2.1. 95% confidence intervals (significance level set at  $P < \text{or} = 0.05$ ) derived from standard least squares regression analyses of log limb bone lengths for bipedally saltating, and consistently quadrupedal (including pentapedal locomotors; see Introduction for gait definitions) macropodoid and outgroup diprotodontian taxa.

Regression analysis	Consistent saltating bipeds		Consistent quadrupeds	
	95% CI	P	95% CI	P
Log tibia length versus log femur length	1.157 to 1.311	<0.0001	0.7681 to 1.144	<0.0001
Log metatarsal IV length versus log femur length	0.8832 to 1.185	<0.0001	0.4134 to 1.262	0.0008
Log metatarsal IV length versus log tibia length	0.7731 to 0.9420	<0.0001	0.6463 to 1.276	<0.0001

in *T. billiarderii*, 124.9 in *T. thetis*) have values comparable to those of potoroides. *Dorcopsis* in particular has an unusual locomotor mode, favouring slow pentapedal progression with the tail used as an arched prop rather than laying flat on the ground (Bourke, 1989). However, both *Dorcopsis* and *Thylogale* regularly use bipedal hopping at higher speeds (as in potoroides; see Bourke, 1989; Strahan, 1998), and it is probably this habitus that is reflected in the elongation of the tibia relative to the femur (a feature thought to be intimately linked to the use of more efficient high speed bipedal progression; Windsor and Dagg, 1971).

The majority of both fossil and Recent macropodids have high T/F values. Most modern macropodines have means >126 (e.g., 126.7 in *Petrogale penicillata* to 185.5 in *Macropus fuliginosus*), reflecting their consistent use of high-speed bipedal hopping. Interestingly, the bulungamayine *Ganguroo bilamina* also falls within this range (143.2), suggesting that some of the hind limb adaptations necessary for effective bipedal saltation may have already evolved within the macropodid clade by at least the early Miocene.

The Plio-Pleistocene species of *Protemnodon* (Macropodinae) show considerable disparity in their T/F values. For example, those of the large-bodied *P. anak* from southeastern Australia (152.4) are comparable to modern *Macropus* species (see Appendix), whereas the New Guinean *P. hopei* and *P. tumbuna* show values (see above) closer to those of tree kangaroos (*Dendrolagus*). Such high variability within a single genus is surprising, but is consistent with recent indications of taxonomic diversity within the clade (Dawson, 2004). In terms of locomotor behavior, this suggests that the species of *Protemnodon* were adapted for a number of primary gait types, ranging from quadrupedal bounding (*P. hopei* and *P. tumbuna*) to full bipedal hopping (*P. anak*). This may have occurred in response to differing habitat preferences between individual species, with some (e.g., *P. anak*) favoring more open woodland and grassland environments (typifying southern mainland Australia in the Late Pleistocene; Macphail, 1997), as opposed to closed dense forest conditions (i.e., New Guinea) in which quadrupedal progression enables easier directional changes when moving among obstacles covering the ground (Windsor and Dagg, 1971).

The highest T/F values within Macropodoidea occur within the extinct giant Plio-Pleistocene sthenurines (Macropodidae).

These include species of *Sthenurus* (approximating some of the larger macropodines in size; Wells and Tedford, 1995), which has values (*S. tindalei*, 154.9; *S. stirlingi*, 172.4; *S. andersoni*, 178.1) comparable to *Macropus* (see Appendix), and *Procoptodon goliah*, which has the highest T/F values of any macropodoid tested (189.1). Wells and Tedford (1995) suggested that *Sthenurus* might have been a habitual bipedal hopper with little or no dependence on pentapedal or quadrupedal movement. Similarly, *Procoptodon* is thought to have been specialized for bipedal progression (Murray, 1991). Indeed, the extreme elongation of the hind limb bones in both *Sthenurus* and *Procoptodon* is likely to have conferred some selective advantage towards this habitus by increasing stride length (critical for bipedal hopping at larger body sizes; see Windsor and Dagg, 1971) and/or height when standing erect for browsing.

### 2.3.2.2 Femoro-Metatarsal Index

As with the T/F index, bipedal hopping mammals are known to show consistent Mt/F values ranging from around 40 to 60 (Howell, 1944; Finch and Freedman, 1988). This trend is also evident in the present sample, with most macropodoids scoring between 45 and 65 (see Appendix). Notably, however, some taxa, namely the habitually quadrupedal species of *Dendrolagus* (*D. matschei*, 27.3; *D. goodfellowi*, 29.6; *D. lumholtzi*, 33; *D. bennettianus*, 34.7) and *Dorcopsis* (*D. atrata*, 29.6; *D. luctosa*, 34.9; *Dorcopsis* sp., 37.1), *H. moschatus* (30), *S. brachyurus* (38.1), the Oligo-Miocene *Purtia* (36.6), and the enigmatic species of *Protemnodon* (*P. tumbuna*, 26; *P. hopei*, 30; *P. anak*, 35.4), have considerably lower values. Despite this, these figures are still significantly higher than any of those for the outgroup taxa (*V. ursinus*, 15.8; *P. cinereus*, 21.2; *T. vulpecula*, 21.6), suggesting that marked metatarsal elongation may be a common feature shared by all macropodoids.

Most other Recent and fossil potoroids and macropodids in the present study have values that fall within the expected range for bipedal saltators (see Appendix). Taxa with significantly higher values include the larger-bodied species of *Macropus* (*M. giganteus*, 60.4; *M. parryi*, 62.3; *M. fuliginosus*, 63; *M. rufus*, 63.5) and the giant Late Pleistocene sthenurine *P. goliah* (65). Interestingly, the small 'wallaby-

sized' (see Kear and Cooke, 2001) Oligo-Miocene bulungamayine *G. bilamina* (63) and balbarid *Nambaroo* (63.3) also have Mt/F values comparable to these large bipedal macropodids. This is unusual given that both these small-bodied taxa are thought to have utilized a considerable degree of quadrupedal movement in their primary gaits (Cooke and Kear, 1999; Kear et al., 2001a). Regardless of these conflicting locomotor strategies and body sizes, the presence of high Mt/F values in a number of independent macropodoid taxa is important because it indicates that elongate metatarsals evolved several times (perhaps in response to similar environmental constraints) in a number of kangaroo groups during the late Oligocene to Recent.

### 2.3.3 Trends Through Time

The reconstructed, least-squares values for T/F and Mt/F on all branches in the 'extant tree' are shown in Figure 2.2A. On each branch, the lower number (*in italics*) is the T/F value, and the upper number (in plain text) is the Mt/F value. The reconstructed values for each branch in the 'full tree' are shown in Figure 2.2B, using the same notation. The trends through time, namely the inferred values for all lineages existing at each given time slice, are also plotted. The trends through time for T/F are shown in Figure 2.3A (inferred using the 'extant tree') and in Figure 2.3B (inferred using the 'full tree'). Similarly, trends through time for Mt/F are shown in Figures 2.3C and 2.3D (extant and full trees, respectively).

## 2.4 Discussion

### 2.4.1 Limb Proportions Versus Locomotion and Ecology

Macropodoids have been a ubiquitous element of the Australian mammal fauna since at least the late Oligocene (Cooke and Kear, 1999). Their characteristic adaptation to bipedal hopping has led to a number of important modifications in the hind limb skeleton, particularly elongation of the femur, tibia, and metapodium. Windsor and Dagg (1971) examined the relationship between limb morphology and movement, recognizing that kangaroos employ a number of primary locomotor strategies (i.e., walking, slow pentapedal progression, quadrupedal bounding, and bipedal hopping), and that these vary considerably according to habitat preference. Importantly, they found no reliable correlation between bipedal hop pattern and relative lengths of the femur and tibia; however, tibia length was reported to increase over that of the femur in larger-bodied taxa. This is confirmed by the present analysis, which shows that T/F values do not differ greatly between bipedal saltators, although they do tend to reach a maximum in the largest species tested (e.g., *P. goliath*; see Figure 2.2). Conversely, Mt/F values fail to conform to a similar pattern,

instead varying widely between body sizes, major clades, and in taxa through time (Figure 2.3C, 2.3D).

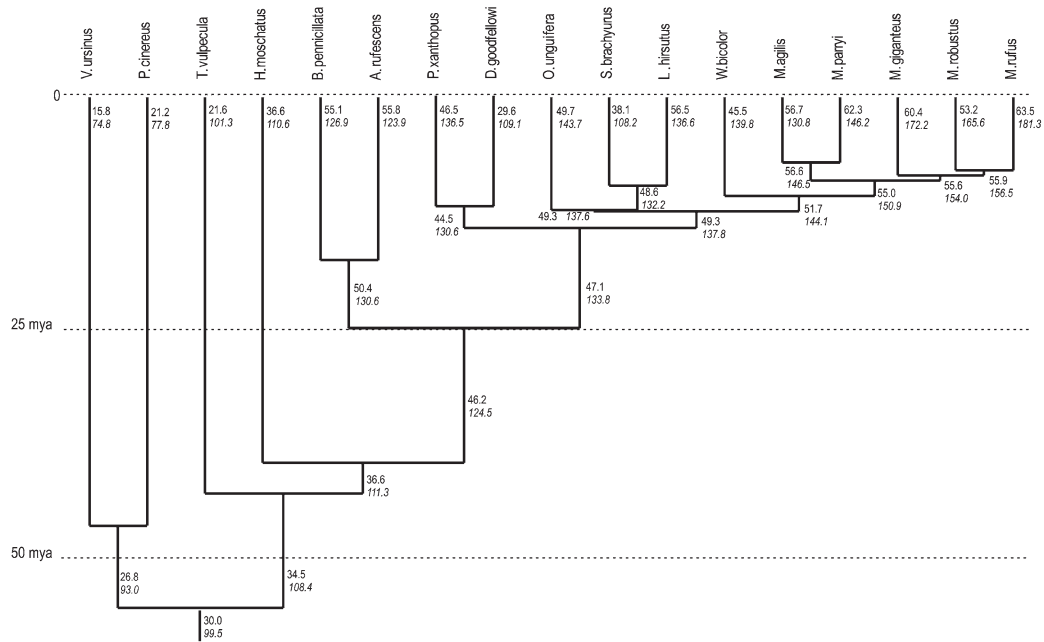
Although unable to discern between bipedal hop patterns, the T/F (and to a lesser degree Mt/F) values recorded here do seem to reflect major differences in primary gait, especially between quadrupedal taxa (which tend to have low scores) and habitual bipedal saltators. In addition, these figures correlate well with preferred habitat in extant taxa (where discernable); primarily quadrupedal macropodoids (e.g., *H. moschatus*, *S. brachyurus*, and species of *Dendrolagus*) generally occupying more densely vegetated environments (see Windsor and Dagg, 1971). However, this trend is less evident in the fossil taxa where low T/F forms such as the apparently quadrupedal New Guinean *Protemnodon tum-buna* and *P. hopei*, and the Riversleigh *Nambaroo* species, correlate with a range of interpreted paleohabitats including closed rainforest to alpine grassland (e.g., Flannery, 1992, 1994; Megirian, 1992; Hope et al., 1993; Archer et al., 1997; Archer et al., 2001; Guerin, 2004).

Some early fossil forms (e.g., the Oligo-Miocene *G. bilamina*, *Purtia* sp.) show high T/F and Mt/F values well within the range of modern bipedal saltators. This suggests that like today, ancient macropodoids probably exhibited a wide variety of locomotor strategies (including quadrupedal bounding to habitual bipedal saltation), and thus were probably able to occupy a similar spectrum of habitats. Indeed, such locomotor diversity, which appears to have been established in a range of taxa (e.g., quadrupedal balbarids and bipedal bulungamayines) by at least the early Miocene, might have facilitated the successful diversification of modern kangaroos (including macropodines and sthenurines, which replaced many of these earlier forms) into the mosaic of open forest and grassland environments that spread across the Australian continent after the onset of aridity in the Miocene-Pliocene (Megirian, 1992; Macphail, 1997; McGowran and Li, 2002).

### 2.4.2 Limb Proportions Versus Phylogeny

As comparison of Figures 2.2A and 2.2B clearly shows, incorporation of fossil taxa demonstrably changes the inferred T/F and Mt/F values for internal branches within macropodoids. This effect is more evident in Mt/F than T/F values. The results for Mt/F will therefore be discussed below; however a similar (but weaker) pattern is also found in the T/F results. Amongst currently living taxa, high (>60%) Mt/F values are restricted to three species of *Macropus* (*M. parryi*, *M. giganteus*, *M. rufus*); consideration of extant taxa alone would thus suggest that this condition evolved fairly recently (<1 mya), with all early lineages having low inferred proportion values. However, some basal fossil macropodoids (*Nambaroo* and *Gangaroo*) have unexpectedly high Mt/F values. Addition of these fossils to the analysis (1) adds lineages with directly observed high Mt/F values to the basal parts of the tree, and (2) increases the inferred values of nearby internal

A



B

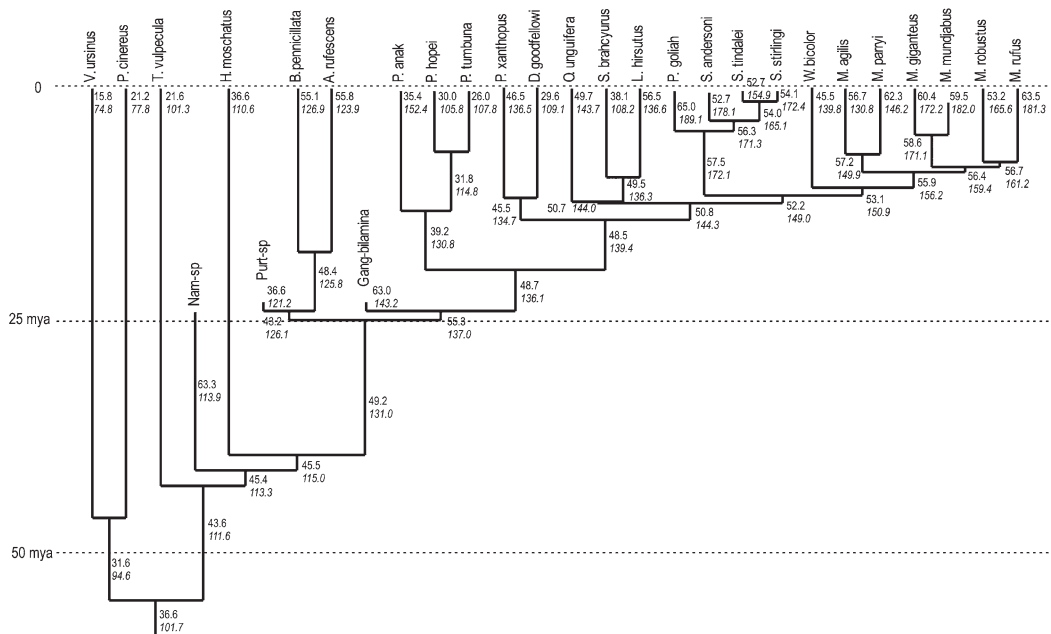


FIGURE 2.2. Macropodoid phylogenies showing reconstructed least-squares values for T/F and Mt/F. A, ‘extant tree’ (fossil taxa excluded), B, ‘full tree’ (fossil taxa included). On each branch, the lower number (in italics) is the T/F value, and the upper number (in plain text) is the Mt/F value.

branches. In the ‘extant tree’ (Figure 2.2A), the inferred value of the branch leading to crown-clade macropodoids (*Hypsiprymnodon* upwards) is 36.6. The inferred value for the same branch increases to 45.5 with the incorporation of the fossil taxa. When plotted through time, the differences

in the trends implied by the extant and full phylogenies are striking (see Figures 2.3C, 2.3D). Consideration of extant species alone suggests that low Mt/F values (<37%) characterized all early macropodoid lineages, and that high Mt/F values (>40%) evolved only recently (around 25 mya) within



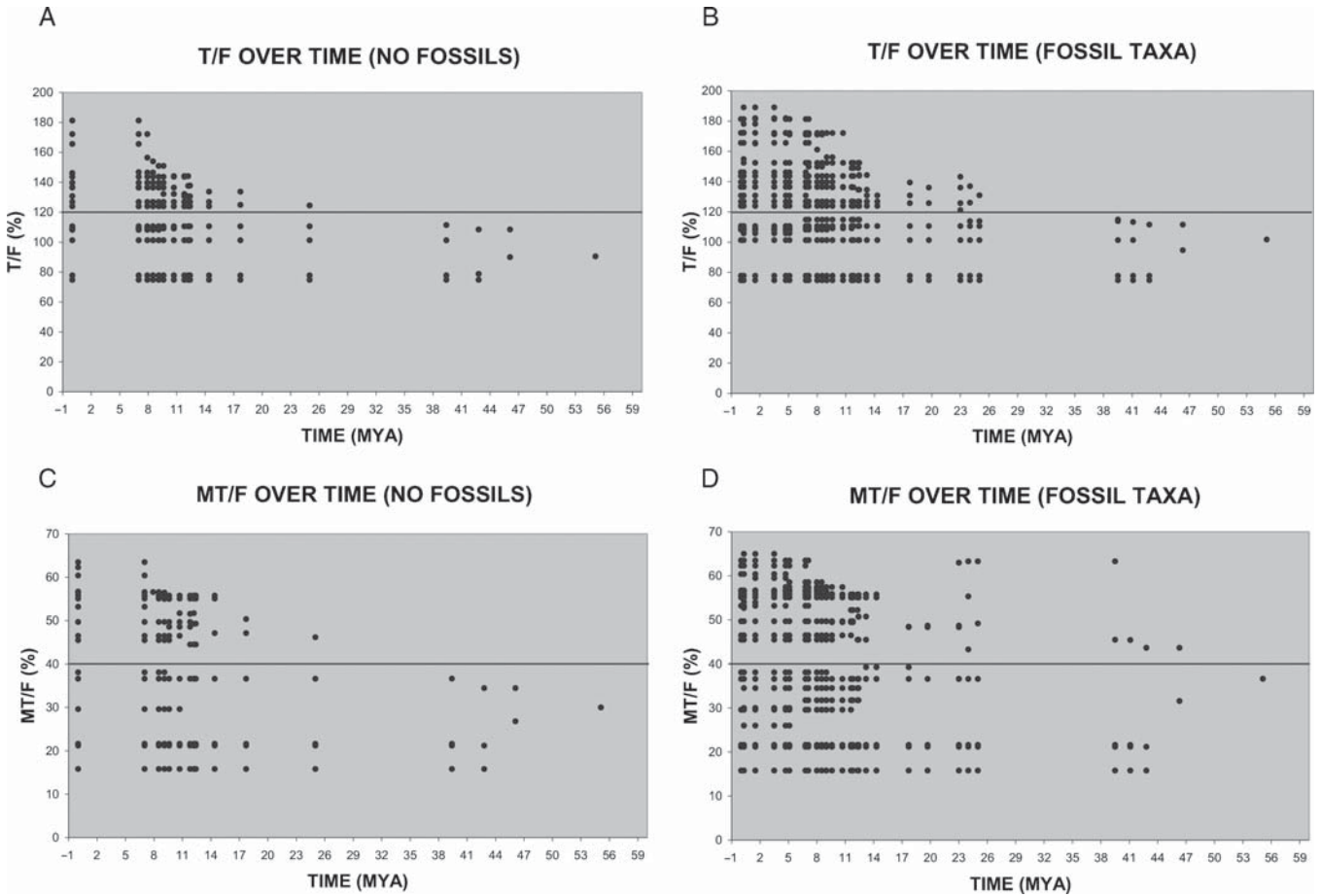


FIGURE 2.3. Plots of reconstructed least-squares values for T/F and Mt/F at each node versus time. A, T/F values inferred using ‘extant tree’; B, ‘full tree’. C, Mt/F values inferred using ‘extant tree’; D, ‘full tree’. Horizontal lines at T/F value 120 (A, B) and Mt/F value 40 (C, D) indicate minimum mean value correlating with habitual bipedal saltation.

macropodids (Figure 2.3C). The timing of this change, functionally related to bipedal saltation, is consistent with previous suggestions that the evolution of derived macropodoid locomotor strategies was driven by the onset of aridity and adaptation to increasingly open environments (e.g., Flannery, 1982). However, inclusion of fossil taxa changes the picture. These demonstrate that some early kangaroos had high Mt/F proportions, and indeed that the ancestors of macropodoids had values over 45. When plotted over time, there is no trend towards gradual increase of Mt/F values; rather macropodoids seem to have established a broad range of metapodial proportions very early in their evolutionary history, and then maintained them through to the present day (see Figure 2.3D). Thus, when the full evidence is considered, there is no clear correlation between the evolution of high Mt/F values and increasing aridity in the late Tertiary. Because living taxa with high Mt/F ratios (*Macropus*) represent only

one of the many clades that evolved this feature, consideration of living taxa alone gives distorted interpretations; such problems will be manifest whenever groups that are ecological analogues replace each other over geological time.

*Acknowledgments.* S. Ingleby (Australian Museum), N. W. Longmore and D. Henry (Museum Victoria), N. Pledge and D. Stemmer (South Australian Museum), M. Archer and H. Godthelp (University of New South Wales) all generously assisted in making information and specimens available. La Trobe University, the Australian Research Council, South Australian Museum, Umoona Opal Mine and Museum, Outback at Isa, Origin Energy, The Advertiser, The Waterhouse Club, the Coober Pedy Tourism Association, Commercial and General Capital Ltd and Kenneth J. Herman Inc. gave financial support for this research.



## Appendix

Hind limb bone measurements and index values of 47 diprotodontian marsupial taxa (mm)

Taxon	N	FL		TL		MtL		T/F		Mt/F	
		Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
<i>Vombatus ursinus</i>	8	9.2		6.2		2.7		74.8	1.8	15.8	0.6
<i>Phascolarctos cinereus</i>	7	9.5		6.4		1.8		77.8	0.8	21.2	0.8
<i>Trichosurus vulpecula</i>	5	14.3		10.2		2.3		101.3	5.9	21.6	1
<i>Nambaroo sp.</i>	1	–		–		–		113.9	–	63.3	–
<i>Hypsiprymnodon moschatus</i>	2	3.5		2.5		0.1		110.6	2.1	36.6	2.3
<i>Potorous tridactylus</i>	6	23.1		83.6	12.9	30.2	2.9	117.6	5.9	43	5.7
<i>Bettongia lesuer</i>	8	83.6	4.7	108.2	5.3	1.2		129.5	3.9	51.8	1.8
<i>Bettongia penicillata</i>	7	4.6		103.9	4.7	45.2	3.2	126.9	3.3	55.1	2.6
<i>Aepiprymnus rufescens</i>	10	15.3		20.3		50.25	10.5	123.9	9.5	55.8	12
<i>Purtia sp.</i>	1	109.4	–	–		–		121.2	–	36.6	–
<i>Ganguroo bilamina</i>	1	64.1	–	91.8	–	–		143.2	–	63	–
<i>Protomnodon hopei</i>	1	–		–		78.1	–	105.8	–	30	–
<i>Protomnodon tumbuna</i>	1	319	–	–		–		107.8	–	26	–
<i>Protomnodon cf. anak</i>	2	40.3		506.5	105.4	14.1		152.4	13.3	35.4	–
<i>Dorcopsis sp.</i>	3	132.7	8	6.5		3.4		121.7	2.3	37.1	0.7
<i>Dorcopsis luctosa</i>	2	137.9	11.7	163.9	3.7	0.8		119.1	7.4	34.9	2.4
<i>Dorcopsis atrata</i>	1	–		170.8	–	46	–	109.8	–	29.6	–
<i>Dendrolagus goodfellowi</i>	2	134.3	0.4	1		0.1		109.1	4.2	29.6	1.3
<i>Dendrolagus matschei</i>	1	–		135	–	36.5	–	101.1	–	27.3	–
<i>Dendrolagus bennettitanus</i>	1	153.2	–	–		53.2	–	101.8	–	34.7	–
<i>Dendrolagus lumholtzi</i>	2	124.5	11.7	129.9	8.6	41.1	3.3	104.5	2.9	33	0.5
<i>Petrogale godmani</i>	1	162	–	206.1	–	60.8	–	127.2	–	37.5	–
<i>Petrogale xanthopus</i>	3	152.1	6.9	207.5	8.2	70.7	3.8	136.5	1.6	46.5	3.4
<i>Petrogale penicillata</i>	4	143.5	5.5	181.8	6.6	59.3	2.4	126.7	1.5	41.1	0.6
<i>Thylogale thetis</i>	2	126.7	13.2	158.8	27.2	53.1	0.2	124.9	8.4	42.1	4.2
<i>Thylogale billardieri</i>	5	139.7	13.4	168	16	56.2	1.5	120.3	1.5	40.5	4.8
<i>Onychogalea fraenata</i>	10	124.7	19.4	176.4	8.2	60.5	3.5	143.7	17.1	49.7	7
<i>Setonix brachyurus</i>	3	105.9	6.1	114.6	6.7	40.3	1.9	108.2	1.6	38.1	0.4
<i>Lagorchestes hirsutus</i>	3	91.7	6.4	125.1	5.6	51.7	1.3	136.6	4	56.5	2.9
<i>Wallabia bicolor</i>	8	183	12.1	255.5	11.3	83.1	4.1	139.8	4.4	45.5	3.1
<i>Macropus agilis</i>	3	156.7	14	205.8	35.3	97.5	–	130.8	10.7	56.7	–
<i>Macropus parryi</i>	6	170.1	31.5	241	55	104.3	9.1	146.2	4.9	62.3	6.4
<i>Macropus giganteus</i>	7	242.2	39.4	420.7	91.5	147	28.8	172.2	56.3	60.4	6.2
<i>Macropus fuliginosus</i>	12	253.3	18.5	465.4	45.5	157.8	10.7	185.5	16.6	63	6
<i>Macropus mundjabus</i>	1	–		434	–	–		182	–	59.5	–
<i>Macropus robustus</i>	4	39.2		74.8		16.7		165.6	5.9	53.2	2.5
<i>Macropus rufus</i>	5	281	42.4	486	97.7	168.7	14.4	181.3	11.6	63.5	7.1
<i>Macropus irma</i>	1	–		–		–		154.7	–	57.9	–
<i>Macropus dorsalis</i>	6	17.5		213.3	16	79.5	4	142.8	5.5	52.9	3.5
<i>Macropus parma</i>	6	119.3	6.8	147.4	14.6	2.6		127.4	2	49.2	3
<i>Macropus rufogriseus</i>	8	18.5		21.3		13.3		144.6	9.9	54.3	5.7
<i>Macropus eugenii</i>	9	126.8	7.5	11.3		60.6	1.3	138.2	4.1	47.7	2.2
<i>Macropus greyi</i>	2	4.6		8.5		–		151	0.9	59.5	–
<i>Procoptodon goliah</i>	1	320	–	605	–	208	–	189.1	–	65	–
<i>Sthenurus andersoni</i>	1	–		–		130.5	–	178.1	–	56.6	–
<i>Sthenurus tindalei</i>	1	319	–	494	–	168.1	–	154.9	–	52.7	–
<i>Sthenurus strirlingi</i>	4	316.1	24.6	544.5	33.7	170.5	6.3	172.4	3.3	54.1	2.3

## References

- Aplin, K. P., Archer, M., 1987. Recent advances in marsupial systematics with a new syncretic classification. In: Archer, M. (Ed.), Possums and Opossums: Studies in Evolution, Volume 1. Surrey Beauty, Chipping Norton, New South Wales, pp. 15–72.
- Archer, M., Hand, S. J., Godthelp, H., 2001. Australia's Lost World: Prehistoric Animals of Riversleigh. Indiana University Press, Bloomington, MN.
- Archer, M., Hand, S. J., Godthelp, H., Creaser, P., 1997. Correlation of the Cainozoic sediments of the Riversleigh world heritage fossil property, Queensland, Australia. In: Aguilar, J. P., Legendre, S., Michaux,

- J. (Eds.), Actes du Congrès Biochrom'97. Ecole Pratique des Hautes études Institut de Montpellier, Montpellier, France, pp. 131–152.
- Argot, C., 2001. Functional-adaptive anatomy of the forelimb in Didelphidae, and the palaeobiology of the Paleocene marsupials *Mayulestes ferox* and *Pucadelphys andinus*. *Journal of Morphology* 247, 51–79.
- Argot, C., 2002. Functional-adaptive anatomy of the hindlimb anatomy of extinct marsupials, and the palaeobiology of the Paleocene marsupials *Mayulestes ferox* and *Pucadelphys andinus*. *Journal of Morphology* 253, 76–108.
- Argot, C., 2003a. Postcranial functional adaptations in the South American Miocene borhyaenoids (Mammalia: Metatheria): *Cladosictis*, *Pseudonotictis* and *Sipalocyon*. *Alcheringa* 27, 303–356.
- Argot, C., 2003b. Functional adaptations of the postcranial skeleton of two Miocene borhyaenoids (Mammalia: Metatheria), *Borhyaena* and *Prothylacinus* from South America. *Palaeontology* 46, 1213–1267.
- Argot, C., 2004. Functional-adaptive features and palaeobiologic implications of the postcranial skeleton of the Late Miocene sabretooth borhyaenoid *Thylacosmilus atrox* (Metatheria). *Alcheringa* 28, 229–266.
- Bishop, N., 1997. Functional anatomy of the macropodid pes. *Proceedings of the Linnean Society, New South Wales* 117, 17–50.
- Bourke, D. W., 1989. Observations on the behaviour of the Grey Dorcopsis Wallaby *Dorcopsis luctosa* (Marsupialia: Macropodidae) in captivity. In: Grigg, G., Jarman, P., Hume, I. (Eds.), Kangaroos, Wallabies and Rat Kangaroos. Surrey Beatty, Sydney, pp. 633–640.
- Buchmann, O. L. K., Guiler, E. R., 1974. Locomotion in the potoroo. *Journal of Mammalogy* 55, 203–206.
- Case, J. A., 1984. A new genus of potoroinae (Marsupialia: Macropodidae) from the miocene Ngapakaldi local fauna, South Australia, and a definition of the potoroinae. *Journal of Paleontology* 58, 1074–1086.
- Christiansen, P., 2002. Locomotion in terrestrial mammals: the influence of body mass, limb length and bone proportions on speed. *Zoological Journal of the Linnean Society* 136, 685–714.
- Cooke, B. N., Kear, B. P., 1999. Evolution and diversity of kangaroos (Macropodoidea: Marsupialia). *Australian Mammalogy* 21, 27–29.
- Dawson, L., 2004. A new fossil genus of forest wallaby (Marsupialia: Macropodinae) and a review of *Protemnodon* from eastern Australia and New Guinea. *Alcheringa* 28, 275–290.
- Eftman, H. O., 1929. Functional adaptations of the pelvis in marsupials. *Bulletin of the American Museum of Natural History* 58, 189–232.
- Finch, M. E., Freedman, L., 1988. Functional morphology of the limbs of *Thylacoleo carnifex* Owen (Thylacoleonidae: Marsupialia). *Australian Journal of Zoology* 36, 251–272.
- Flannery, T. F., 1980. *Macropus mundjabus*, a new kangaroo (Marsupialia: Macropodidae) of uncertain age from Victoria, Australia. *Australian Mammalogy* 3, 35–51.
- Flannery, T. F., 1982. Hindlimb structure and evolution in the kangaroos (Marsupialia: Macropodoidea). In: Rich, P. V., Thompson, E. M. (Eds.) *The Vertebrate Fossil Record of Australasia*. Monash University Press, Clayton, Australia, pp. 508–524.
- Flannery, T. F., 1992. New pleistocene marsupials (Macropodidae, Diprotodontidae) from subalpine habitats in Irian Jaya. *Alcheringa* 16, 321–331.
- Flannery, T. F., 1994. The fossil land mammal record of New Guinea: a review. *Science in New Guinea* 20, 39–48.
- Flannery, T. F., Archer, M., 1987. *Hypsiprymnodon bartholomaii* (Potoroidae: Marsupialia), a new species from the Dwornamor local fauna and a reassessment of the phylogenetic position of *H. moschatus*. In: Archer, M. (Ed.), *Possums and Opossums: Studies in Evolution*. Surrey Beatty, Sydney, pp. 749–758.
- Flannery, T. F., Martin, R., Szalay, A., 1996. *Tree Kangaroos: A Curious Natural History*. Reed Books, Melbourne, Australia.
- Flannery, T. F., Rich, T. H., Turnbull, W. D., Lundelius, E. L. Jr., 1992. The macropodoidea of the early Pliocene Hamilton local fauna from Victoria, Australia. *Fieldiana Geology* 25, 1–37.
- Garland, T. Jr, Janis, C. M., 1993. Does metatarsal/femur ratio predict the maximum running speed in cursorial mammals? *Journal of Zoology, London* 229, 133–151.
- Goldfinch, A. J., Molnar, R. E., 1978. Gait of the brush-tail possum (*Trichosurus vulpecula*). *Australian Zoology* 19, 277–289.
- Guerin, G., 2004. Plant macrofossils associated with the Riversleigh macrofauna. *Australian Biology* 17, 55–62.
- Hildebrand, M., 1985. Digging in quadrupeds. In: Hildebrand, M., Bramble, D. M., Leim, K. F., Wake, D. B. (Eds.), *Functional Vertebrate Morphology*. Belknap, Cambridge, MA, pp. 89–109.
- Hildebrand, M., 1988. *Analysis of Vertebrate Structure*, 3rd ed. Wiley, New York.
- Hope, G. S., Flannery, T. F., Boardi, N., 1993. A preliminary report of changing quaternary mammal faunas in subalpine New Guinea. *Quaternary Research* 40, 117–126.
- Howell, B. A., (1944). *Speed in Animals. Their Specialisation for Running and Leaping*. University of Chicago Press, Chicago.
- Huey, R. B., Bennett, A. F., 1987. Phylogenetic studies of co-adaptation: preferred temperatures versus optimal performance temperatures of lizards. *Evolution* 41, 1098–1115.
- Jenkins, F. A. Jr., 1971. Limb posture and locomotion in the Virginia opossum (*Didelphis marsupialis*) and in other non-cursorial mammals. *Journal of Zoology, London* 165, 303–315.
- Johnson, P. M., Strahan, R., 1982. A further description of the musky rat kangaroo, *Hypsiprymnodon moschatus* Ramsay, 1876 (Marsupialia: Potoroidae), with notes on its biology. *Australian Zoology* 21, 27–46.
- Kear, B. P., Cooke, B. N., 2001. A review of macropodoid systematics with the inclusion of a new family. *Memoirs of the Association of Australasian Palaeontologists* 25, 83–101.
- Kear, B. P. Archer, M., Flannery, T. F., 2001a. Postcranial morphology of *Ganguroo bilamina* Cooke, 1997 (Marsupialia: Macropodidae) from the middle Miocene of Riversleigh, northwestern Queensland. *Memoirs of the Association of the Australasian Palaeontologists* 25, 123–138.
- Kear, B. P. Archer, M., Flannery, T. F., 2001b. Bulungamayine (Marsupialia: Macropodoidea) postcranial remains from the late Miocene of Riversleigh northwestern Queensland. *Memoirs of the Association of the Australasian Palaeontologists* 25, 103–122.
- Macphail, M. K., 1997. Late Neogene climates in Australia: fossil pollen- and spore-based estimates in retrospect and prospect. *Australian Journal of Botany* 45, 425–464.
- Maddison, W. P., Maddison, D. R., 2003. *Mesquite*: a modular system for evolutionary analysis. Version 1.0. <http://mesquiteproject.org>.

- McGowran, B., Li, Q. Y., 2002. Sequence biostratigraphy and evolutionary palaeoecology: foraminifera in the Cenozoic Era. *Memoirs of the Association of the Australasian Palaeontologists* 27, 167–188.
- Megirian, D., 1992. Interpretation of the Miocene Carl creek limestone, northwestern Queensland. *The Beagle, Records of the Northern Territory of Museum of Arts and Science* 9, 219–248.
- Menzies, J. I., Ballard, C., 1994. Some new records of pleistocene megafauna from New Guinea. *Science in New Guinea* 20, 113–139.
- Muizon, C. de., 1998. *Mayulestes ferox*, a borhyaenoid (Metatheria: Mammalia) from the early Paleocene of Bolivia. Phylogenetic and palaeobiologic implications. *Geodiversitas* 20, 19–142.
- Munson, C. J., 1992. Postcranial morphology of *Ilaria* and *Ngapakaldia* (Vombatiformes: Marsupialia) and the phylogeny of the vombatiforms based on postcranial morphology. *University of California Publications in Zoology* 125, 1–99.
- Murray, P. F., 1991. The Pleistocene megafauna of Australia. In: Vickers-Rich, P., Monaghan, J. M., Baird, R. F., Rich, T. H. (Eds.), *Vertebrate Palaeontology of Australasia*. Pioneer Design Studio, Monash University, Melbourne, Australia, pp. 1071–1164.
- Posada, D., Crandall, K., 1998. Modeltest: testing the model of DNA substitution. *Bioinformatics* 14, 817–818.
- Prideaux, G., 2004. Systematic and evolution of the sthenurine kangaroos. *University of California Publications in Geological Sciences* 146, 1–646.
- Ride, W. D. L., Pridmore, P. A., Barwick, R. E., Wells, R. T., Heady, R. D., 1997. Towards a biology of *Propleopus oscillans* (Marsupialia: Propleopinae: Hysiprymnodontidae). *Proceedings of the Linnean Society, New South Wales* 117, 243–328.
- Strahan, R., 1998. *The Mammals of Australia*. Reed New Holland, Sydney, Australia.
- Swofford, D. L., 2000. PAUP\*. Phylogenetic Analysis Using Parsimony (\*and Other Methods). Version 4. Sinauer, Sunderland, MA.
- Szalay, F. S., 1994. *Evolutionary History of the Marsupials and an Analysis of Osteological Characters*. Cambridge University Press, New York.
- Szalay, F. S., Sargis, E. J., 2001. Model-based analysis of postcranial osteology of marsupials from the Paleocene of Itaborai, Brazil, and the phylogenetics and biogeography of Metatheria. *Geodiversitas* 23, 139–302.
- Tedford, R. H., 1967. The fossil Macropodidae from Lake Menindee, New South Wales. *University of California Publications in Geological Sciences* 64, 1–156.
- Van Valkenburgh, B., 1987. Skeletal indicators of locomotor behaviour in living and extant carnivores. *Journal of Vertebrate Paleontology* 7, 162–182.
- Webster, A. J., Purvis, A., 2001. Testing the accuracy of methods for reconstructing ancestral states of continuous characters. *Proceedings of the Royal Society of London, Biological Sciences* 269, 143–149.
- Wells, R. T., Tedford, R. H., 1995. *Sthenurus* (Macropodidae: Marsupialia) from the Pleistocene of Lake Callabonna, South Australia. *Bulletin of the American Museum of Natural History* 225, 1–111.
- Westerman, M., Burk, A., Amrine-Madsen, H., Prideaux, G., Case, J. A., Springer, M. S., 2002. Molecular evidence for the last survivor of an ancient kangaroo lineage. *Journal of Mammalian Evolution* 9, 209–223.
- Windsor, D. E., Dagg, A. I., 1971. Gaits in the Macropodinae (Marsupialia). *Journal of Zoology, London* 163, 165–175.
- Woodburne, M. O., MacFadden, B. J., Case, J. A., Springer, M. S., Pledge, N., Power, J. D., Woodburne, J. M., Springer, K. B., 1993. Land mammal biostratigraphy of the Etadunna formation (late Oligocene) of South Australia. *Journal of Vertebrate Paleontology* 14, 483–515.
- Wroe, S., 1996. An investigation of phylogeny in the giant extinct rat kangaroo *Ekaltadeta* (Propleopinae: Potoroidae: Marsupialia). *Journal of Paleontology* 70, 681–690.