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Palaeoecology of Oligo-Miocene macropodoids determined from craniodental and calcaneal data

Christine M. Janis[1,2,*], John Damuth[3], Kenny J. Travouillon[4,5], Borja Figueirido[6], Suzanne J. Hand[7], and Michael Archer[7]

[1] Department of Ecology and Evolutionary Biology, Brown University, Providence, RI 02912, USA (christine_janis@Brown.edu)
[2] School of Earth Sciences, University of Bristol, Bristol BS8 1RJ, UK
[3] Department of Ecology, Evolution and Marine Biology, University of California Santa Barbara, Santa Barbara, CA 93106, USA (john.damuth@lifsci.ucsb.edu)
[4] School of Earth Sciences, University of Queensland, St. Lucia, Queensland 4072, Australia (k.travouillon@uq.edu.au)
[5] Western Australian Museum, Locked Bag 49, Welshpool DC, WA 6986, Australia (Kenny.Travouillon@museum.wa.gov.au) (current address)
[6] Departmento Ecología y Geología, Facultad de Ciencias, Universidad de Málaga, 29071-Málaga, Spain (Borja.Figuirido@uma.es)
[7] PANGEA Research Centre, School of Biological, Earth and Environmental Sciences, University of New South Wales, New South Wales 2052, Australia (s.hand@unsw.edu.au, m.archer@unsw.edu.au)
* To whom correspondence should be addressed. E-mail: christine_janis@Brown.edu

Abstract

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Analyses of craniodental and calcaneal material of extant macropodoids show that both dietary and locomotor types are statistically distinguishable. Application of the craniodental data to fossil macropodoids from the Oligo-Miocene of South Australia (Lake Eyre Basin) and Queensland (Riversleigh World Heritage Area) shows that these taxa were primarily omnivores or browsers. Specialized folivorous browsers were more prevalent in the Queensland deposits than in those of South Australia, suggesting more mesic conditions in the former. The calcaneal data showed that the Oligo-Miocene taxa clustered with extant generalized hoppers, in contrast to prior speculation that balbarids were quadrupedal rather than bipedal.

Keywords

Macropodoidea, palaeocology, Riversleigh, Lake Eyre Basin, craniodental measurements, dietary behaviour, calcaneal measurements, locomotion.

Introduction

The Macropodoidea (kangaroos and rat-kangaroos) first radiated in the late Oligocene to early Miocene. The Oligo-Miocene record of these marsupials is primarily from the deposits in Queensland (Riversleigh World Heritage Area) and South Australia (Lake Eyre Basin) and the Northern Territory. The total age range of these fossil deposits range from around 25 Ma to 7 Ma (Black et al., 2012). The relative abundance of macropodoids in the late Oligocene localities suggests that they may have had origins earlier in the Palaeogene, with the molecular data suggesting the Eocene (e.g., Meredith et al., 2008), but they are absent from the possibly earlier Oligocene locality, the Pwerte Marnte Marnte local fauna in the Northern Territory (Murray and Megirian, 2006), as well as from the Eocene Tingamara deposit in south-eastern Queensland (Black et al., 2012).

The Oligo-Miocene macropodoids were small to medium-sized animals, generally ranging in size from forms about the size of a modern-day bettong (*Bettongia* spp., mass 0.5–2.5 kg) to a pademelon (*Thylogale* spp., mass 4–12 kg). The largest one considered here, *Rhizosthenurus flanneryi* from the early-late Miocene Encore Local Fauna, was about the size of a Red-necked Wallaby (*Macropus rufogriseus*, mass 11–30 kg). In contrast, the extant large kangaroos, such as the Eastern Grey and Red Kangaroos (*Macropus giganteus* and *M. rufus*), weigh between 35 and 80 kilograms. The Oligo-Miocene macropodoids mainly had thin-enamelled brachydont (low-crowned) dentitions and no evidence of the molar progression seen in many extant kangaroos (primarily species of *Macropus*). These taxa have thus been considered to be forest-dwelling browsers or omnivores, especially in the Riversleigh deposits, where habitats have been interpreted to include cool

temperate rainforests, at least during the early and middle Miocene (Archer et al., 1989, 1997, 2006; Travouillon et al., 2009). The limited postcranial material available for these macropodoids has led to speculation that some of them (e.g., the balbarid *Nambaroo*, see Kear et al., 2007) were not hoppers, but instead were quadrupedal bounders, like the extant Musky Rat-kangaroo (*Hypsiprymnodon moschatus*).

This paper attempts to make a more quantitative determination of the palaeoecology of these extinct macropodoids by comparing their morphology with that of extant macropodoids whose behaviours are known. Specifically we examine craniodental morphology in relation to dietary behaviour, and calcaneal morphology in relation to locomotor behaviour (the calcaneum has been shown to be an extremely informative bone in assessing marsupial locomotor habits: Bassarova et al., 2009). We use the craniodental data to investigate two issues in palaeoecology: first we investigate whether there were dietary differences in the animals, indicative of environmental differences, between the late Oligocene and early Miocene macropodoids from South Australia and Queensland; and secondly we investigate whether, over the Oligo-Miocene time span in each region, there were changes in the dietary behaviours that reflect environmental changes. We also use the calcaneal data to investigate the issue of the range of locomotor behaviours of these macropodoids, specifically to see if there was a prevalence of non-hopping-adapted forms.

Materials And Methods

Taxa included. For the craniodental data our reference group of extant macropodoids included 42 individuals (representing 42 species: including *Hypsiprymnodon moschatus*, five potoroines, and at least one representative of every extant macropodine genus: see appendix table A1). These individuals were drawn from a much larger dataset, but we were limited for this analysis to those specimens with a completely erupted but relatively unworn dentition (at least an unworn last molar), as explained below. For the calcaneal data our reference group of extant macropodoids included 44 individuals (representing 33 species: including *Hypsiprymnodon moschatus*, seven potoroines, and at least one representative of every extant macropodine genus: see appendix table A3). For these data, we were limited to specimens for which a disarticulated calcaneum was available.

Three families of macropodoids are represented in Oligo-Miocene assemblages in Australia (systematics following that of Prideaux and Warburton, 2010). Unfortunately, most are represented only by fragmentary dental material, but we were able to include in our sample a number of representative taxa: 37 individuals (representing 30 species) for the craniodental data (see appendix table A2), three of which were represented by complete crania and jaws, and the rest by mandibles; and ten individuals (representing ten species) for the calcaneal data (see appendix table A4).

1. The Hypsiprymnodontidae, the basal family among extant macropodoids, is represented today by the Musky Rat-kangaroo, *Hypsiprymnodon moschatus*, and in the Oligo-Miocene by extinct species of this genus and larger, possibly more faunivorous forms, such as *Ekaltadeta ima*. The earliest known hypsiprymnodontid is from the early Miocene (Riversleigh Faunal Zone B) (Bates et al., 2014). The extant Musky Rat-kangaroo is omnivorous/frugivorous (Dennis, 2002, 2003), with relatively long forelimbs and short hindlimbs, and is the only extant macropodoid that is a quadrupedal bounder rather than a hopper (Windsor and Dagg, 1971). This form of locomotion is thought to represent the primitive condition for macropodoids. Dental material (maxillae and dentaries) of extinct hypsiprymnodontids suggests a similar diet to that of the living species (Bates et al., 2014). We did not include any extinct hypsiprymnodontids in this study because our interest was in the more herbivorous taxa, and how they reflected Australian habitats.

2. The Balbaridae, an extinct group of kangaroos, has been sometimes considered to be more primitive than all other macropodoids, and is either the sister taxon to the Hypsiprymnodontidae, or the Macropodidae (see Kear and Cooke, 2001). The earliest known balbarids are from the late Oligocene (Etadunna Formation, Zone C [Woodburne et al., 1994]; Riversleigh Faunal Zone A [Cooke, 1997b; Archer et al., 2006; Travouillon et al., 2006, 2011]), while the youngest one is from the late middle or early late Miocene Encore Site, also from Riversleigh (K. J. T. pers. observ.). Balbarids (e.g., species of *Balbaroo* and *Nambaroo*) paralleled macropodines in their possession of distinctly bilophodont molars (a derived condition), but retained more primitive postcrania (especially retention of the hallux). The argument has been presented that balbarids, like *H. moschatus*, did not hop (e.g., Kear et al., 2007; Black et al., 2014). Sixteen individuals (representing five genera and up to 13 species) are included in the craniodental data, and six individuals (representing two genera and up to six species) are included in the calcaneal data.

3. The Macropodidae (kangaroos and most rat-kangaroos), are represented today by three subfamilies: Potoroinae (rat-kangaroos, excluding *H. moschatus*); Lagostrophinae (the Banded Hare-wallaby, *Lagostrophus fasciatus*); and Macropodinae (kangaroos and wallabies, including tree-kangaroos). Macropodids comprise 14 extant genera and several extinct ones. They were represented in the Oligo-Miocene by one extant subfamily (the Potoroinae) and two extinct subfamilies, the Bulungamayinae and the Sthenurinae.

The Potoroinae, represented today by three extant genera and one recently extinct one, are regarded here as the most basal macropodid subfamily (e.g., Prideaux and Warburton, 2010), but some authors place them as a separate family within the Macropodoidea. The earliest potoroine (“*Kyeema mahoneyi*” [nomen nudum]) is known from the late Oligocene Etadunna Formation, Zone A [Woodburne et al., 1994], although they do not appear in Riversleigh until the middle Miocene in Faunal Zone C assemblages as *Bettongia moyesi* [Flannery and Archer, 1987]). Extant potoroines are small forms (the largest, the Rufous Bettong, *Aepyprymnus rufescens*, has a mass of ~3 kg). While they can all hop, some taxa more frequently bound quadrupedally (e.g., species in the genus *Potorous*: Baudinette et al., 1993). All potoroines have bunolophodont molars, reflecting a more omnivorous (i.e., fungivory or frugivory) diet than that of the more strictly

herbivorous (folivorous) kangaroos (subfamily Macropodinae). Extinct potoroines (e.g. "*Kyeema"*) appear to have been similar to the extant ones, and share with them the feature of a long sectorial third premolar. Three extinct potoroine individuals (representing two species) are included in the craniodental data, and one extinct species in the calcaneal data.

The bulungamayines, which may be a basal paraphyletic stem group rather than a monophyletic subfamily (e.g., Cooke, 1997a), had more derived postcrania than the balbarids and there is no speculation that they were not hoppers. However, their dentition is less derived; most were bunolophodont, such as species of *Purtia* and *Bulungamaya*, while some were bilophodont, such as species of *Ganguroo* and *Wabularoo*. Bulungamayines are first known from the late Oligocene (Etadunna Formation Zone C [Woodburne et al., 1994]) and Riversleigh Fauna Zone A [Cooke et al., 2015; Travouillon et al., 2006, 2011, 2014, 2016]). Their last appearance is in the late middle to early late Miocene (Riversleigh Faunal Zone D [Travouillon et al., 2006, 2011, 2014]). Thirteen individuals (representing four genera and seven species) are included in the craniodental data. Unfortunately, we were unable to obtain any calcaneal data for bulungamayines.

Sthenurines, the sister taxon to the macropodines, are best known as the giant short-faced kangaroos of the Plio-Pleistocene. While some Pleistocene species had body masses two or three times greater than any extant kangaroo (Helgen et al., 2006), the Miocene taxa were smaller, but still relative giants in the macropodoid fauna of the time (Travouillon et al., 2009). Sthenurines, like macropodines, have bilophodont molars. The earliest known sthenurine is *Wanburoo hilarus* from the middle Miocene of Riversleigh (Faunal Zone C [Cooke, 1999; Prideaux and Warburton, 2010; Travouillon et al., 2014]). *Wanburoo hilarus* is slightly smaller than *Rhizosthenurus flanneryi,* ranging in body mass between 7–8kg, versus 9–15kg for the latter (Travouillon et al., 2009). Three individuals (representing two genera and two species) are represented in the craniodental data and one individual in the calcaneal data.

The earliest undoubted macropodine is *Dorcopsoides fossilis* (Woodburne, 1967) from the late Miocene Alcoota Local Fauna in the Northern Territory. This faunal assemblage has been interpreted (Murray and Megirian, 1992) to be approximately seven Ma. One individual of *D. fossilis* was included in the calcaneal data, but none in the craniodental data. Various undescribed taxa from the late Oligocene Etadunna assemblages have been proposed as macropodines, such as the taxon "Macropodine Genus P. sp. A" included here in both the craniodental and calcaneal data (Woodburne et al., 1994). However, one of us (KJT) considers this taxon to likely be a balbarid (due to the presence of posterior cingulid on the lower molars and large upper canines).

Measurements. Fourteen craniodental measurements were taken (see fig. 1, and table 1), and 25 calcaneal measurements (see fig. 2, and table 2). All measurements were in millimetres using digital callipers. The craniodental measurements were based on those known to distinguish extant ungulates according to dietary behaviour (grazer, browser, and mixed feeder: see Janis, 1990a, b; Mendoza et al., 2002). The measurement "wear rate" was determined as the height of the third molar minus the height of the first molar (in a dentition where the fourth molar

Table 1. Craniodental measurements.

SKL	Total cranium length, measured from the tip of the premaxilla to the occipital condyle.
SNL	Snout length, measured from the tip of the premaxilla to the boundary between the molars and premolars.
MZW	Muzzle width, measured on the underside of the cranium at the premaxilla/maxilla boundary (a minimal width measurement).
PAW	Palatal width, measured as the greatest width between the upper teeth (usually at the level of the third molar).
ZY1	Depth of the zygomatic arch at its narrowest point.
ZY2	Depth of the zygomatic arch at its broadest point (including the masseteric process).
JL	Length of the mandible from the tip of the dentary to the jaw condyle.
JMB	Depth of the jaw angle, measured from the jaw condyle to the base of the angle of the jaw.
JD	Depth of the jaw ramus, measured at the level between the second and third molars.
LPRL	Length of the lower premolar, measured along the base of the tooth (i.e., an alveolar measurement).
LMRL	Length of the lower molar row, measured along the base of the tooth (i.e., an alveolar measurement).
M4H	Unworn height of the fourth molar.
M3H	Height of the third molar in a jaw with M4 erupted but unworn.
M1H	Height of the first molar in a jaw with M4 erupted but unworn.

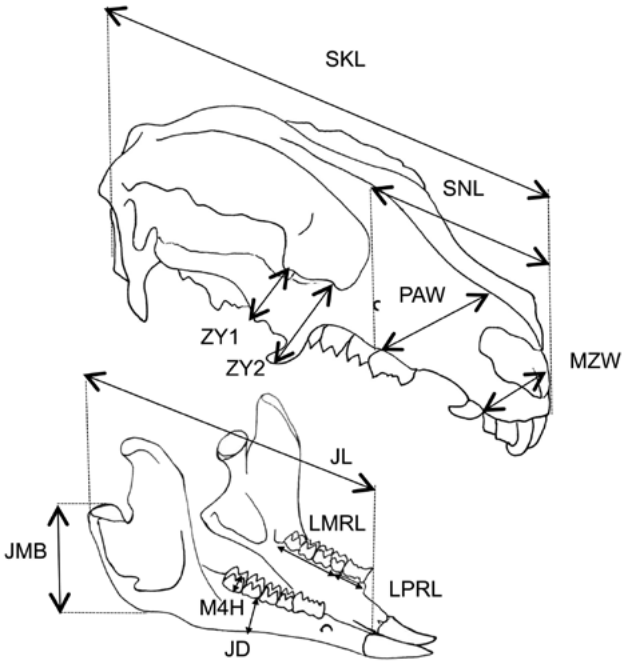

Figure 1. Craniodental measurements (skull of *Dendrolagus lumholtzi*): for description of the variables see table 1. Artwork by Gina Roberti.

had erupted, but showed little or no wear): this provided an estimate of how rapidly the first molar had been worn down in the time of the eruption sequence, from the eruption of the first molar to the eruption of the fourth.

The calcaneal measurements were based in part on those taken by Bassarova et al. (2009), which distinguished extant marsupials according to substrate use/locomotor type (terrestrial, arboreal, hopping), with the inclusion of some additional measurements that we considered might further distinguish between different types of hopping behaviour. These same measures were used in the study of sthenurine locomotion by Janis et al. (2014).

Statistical Analyses. The multivariate analyses included both Principal Components Analysis (PCA) of log-transformed variables and Linear Discriminant Analysis. All the discriminant analyses were performed by the stepwise approach. This approach was preferred over the direct method because it only uses the best set of variables for discriminating among the groups compared (e.g., Mendoza et al., 2002; Figueirido et al., 2010; Samuels et al., 2014). The selection criterion in the stepwise model was the inclusion of variables with F probability between < 0.05–0.01 (depending on sample size and the number of variables), and the exclusion of variables with F probability > 0.1. The first analysis was run with an F probability < 0.05 of inclusion and, if this analysis included too many variables for the sample size of each specific analysis (see above), we modified the F probability up to < 0.01. The F probability for excluded variables was not modified in all of the analyses performed. The power of the discriminant functions was evaluated from the value of the Wilks' lambda statistic (λ). The effectiveness of the discrimination function was assessed with the percentage of correct assignments using the leave-one-out cross-validation

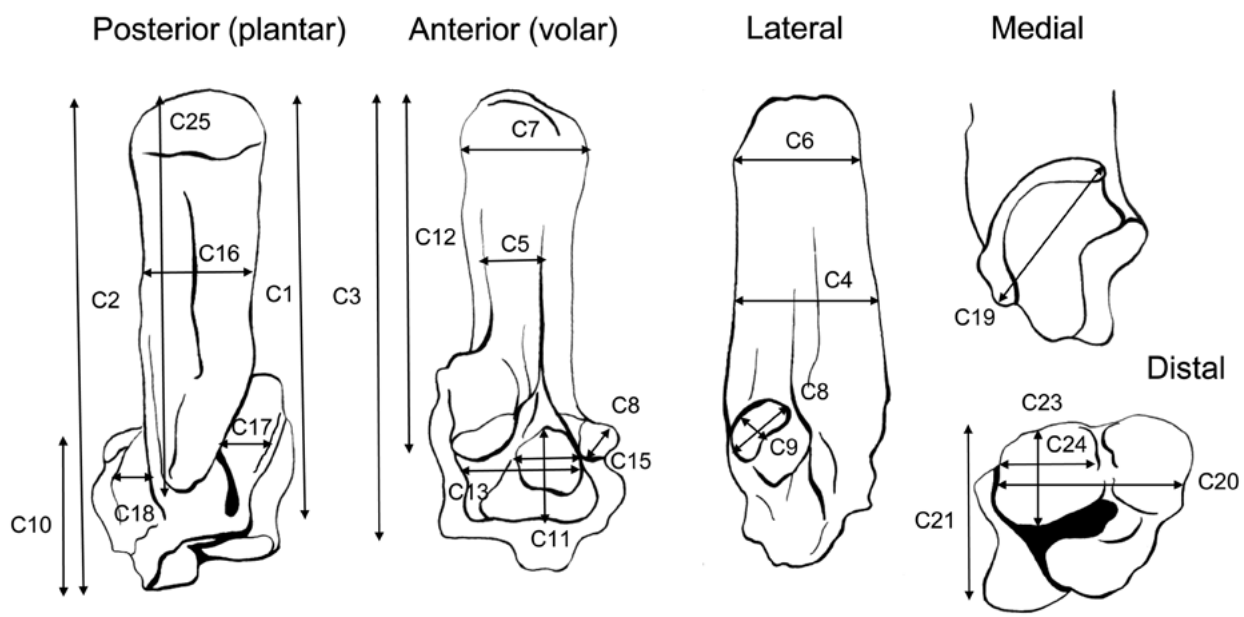

Figure 2. Calcaneal measurements (calcaneum of *Macropus agilis*): for description of the variables see table 2. Artwork by Nativad Chen.

approach described in Mendoza et al. (2002). The discriminant functions for the Stepwise Discriminant Analyses are provided in appendix table A5.

The extant macropodoids were classified as to dietary type (grazer, browser, mixed feeder, and omnivore) (see appendix table A1: data obtained primarily from Cronin, 2008, and Martin, 2005). The extant kangaroos were classified as "rare hopper or non-hopper" (tree-kangaroos and the musky rat-kangaroo), "specialized hopper" (species of the genus *Macropus*), and "regular hopper" (all other macropodoids) (see appendix table A3).

Results

Craniodental analyses with full set of measurements. The measurements shown in Figure 1 and Table 1 represent a subset of a larger set of measurements, many of which proved unsuitable for use in these analyses. For example, the variables removed included the height of the coronoid process (almost never preserved in fossils, and not a strong indicator of dietary preference when used in extant taxa alone), the length of the jaw symphysis (the variation in this measurement was excessive), and measures of the widths of the incisors (which appear to carry a phylogenetic signal rather than a dietary

Table 2. Calcaneal measurements.

C1	Maximum plantar (posterior) anterioposterior (dorsoventral) length (measured from tip of calcaneal tuber to posterior border of calcaneocuboid facet).
C2	Maximum lateral anterioposterior (dorsoventral) length (measured from tip of calcaneal tuber to anterior border of lateral calcaneocuboid facet).
C3	Maximum medial anterioposterior (dorsoventral) length (measured from tip of calcaneal tuber to medial anterior border of calcaneocuboid facet).
C4	Dorsoplantar width of midshaft of calcaneal tuber.
C5	Mediolateral width of midshaft of calcaneal tuber measured on anterior (volar) side (main dorsal ridge only).
C6	Dorsoplantar width of top of calcaneal tuber.
C7	Mediolateral width of top of calcaneal tuber.
C8	Anteroposterior (dorsoventral) width of fibular facet.
C9	Mediolateral width of fibular facet.
C10	Anterposterior (dorsoventral) length of calcaneal head on lateral side, from top of fibular facet to base of lateral cubonavicular facet.
C11	Anterposterior (dorsoventral) length continuous lower ankle joint (CLAJ) measured from the top of the ectal facet to the bottom of joint articulation.
C12	Anterioposterior (dorsoventral) length of calcaneal heel (measured from tip of calcaneal tuber to base of sustentacular facet).
C13	Mediolateral width across CLAJ.
C14	Maximum width across calcaneal head, measured on posterior (plantar) side.
C15	Length (mediolateral) of ectal facet.
C16	Mediolateral width of midshaft of calcaneal tuber measured on posterior (plantar) side.
C17	Width of sulcus for tendon of peroneus longus (taken as inside measurement).
C18	Width of sulcus for tendon of flexor digitorum longus (taken as inside measurement).
C19	Length of the ridge along the lateral/dorsal side of the sustentaculum tali.
C20	Width (mediolateral) across anterior surface of cubonavicular facet.
C21	Length (anteroposterior/dorsoplantar) across surface of cubonavicular facet.
C22	Width (mediolateral) across posterior base of calcaneum, including the cubonavicular facet, and the base of the sustentacular ridge (if flush with CN facet).
C23	Width (dorsoplantar) of medial cubonavicular facet.
C24	Width (mediolateral) of the medial surface of the cubonavicular facet.
C25	Length of the roughened area on the plantar side of the calcaneal heel.

one). Even with this reduced set of measurements, only three fossil taxa had a complete set: "Genus P sp. A" (possibly a balbarid), *Ganguroo robustiter* (a bulungamayine), and *Rhizosthenurus flanneryi* (a sthenurine).

The PCA of the extant macropodoid skulls yielded two significant principal components (PCs), which jointly explained more than 85% of the original variance (fig. 3). The first PC, which explains 74.13% of the variance, appears to be largely, but not entirely, a size axis: most of the variables have high positive loadings (ranging from 0.808 for muzzle width [MZW] to 0.976 for jaw length [JL]), but the "wear rate" measure has much lower positive loadings (0.462), and the loadings for the lower premolar length has weakly negative loadings (-0.169). These low loadings may, respectively, simply reflect the fact that tooth wear rate is independent of body size (see Damuth and Janis, 2014), and that potoroines (among the smallest taxa) have long, sectorial premolars.

The second PC, which explains 11.02% of the variance, appears to be largely a shape axis. Variables with relatively high positive loadings are lower premolar length (LPRL: 0.895), muzzle width (MZW: 0.484), snout length (SNL: 0.171), and total cranium length (SKL: 0.165). Variables with relatively high negative loadings are wear rate (M3H–M1H: -0.369), both the minimum (ZY1) and maximum (ZY2) depth of the zygomatic arch (-0.205 and -0.264, respectively), the depth of the angle of the mandible (JMB: -0.175), and the lower fourth molar crown height (M4H: -0.152). As can be seen in Figure 3, the second component mainly separates the browsers (with positive scores) from the omnivores, mixed feeders and grazers (with negative scores). Note that, while they were not coded separately in the analyses, the tropical forest browsers, species of *Dendrolagus* (tree-kangaroos) and *Dorcopsis* (New Guinea forest wallabies) are clearly distinguished from the other browsers: *Wallabia* (the Swamp Wallaby), *Setonix* (the Quokka), and species of *Dorcopsulus* (New Guinea woodland wallabies). In this and all other analyses the less specialized browsers mainly fall at the positive end of the clustering of the mixed feeders (*Setonix* is the exception). Because *Dendrolagus* and *Dorcopsis* do not form a clade (Meredith et al., 2008) this craniodental similarity must represent convergence related to diet. We term these browsers "specialized folivores" to avoid linking a dietary style with a particular modern type of habitat.

The variables with high negative scores on the second component mainly relate to the size of the masseter muscle (the deep angle of the jaw and zygomatic arch) and the wear experienced by the dentition (the wear rate and the height of the fourth molar), all of these variables reflecting the demands of mastication relating to the more abrasive diet of the grazers and mixed feeders. The species of *Macropus* have slightly higher scores on the second component than some of the mixed feeders, possibly because they share with some of the browsers (*Dorcopsulus* spp. and *Wallabia*) the features of a long cranium and long snout (which have weakly positive scores on this component). Performing the PCA with the inclusion of the fossil taxa (see fig. 3) did little to change the placement of the extant taxa. All three of the extinct species fall within the realm of the browsers, with *Rhizosthenurus flanneryi* being the most similar to the extant specialized folivorous browsers.

The stepwise discriminant analysis of the extant kangaroos showed excellent discrimination among the dietary categories, with 85.7% of the taxa being correctly classified (fig. 4). We considered reanalyzing the data with these two types of browsers as separate groups, but the sample size of the "regular browsers" (limited by nature, not by our data sampling) is too small. Appendix table A6 shows the probabilities for group assignment: misclassifications include *Bettongia penicillata* (taxon #5, classified as a mixed feeder rather than an omnivore, but with very similar probabilities for both categories); both species of

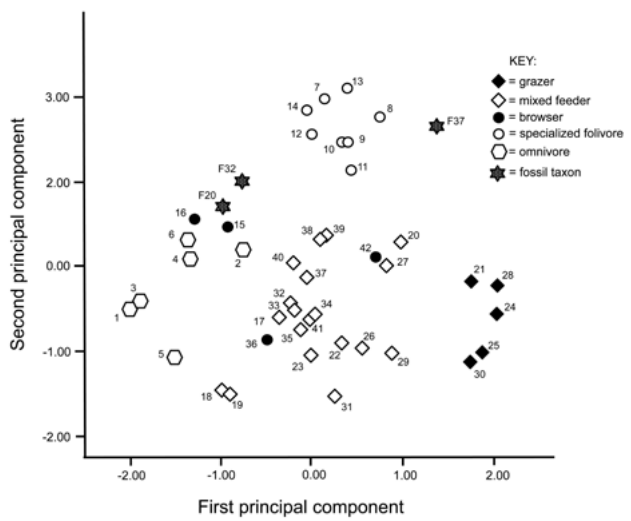

Figure 3. Principal Components Analysis of the complete set of craniodental data. Tables 3 and 4 provide the key to the numbers of the taxa in this figure. Specialized folivore" = species of *Dendrolagus* and *Dorcopsis*.

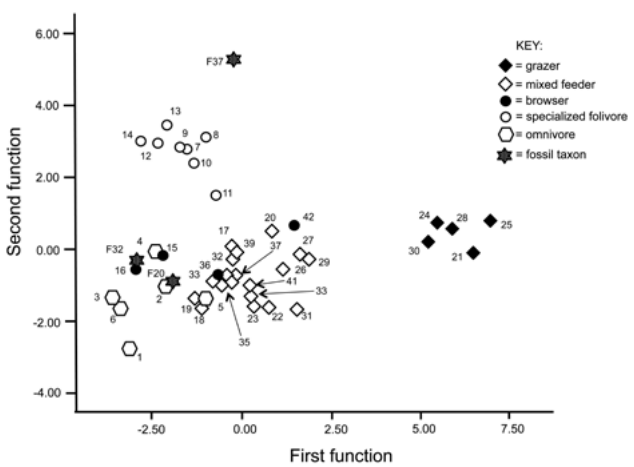

Figure 4. Stepwise discriminant analysis of the complete set of craniodental data. Tables 3 and 4 provide the key to the numbers of the taxa in this figure.

Dorcopsulus (taxa #15 and #16, classified as omnivores rather than as browsers); *Lagostrophus fasciatus* (taxon #19, classified as an omnivore rather than as a mixed feeder); and *Setonix brachyurus* and *Wallabia bicolor* (taxa #36 and #42, respectively, classified as mixed feeders rather than as browsers).

Although only three variables were selected by this analysis, the pattern of clustering of the taxa is strikingly similar to that in the PCA. The first function, accounting for 79.6% of the variance, has positive loadings for wear rate (M3H–M1H: 0.733) and mandibular depth (JMB: 0.183), and negative loadings for the length of the lower premolar (LPRL: -0.268). This axis clearly separates the grazers (with high positive scores) from the omnivores and the browsers (with negative scores), with the mixed feeders falling in the middle, with slightly positive scores. While the similar distribution of taxa to the PCA might lead to the conclusion that this discriminant function is also largely a size axis, note that the highest loading variable is for the wear rate, which is independent of body size (in terms of the statistical bias of the analysis; see Damuth and Janis, 2014), and that the premolar row length has negative values on this axis. However, it is true that it is the larger extant taxa that have the highest wear rates, so this variable is indeed correlated with body size ecologically if not statistically. Thus large extinct species with low wear rates would not have high scores on this function. Note the position of *Rhizosthenurus flanneryi*, which is of similar size to the smaller grazing *Macropus* species: in Figure 3 it clusters with *Macropus* spp. on the first principal component, but in Figure 4 it does not cluster with them on the first discriminant function.

The second function, accounting for almost all of the rest of the variance (20.3%), has positive values for the length of the lower premolar (LPRL: 0.619) and the depth of the angle of the mandible (JMB: 0.135), and negative values for the rate of tooth wear (M3H–M1H: -0.742). This function further separates the specialized folivore browsers from the other taxa, as they combine a long lower premolar with relatively low rates of tooth wear: the Musky Rat-kangaroo is distinguished by having the lowest scores on factor 2, possibly because of its relatively gracile mandible.

The inclusion of the three fossil taxa shows a similar placement for these taxa as with the PCA (fig. 3). "Genus P sp. A" (taxon #F20) and *Ganguroo robustiter* (taxon #F32) cluster with the omnivorous potoroines and the woodland browsing New Guinea wallabies (*Dorcopsulus* spp.): they are assigned a probability of being omnivores of 84.6% and 91.43%, respectively (see appendix table A6). *Rhizosthenurus flanneryi* (taxon #F37) again clusters with the specialized folivorous browsers (probability of being a browser of 100%), but now with higher scores on factor two than any extant taxon.

Craniodental analyses with reduced measurements: comparison of South Australian and Queensland fossil taxa. Because the Oligo-Miocene fossils tend to be so fragmentary (even if a complete cranium exists it may not come associated with a complete mandible), we did some experimental analyses of removing variables that were least likely to be preserved from the analysis, but retaining enough variables to obtain a signal that separated the extant taxa. Interestingly, we found that with only five mandibular variables (the depth of the mandible [JMB], the length of the premolar [LPRL], the length of the molar row [LMRL], the fourth molar crown height [M4H], and the wear rate [M3H–M1H]) we were still able to achieve an excellent level of discrimination among dietary categories in extant macropodoids, with a similar pattern of taxon clustering in the stepwise discriminant analysis as in the analysis with the full set of variables (see figs. 5 and 6). This set of variables could be obtained in a wide variety of extinct taxa, although there is still the restriction that they have to be of a specific stage of tooth eruption (i.e., with a fully erupted, but as yet unworn, or lightly worn, fourth lower molar, so that the variable "wear rate" could be obtained).

The discriminant analyses performed from the restricted set of measurements to separate among the dietary groups correctly classified 88% of the taxa. As in the analysis with the complete dataset, the regular browsers were classified either as omnivores (species of *Dorcopsulus*) or as mixed feeders (*Wallabia*) (see appendix table A6). *Setonix*, classified as a mixed feeder in the analysis with the complete dataset, is here assigned almost equal probabilities of being an omnivore or a mixed feeder. The only other misclassification is *Aepyprymnus rufescens* (classified as a mixed feeder rather than an omnivore).

The first significant function explains 82.7% of the variance: the variables with positive loadings are wear rate (M3H–M1H: 0.682), fourth lower molar height (M4H: 0.210), lower molar row length (LMRL: 0.108), and mandible depth (JMB: 0.095), and the variable with negative loadings is lower premolar length (LPRL: -0.475). The second significant function explains 16.4% of the variance: variables with positive loadings are lower premolar row length (LPRL: 0.469), depth of the mandible (JMB: 0.180), fourth lower molar height (M4H: 0.088), and lower molar row length (LMRL: 0.057), and the variable with negative loadings is wear rate (M3H–M1H: -0.553). The first function again separates the grazers (with high crowned molars and a high wear rate) from the browsers and the omnivores (with a long lower premolar). The second function separates the specialized folivorous browsers from other feeding types, again probably based on the length of the premolar, and also a low rate of tooth wear. The possession of a deep mandible is probably the reason for the moderately positive scores of the grazers and some of the mixed feeders, and a gracile mandible probably accounts for the low scores of the potoroines (plus *Hypsiprymnodon moschatus*) and the smaller macropodines on this function.

Adding fossil taxa as unknowns to this analysis produced the following results. In the South Australia sample (fig. 5), most of the late Oligocene taxa (balbarids [*Nambaroo,* taxon #4], the potoroine "*Keemya mahonyi*" [taxon #F1] and the possible balbarid "Genus P sp. A" [taxon #F20]) have low scores on both functions, clustering with the omnivorous extant potoroines. These taxa are all classified as omnivores, although *Nambaroo* has an almost equal probability of being a browser (see appendix table A6). However, *Ngamaroo archeri* (Macropodidae incertae sedis [taxa #F2 and #F3]) has higher scores on function two, falling closer to the specialized folivorous browsers, and both individuals are assigned to this category with high probability. In the early Miocene, some balbarids (the species of *Balbaroo*

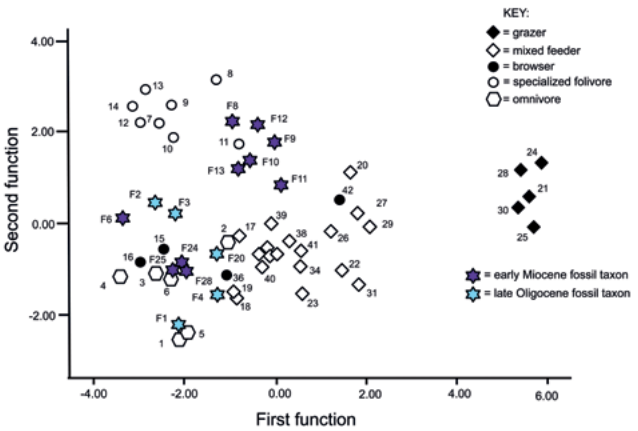

Figure 5. Stepwise discriminant analysis of the reduced set of craniodental data, with the inclusion of South Australian fossils. Tables 3 and 4 provide the key to the numbers of the taxa in this figure.

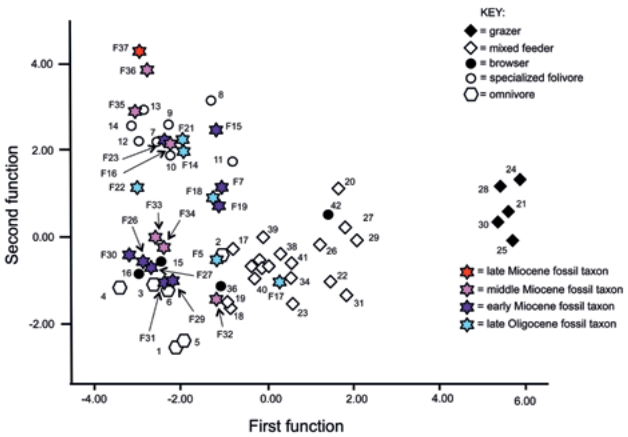

Figure 6. Stepwise discriminant analysis of the reduced set of craniodental data, with the inclusion of Queensland fossils. Tables 3 and 4 provide the key to the numbers of the taxa in this figure.

[taxa #F8–#F13]) cluster in the region of the specialized folivorous browsers; all but one of these are assigned a high probability of being browsers, the one exception being *Balbaroo* sp. B1 (taxon #F11), which is assigned as a mixed feeder. The species of *Nambaroo* (taxon #F6) still clusters close to the omnivores, and although it is assigned as an omnivore it has almost equal probability of being a browser (see appendix table A6). The three bulungamayine taxa, (species of the genera *Bulungamaya* and *Ganguroo* [taxa #F24, #F25, and #F28]), are firmly clustered with the omnivores, and all are assigned high probabilities of belonging to this category (appendix table A6). None of the bulungamayines cluster with the specialized folivorous browsers.

In the Queensland sample (fig. 6), among the late Oligocene taxon set some of the balbarids (*Galanarla tessellata* [taxon #F17] and *Nambaroo couperi* [taxon #F5]) cluster with the mixed feeders and omnivores respectively, and both are assigned high probabilities of belonging to these groupings (see appendix table A6). But other balbarids (*Wururoo dayamayi* [taxon #F14] and *Ganawamaya aediculus* [taxon #F18]) cluster with, or near to, the specialized folivorous browsers, as do the bulungamayines *Gumardee springae* (taxon #F22) and *Wabularoo naughtoni* (taxon #F21), and all of these taxa are assigned high probabilities of belonging to this grouping (see appendix table A6).

In the early Miocene *Cookeroo hortusensis* (Butler et al. 2016) (taxon #F23) clusters more definitively with the specialized folivorous browsers, as do all of the balbarids (species of *Nambaroo*, *Balbaroo*, and *Ganawamaya* [taxa #F7, #F15, and #F19]); all are assigned to the browser category, with *Balbaroo fangaroo* having the highest probability (99.22%) and *Ganawanamaya acris* the lowest (67.5%). The other bulungamayines (species of *Bulungamaya* and *Ganguroo* [taxa #F26, #F27, and #F29–31]) cluster with the omnivores (as they do in the South Australia sample); all are assigned to this category with high probabilities (see appendix table A6).

In the middle Miocene, the individuals of the bulungamayine *Ganguroo robustiter* (taxa #F32–#F34) still cluster with the omnivores; two of these individuals are assigned to the omnivore category with high probability, but one (taxon #F32) has almost equal probabilities of being a browser (see appendix table A6), although it actually clusters closer to the mixed feeders, but close to the extant browser *Setonix*. However, the one surviving balbarid (*Balbaroo nalima* [taxon #F16]), and the first appearing sthenurine (*Wanburoo hilarus* [taxa #F35–#F36]) cluster well within the extant specialized folivorous browsers, and are assigned to this category with near 100% probability (see appendix table A6). The only later Miocene taxon available for this part of the study, the sthenurine *Rhizosthenurus flanneryi* (taxon #F37), clusters with the specialized folivorous browsers on function one, and has higher scores than the extant forms on function two (as does the middle Miocene *Wanburoo hilarus* from Henk's Hollow, taxon #F36), falling in a similar position in the morphospace as in the analysis with the complete set of craniodental data, and again being assigned as a browser with 100% probability.

Calcaneal analysis. A stepwise discriminant analysis was performed on the calcaneal data for the extant species (see fig. 7 and appendix tables A3–4) to determine those morphological features that best distinguished among the three locomotor modes (rare or non-hopper, regular hopper, and specialized hopper). The three groups were distinguished with 93% correct classification. The misclassifications include *Hypsiprymnodon moschatus*, classified as a regular hopper rather than a non-hopper (probably because it does not occupy the same portion of the morphospace as the tree kangaroos), and the smaller species of *Macropus*, *M. eugenii* and *M. irma*, which were classified as regular hoppers rather than specialized hoppers (see appendix table A8). In analyses of other aspects of hindlimb anatomy these *Macropus* species also cluster with other kangaroos, rather than with the larger species of *Macropus* (Janis et al., 2014).

Four variables were selected by the analysis: the dorsoventral length of the continuous lower ankle joint (CLAJ where the calcaneum and astragalus articulate: variable C11); the mediolateral width across the CLAJ (variable C13); the

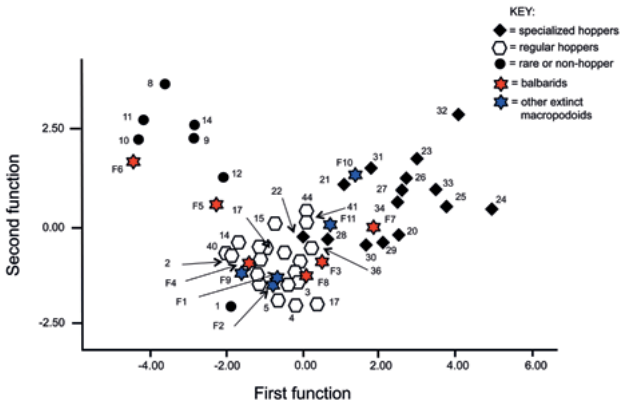

Figure 7. Stepwise discriminant analysis of the calcaneal data. Table 5 provides the key to the numbers of the taxa in this figure.

dorsoventral length of the calcaneal tuber (variable C12); and the mediolateral width of the midshaft of the calcaneal tuber on the anterior side (variable C5).

The first function explains 77.8% of the variance: variables with positive loadings are the length of the calcaneal tuber (0.933) and (very weakly positive) the mediolateral width of the CLAJ (0.14); variables with negative loadings are the mediolateral width of the calcaneal tuber (-0.615) and the dorsoventral length of the CLAJ (-0.533). This function basically separates the "specialized hoppers", the species of *Macropus* (with a long, narrow calcaneal tuber and a narrow articulation with the astragalus) from the tree-kangaroos (with a short, wide calcaneal tuber and a broad articulation with the astragalus). The "regular hoppers" fall in the middle of these two groupings, although the non-hopping Musky Rat-kangaroo has negative scores that are almost within the scores of the tree-kangaroos. "Regular hoppers" with similarly low scores on function one include closed habitat forms, such as the New Guinea forest wallabies (*Dorcopsis* spp.), and the Quokka (*Setonix brachyurus*), but also more open-habitat species such as the Banded Hare-wallaby (*Lagostrophus fasciatus*).

The second function explains 22.2% of the variance; variables with positive loadings are the mediolateral width and the dorsoventral length of the CLAJ (0.586 and 0.239 respectively); variables with negative loadings are the dorsoventral length and mediolateral width of the calcaneal tuber (-0.641 and -0.111 respectively). This variable separates the tree-kangaroos and the larger species of *Macropus* with positive scores, from other macropodoids. This function may be separating taxa on a combination of size and shape, the tree-kangaroos having positive scores because of a relatively broad CLAJ, and the largest kangaroos having absolutely large values for these measurements. Tree-kangaroos are also separated from the other taxa by their short and broad calcaneal tubers, although the species of *Macropus* with relatively high positive scores do not have this calcaneal morphology, and their scores on function two may reflect larger body size, as previously discussed. This size aspect of the second function seems to be confirmed by the fact that the taxa with the most negative scores on this function are the Musky Rat-kangaroo, the potoroines, and small macropodines (while the larger macropodines, such as the Swamp Wallaby, have positive scores).

The inclusion of the fossil taxa shows that most of them fall with the regular hoppers, mostly with a high probability of assignment to this group (see appendix table A8), but with a few interesting exceptions. The macropodine *Dorcopsoides fossilis* (taxon #F11) has only a moderately high probability of belonging to the regular hopper category (60.51%), and also has rather high scores for the specialized hopper category (39.45%): if, however, the small *Macropus* species *M. eugenii* and *M. irma* are recoded as belonging to category 2 (regular hoppers, probably a more realistic assignment), then *Dorcopsoides* has a much higher probability (89.16%) of also belonging to this group. The sthenurine *Rhizosthenurus flanneryi* (taxon #F10) clusters with the specialized hoppers, possibly because of its relatively large size, as it does not cluster with *Macropus* species in other aspects of its hindlimb anatomy (Janis et al., 2014).

While most of the balbarids were predicted to be regular hoppers, two of the early Miocene species of *Balbaroo* from South Australia (taxa #F5 and #F6) cluster with the tree-kangaroos. Both have high probabilities of belonging to this group, whose calcaneal morphology clearly reflects arboreality (as the non-hopping *Hypsiprymnodon* does not fall into this portion of the morphospace): taxon #F6 with almost 100% probability, and taxon #F5 with a probability of 79.02% (see appendix table A8). However, the middle Miocene *Balbaroo nalima* (taxon #F7) is assigned to the specialized hopping group (probability of 98.61%). Caution should be taken in interpreting this preliminary result: while this late surviving balbarid may indeed have evolved a more specialized type of locomotion, this specimen was also measured by a different person (KJT) than the others (CMJ), and there may be a difference in user measurements.

The discriminant functions for all of the analyses are shown in appendix table A5.

Discussion

The analyses of the craniodental data clearly show that extant kangaroos can be distinguished on the basis of even limited measurements. The main distinction is of the specialized folivorous browsers (with low scores on the first function in the discriminant analyses, and high scores on the second function) and the grazers (with high scores on the first function, and scores near zero on the second function) from other dietary types. Among the browsers, the Swamp Wallaby (*Wallabia bicolor*) has somewhat more positive scores than the others; this may reflect a more abrasive diet, even if selecting predominantly browse. The other browsers and the omnivorous potoroines resemble the specialized folivorous browsers in having low scores on function one: however, it is likely that this axis is also making some determinations on the basis of body size, because the browsers other than the Swamp Wallaby also resemble the potoroines in their relatively small body size. But also note that both the potoroines and the browsing macropodines retain a long lower premolar (which may be the

Table 3. Key to extant taxa measured in craniodental analyses, numbers shown in figs 4-6. (More detailed information is available in appendix table A1).

Taxon	Key
Hypsiprymnodon moschatus	1
Aepyprymnus rufescens	2
Bettongia gaimardi	3
Bettongia lesueuri	4
Bettongia penicillata	5
Potorous tridactylus	6
Dendrolagus bennettianus	7
Dendrolagus dorianus	8
Dendrolagus inustus	9
Dendrolagus lumholtzi	10
Dendrolagus matschiei	11
Dorcopsis atrata	12
Dorcopsis hageni	13
Dorcopsis muelleri	14
Dorcopsulus macleayi	15
Dorcopsulus vanheurni	16
Lagorchestes conspicillatus	17
Lagorchestes hirsutus	18
Lagostrophus fasciatus	19
Macropus agilis	20
Macropus antilopinus	21
Macropus dorsalis	22
Macropus eugenii	23
Macropus fuliginosus	24
Macropus giganteus	25
Macropus irma	26
Macropus parryi	27
Macropus robustus	28
Macropus rufogriseus	29
Macropus rufus	30
Onychogalea unguifera	31
Petrogale brachyotis	32
Petrogale godmani	33
Petrogale inornata	34
Petrogale lateralis	35
Setonix brachyurus	36
Thylogale billardierii	37
Thylogale browni	38
Thylogale brunii	39
Thylogale stigmatica	40
Thylogale thetis	41
Wallabia bicolor	42

Table 4. Key to extinct taxa measured in craniodental analyses, numbers shown in figs. 3-6. (More detailed information is available in appendix table A2).

Taxon	Key
"Kyeema mahoneyi"	F1
Ngamaroo archeri	F2
Ngamaroo archeri	F3
Nambaroo sp. A	F4
Nambaroo couperi	F5
Nambaroo sp.	F6
Nambaroo gillespieae	F7
Balbaroo sp. A #1	F8
Balbaroo sp. A #2	F9
Balbaroo sp. A #3	F10
Balbaroo sp. B #1	F11
Balbaroo sp. B #2	F12
Balbaroo sp. (? *Nambaroo*)	F13
Wururoo dayamayi	F14
Balbaroo fangaroo	F15
Balbaroo nalima	F16
Galanarla tessellata	F17
Ganawanamaya aediculus	F18
Ganawanamaya acris	F19
"Genus P, sp. A"	F20
Wabularoo naughtoni	F21
Gumardee springae	F22
Cookeroo hortusensis	F23
Bulungamaya sp. A	F24
Bulungamaya sp. B	F25
Bulungamaya delicata	F26
Bulungamaya delicata	F27
Ganguroo bilamina	F28
Ganguroo bilamina	F29
Ganguroo bilamina	F30
Ganguroo bilamina	F31
Ganguroo robustiter #1	F32
Ganguroo robustiter #2	F33
Ganguroo robustiter #3	F34
Wanburoo hilarus (G)	F35
Wanburoo hilarus (HH)	F36
Rhizosthenurus flanneryi	F37

Table 5. Key to extant taxa measured in calcaneal analyses, numbers shown in fig 7. (More detailed information is available in appendix table A3).

Taxon	Key
Hypsiprymnodon moschatus	1
Aepyprymnus rufescens #1	2
Aepyprymnus rufescens #2	3
Bettongia gaimardi	4
Bettongia penicillata	5
Potorous tridactylus #1	6
Potorous tridactylus #2	7
Dendrolagus bennettianus	8
Dendrolagus dorianus	9
Dendrolagus lumholtzi	10
Dendrolagus lumholtzi	11
Dendrolagus matschiei	12
Dendrolagus scotti	13
Dorcopsis luctosa	14
Dorcopsis muelleri	15
Dorcopsulus vanheurni	16
Lagorchestes conspicillatus	17
Lagorchestes hirsutus	18
Lagostrophus fasciatus	19
Macropus agilis #1	20
Macropus agilis #2	21
Macropus eugenii	22
Macropus fuliginosus	23
Macropus giganteus #1	24
Macropus giganteus #2	25
Macropus giganteus #3	26
Macropus giganteus #4	27
Macropus irma	28
Macropus robustus	29
Macropus rufogriseus #1	30
Macropus rufogriseus #2	31
Macropus rufus #1	32
Macropus rufus #2	33
Macropus rufus #2	34
Onychogalea fraenata #1	35
Onychogalea fraenata #2	36
Petrogale assimilis	37
Petrogale lateralis	38
Petrogale pencillata	39
Setonix brachyurus	40
Thylogale billardierii	41
Thylogale stigmatica	42
Thylogale thetis	43
Wallabia bicolor	44

Table 6. Key to extinct taxa measured in calcaneal analyses, numbers shown in fig 7. (More detailed information is available in appendix table A4).

Taxon	Key
Ngamaroo archeri	F1
Nambaroo sp.	F2
Nambaroo gillespieae	F3
Balbaroo sp. #1	F4
Balbaroo sp. #2	F5
Balbaroo sp. #3	F6
Balbaroo nalima	F7
Balbaroo camfieldensis	F8
"Genus P, sp. A"	F9
Rhizosthenurus flanneryi	F10
Dorcopsoides fossilis	F11

reason why they group together on this function), whereas in the mixed feeders and (especially) the grazers the premolars have been greatly reduced in length, and may be lost after moderate tooth wear. In practice the omnivores could be distinguished from the browsers by the occlusal morphology of their molars (bunolophodont versus bilophodont, respectively). Note that most of the bulungamayines, which are usually bunolophodont forms, cluster with the extant omnivores and the small New Guinea woodland browsers (species of *Dorcopsulus*) in all of the analyses. The exceptions are *Wabularoo naughtoni* (which is bilophodont), *Gumardee springae,* and *Cookeroo hortusensis*, which cluster with the specialized folivorous browsers.

The calcaneal analyses mainly show that specialized hoppers, such as the larger species of *Macropus*, and the arboreal forms (the tree-kangaroos), can be distinguished both from each other and from the "regular hoppers". The more specialized hoppers have a long, narrow calcaneal tuber, reflecting a long moment arm for the gastrocnemius muscle (which powers the lift off from the foot in hopping), and a narrow articulation with the astragalus (which would limit any motion between the astragalus and calcaneum, and restrict ankle motion to the parasagittal plane). In contrast, in the tree-kangaroos possess the opposite suite of features; the short broad calcaneal tuber is reflective of their relative lack of hopping locomotion, and the broad articulation with the astragalus reflects their ability for a degree of inversion and eversion of the foot (a secondarily derived function amongst macropodoids).

Note that the Musky Rat-kangaroo (*Hypsiprymnodon moschatus*), the only extant macropodoid that is not known to hop at any time, does not cluster with the tree-kangaroos, presumably because it retains the more generalized macropodoid feature of a relatively narrow articulation

between the astragalus and calcaneum. Both the Musky Rat-kangaroo and the potoroines have lower scores on function two than the other "regular hoppers", but this may be related to small body size: as discussed in the results section, function two seems to carry a size component, which may be the reason why the relatively unspecialized (to judge from its overall postcranial anatomy) *Rhizosthenurus flanneryi* clusters with the larger species of *Macropus*.

Adding the fossil taxa to the analysis is not especially informative, except to note that the balbarids mainly cluster with the "regular hoppers", and are not close to the non-hopping Musky Rat-kangaroo. Thus, based on the calcaneal data at least, there is no support for the hypothesis that the balbarids were unable to hop. However, a surprising finding is that two of the balbarids, both individuals of the genus *Balbaroo* from the early Miocene of South Australia, cluster with the tree-kangaroos, with the implication that they may have been arboreal. Interestingly, among the balbarids, the more bunolophodont (i.e., likely omnivorous) *Nambaroo* is the form whose calcaneum shows terrestrial habits, while more bilophodont (i.e., likely folivorous) species of *Balbaroo* are the ones with calcanea hinting at arboreal habits.

Although these data are admittedly preliminary because they do not include all of the known fossil species, there are some interesting patterns in the comparison of the distribution of dietary habits of macropodoids from the South Australian and Queensland fossil localities (see figs. 5 and 6). A comparison between the late Oligocene of South Australia (Etadunna Formation Zones C and D) and the late Oligocene of Queensland (Riversleigh Faunal Zone A) shows the following pattern. South Australia contained primarily taxa with a likely omnivorous diet: *Ngamaroo archeri* may have been a browser, but not a specialized folivorous browser, while the balbarid *Nambaroo* sp. A and the enigmatic "Genus P sp. A" are likely omnivores or omnivorous browsers, clustering with the Rufous Bettong (*Aepyprymnus rufescens*). The Queensland faunas show a greater number of probable browsing specialists. There are several forms that group with the extant specialized folivorous browsers: the balbarid *Wururoo dayamayi* and the bulungamayine *Wabularoo naughtoni* cluster within the grouping of extant specialized folivorous browsers, while the balbarid *Ganawanamaya aediculus* and the bulungamayine *Gumardee springae* fall close to this cluster (and are assigned to this feeding group). The balbarid *Nambaroo couperi* falls close to the browser-omnivore *Aepyprymnus rufescens*, and is assigned as an omnivore: the balbarid *Galanarla tessellata* clusters with the pademelons (*Thylogale* spp., macropodines that select mainly browse but also include young grass in their diet [Cronin, 2008]), and is assigned as a mixed feeder (see appendix table A8). This difference in distribution of dietary types may indicate a more mesic environment in Queensland during the late Oligocene, with a greater availability of palatable leaves. Interestingly, our interpretation here of a difference in habitats between Queensland and South Australia in the latest Oligocene is supported by vegetational reconstruction based on pollen data (Crisp and Cook, 2013), which shows South Australia as being drier than Queensland at this time (see their fig. 6).

The early Miocene of South Australia (the Kutjamarpu Local Fauna) looks more like the late Oligocene of Queensland, with a mix of omnivorous and tropical browsing species. Again, among the balbarids, *Nambaroo* sp. is still classified as an omnivorous browser (but now falls closer to the specialized folivorous browsers, and has moderately high probability of being included in the browser category), while the taxa clustering with the specialized folivore browsers (and assigned as such with high probabilities) are all individuals of *Balbaroo*. In Queensland the late Oligocene pattern continues into the early Miocene (Riversleigh Faunal Zone B): the specialized folivorous browsers are all balbarids, and the bulungamayines are mainly classified as omnivores (clustering with the species of *Dorcopsulus* and the potoroine species of *Bettongia* and *Potorous*), but *Cookeroo hortusensis* now appears to be a more definitive browser (and is classified as such with a high probability). This slightly greater preponderance of specialized folivorous browsers may indicate more mesic conditions in Faunal Zone B than in Faunal Zone A. This is in agreement with Archer et al. (1989, 1997) and Travouillon et al. (2009) who suggested that the open forest environments of Faunal Zone A were replaced by rainforest in Faunal Zone B.

In the middle Miocene of Queensland (Faunal Zone C), only a few omnivorous bulungamayines remain (individuals of *Ganguroo robustiter*), and there is now the presence of the highly folivorous sthenurine *Wanburoo hilarus*, as well as a persistent species of specialized folivorous browsing *Balbaroo*. These taxa at least indicate the persistence of the mesic conditions from the early Miocene, also in agreement with Archer et al. (1989, 1997) and Travouillon et al. (2009), as the rainforest persists. However in the later Miocene (Faunal Zone D) the number of macropodoid species declined precipitously (although this may be an artefact of there only being one known locality of this age, Encore Site). The sthenurine *Rhizosthenurus flanneryi* continues as a specialized folivorous browser: the bulungamyine *Ganguroo* sp. 2 (an omnivore/browser) is also known in the Encore assemblage (Travouillon et al., 2014), but there was not suitable material to include in this analysis. Archer et al. (1989, 1997) and Travouillon et al. (2009) suggested that rainforest is replaced by open forest at this point in time (see also Black et al., 2012).

Conclusion

Extant macropodoids can be distinguished by dietary type (omnivore, browser, mixed feeder and grazer) with a high degree of success, even when using a limited set of variables belonging to the mandible alone. Based on a comparison with the extant forms of known diet, Oligo-Miocene macropodoids appear to have been mainly generalist omnivores and browsers in their diet, with a few forms tending towards more specialized folivorous browsing, as seen today in the tree-kangaroos and forest wallabies of New Guinea. Comparison between South Australia and Queensland shows an overall greater preponderance of specialized folivores in Queensland. There were no specialized folivores in South Australia in the late Oligocene, and the taxa present appear to have been mainly omnivorous; in contrast, at the same time in Queensland both omnivores and specialized browsers were present. Specialized browsers, as well as omnivores, were present

in the early Miocene in both areas, and in the middle Miocene (where there are no data for South Australia), this combination of dietary types persisted. We interpret these data as indicative of more mesic, tropical-forest like conditions in Queensland than in South Australia, especially during the late Oligocene.

The Oligo-Miocene macropodoids studied here appear to have all been generalized hoppers: there is no compelling evidence that any were unable to hop, as is apparently the case for the extant Musky Rat-kangaroo, *Hypsiprymnodon moschatus*, and as has been suggested for the members of the extinct family Balbaridae. However, some intriguing evidence suggests that some balbarids (in the early Miocene of South Australia) may have been arboreal, because they cluster with the tree-kangaroos in the calcaneal analyses.

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Table A1. Extant taxa measured in craniodental analyses.

Taxon	Key	Common Name	Family/ Subfamily	Diet	Specimen number
Hypsiprymnodon moschatus	1	Musky Rat-kangaroo	Hypsiprymno-dontidae	O	AMNH 62750
Aepyprymnus rufescens	2	Rufous Bettong	Macropodidae/ Potoroinae	O	AMNH 183408
Bettongia gaimardi	3	Tasmanian Bettong	Macropodidae/ Potoroinae	O	AMNH 65268
Bettongia lesueuri	4	Burrowing Bettong/Boodie	Macropodidae/ Potoroinae	O	AMNH 197663
Bettongia penicillata	5	Brush-tailed Bettong/Woylie	Macropodidae/ Potoroinae	O	AMNH 196954
Potorous tridactylus	6	Long-Nosed Potoroo	Macropodidae/ Potoroinae	O	AMNH 65328
Dendrolagus bennettianus	7	Bennett's Tree-kangaroo	Macropodidae/ Macropodinae	B	AMNH 155115
Dendrolagus dorianus	8	Doria's Tree- kangaroo	Macropodidae/ Macropodinae	B	AMNH 192143
Dendrolagus inustus	9	Grizzled Tree- kangaroo	Macropodidae/ Macropodinae	B	AMNH 109467
Dendrolagus lumholtzi	10	Lumholtz's Tree- kangaroo	Macropodidae/ Macropodinae	B	AMNH 65248
Dendrolagus matschiei	11	Matschie's Tree- kangaroo	Macropodidae/ Macropodinae	B	AMNH 194798
Dorcopsis atrata	12	Black Forest Wallaby	Macropodidae/ Macropodinae	B	AMNH 157277
Dorcopsis hageni	13	White-striped Forest Wallaby	Macropodidae/ Macropodinae	B	AMNH 109376
Dorcopsis muelleri	14	Brown Dorcopsis	Macropodidae/ Macropodinae	B	AMNH 222625
Dorcopsulus macleayi	15	Papuan Forest Wallaby	Macropodidae/ Macropodinae	B	AMNH 104086
Dorcopsulus vanheurni	16	Lesser Forest Wallaby	Macropodidae/ Macropodinae	B	AMNH 109664
Lagorchestes conspicillatus	17	Spectacled Hare-wallaby	Macropodidae/ Macropodinae	M	AMNH 196976
Lagorchestes hirsutus	18	Rufus Hare-wallaby /Mala	Macropodidae/ Macropodinae	M	AMNH 155106
Lagostrophus fasciatus	19	Banded Hare- wallaby	Macropodidae/ Lagostrophinae	M	AMNH 155104
Macropus agilis	20	Agile Wallaby	Macropodidae/ Macropodinae	M	AMNH 108111
Macropus antilopinus	21	Antilopine Wallaroo	Macropodidae/ Macropodinae	G	AMNH 194061
Macropus dorsalis	22	Black-Striped Wallaby	Macropodidae/ Macropodinae	M	AMNH 193780
Macropus eugenii	23	Tammar Wallaby	Macropodidae/ Macropodinae	M	AMNH 197003
Macropus fuliginosus	24	Western Grey Kangaroo	Macropodidae/ Macropodinae	G	AMNH 160045
Macropus giganteus	25	Eastern Grey Kangaroo	Macropodidae/ Macropodinae	G	AMNH 42905
Macropus irma	26	Western Brush Wallaby	Macropodidae/ Macropodinae	M	AMNH 197028
Macropus parryi	27	Whiptail Wallaby	Macropodidae/ Macropodinae	M	AMNH 156731
Macropus robustus	28	Common Wallaroo/Euro	Macropodidae/ Macropodinae	G	AMNH 107371
Macropus rufogriseus	29	Red-Necked Wallaby	Macropodidae/ Macropodinae	M	AMNH 65120
Macropus rufus	30	Red Kangaroo	Macropodidae/ Macropodinae	G	AMNH 197114
Onychogalea unguifera	31	Northern Nail-Tail Wallaby	Macropodidae/ Macropodinae	M	AMNH 197524
Petrogale brachyotis	32	Short eared Rock- wallaby	Macropodidae/ Macropodinae	M	AMNH 197510
Petrogale godmani	33	Godman's Rock- wallaby	Macropodidae/ Macropodinae	M	AMNH 107376
Petrogale inornata	34	Unadorned Rock- wallaby	Macropodidae/ Macropodinae	M	AMNH 107704
Petrogale lateralis	35	Black footed Rock- wallaby	Macropodidae/ Macropodinae	M	AMNH 197653
Setonix brachyurus	36	Quokka	Macropodidae/ Macropodinae	B	AMNH 160043
Thylogale billardierii	37	Tasmanian Pademelon	Macropodidae/ Macropodinae	M	AMNH 65217
Thylogale browni	38	Brown's Pademelon	Macropodidae/ Macropodinae	M	AMNH 151857
Thylogale brunii	39	Dusky Pademelon	Macropodidae/ Macropodinae	M	AMNH 108010
Thylogale stigmatica	40	Red-legged Pademelon	Macropodidae/ Macropodinae	M	AMNH 65155
Thylogale thetis	41	Red-necked Pademelon	Macropodidae/ Macropodinae	M	AMNH 106127
Wallabia bicolor	42	Swamp Wallaby	Macropodidae/ Macropodinae	B	AMNH 65127

Key to dietary categories: B = browser, G = grazer, M = mixed feeder, O = omnivore.
AMNH = American Museum of Natural History.

Table A2. Extinct macropodoids measured for craniodental data.

Taxon	Key	Family/ Subfamily	Locality/ Site	Formation	Locality age	State	Specimen number
"Kyeema mahoneyi"	F1	Macropodidae/ Potoroinae	Minkina	Etadunna FZA	Late Oligocene	SA	SAM P36437
Ngamaroo archeri #1	F2	Macropodidae incertae sedis	Mammalon Hill	Etadunna FZD	Late Oligocene	SA	SAM P23623
Ngamaroo archeri #2	F3	Macropodidae incertae sedis	Mammalon Hill	Etadunna FZD	Late Oligocene	SA	SAM P31834
Nambaroo sp. A	F4	Balbaridae	Lake Pitikanta	Etadunna FZC	Late Oligocene	SA	SAM P22357
Nambaroo couperi	F5	Balbaridae	White Hunter	Riversleigh FZA	Late Oligocene	QLD	QM F30401
Nambaroo sp.	F6	Balbaridae	Leaf	Wipajiri	Early Miocene	SA	SAM P24509
Nambaroo gillespieae	F7	Balbaridae	Quantum Leap	Riversleigh FZB	Early Miocene	QL	QM F34532
Balbaroo sp. A #1	F8	Balbaridae	Leaf	Wipajiri	Early Miocene	SA	UCMP 88203
Balbaroo sp. A #2	F9	Balbaridae	Leaf	Wipajiri	Early Miocene	SA	AR 3241
Balbaroo sp. A #3	F10	Balbaridae	Leaf	Wipajiri	Early Miocene	SA	SAM P24222
Balbaroo sp. B #1	F11	Balbaridae	Leaf	Wipajiri	Early Miocene	SA	UCMP 88024
Balbaroo sp. B #2	F12	Balbaridae	Leaf	Wipajiri	Early Miocene	SA	UCMP 99532
Balbaroo sp. (? *Nambaroo*)	F13	Balbaridae	Leaf	Wipajiri	Early Miocene	SA	SAM P24216
Wururoo dayamayi	F14	Balbaridae	White Hunter	Riversleigh FZA	Late Oligocene	QLD	QM F19820
Balbaroo fangaroo	F15	Balbaridae	MIM	Riversleigh FZB	Early Miocene	QLD	QM F30456
Balbaroo nalima	F16	Balbaridae	AL90	Riversleigh FZC	Middle Miocene	QLD	QM F52809
Galanarla tessellata	F17	Balbaridae	D	Riversleigh FZA	Late Oligocene	QLD	QM F10644
Ganawanamaya aediculus	F18	Balbaridae	White Hunter	Riversleigh FZA	Late Oligocene	QLD	QM F16843
Ganawanamaya acris	F19	Balbaridae	RSO	Riversleigh FZB	Early Miocene	QLD	QM F16841

Taxon	Key	Family/ Subfamily	Locality/ Site	Formation	Locality age	State	Specimen number
"Genus P sp. A"	F20	Macropodidae/ ?Macropodinae	Lake Pitikanta	Etadunna FZC	Late Oligocene	SA	UCMP 55339
Wabularoo naughtoni	F21	Macropodidae Bulungamayinae	D	Riversleigh FZA	Late Oligocene	QLD	QM F9177
Gumardee springae	F22	Macropodidae Bulungamayinae	White Hunter	Riversleigh FZA	Late Oligocene	QLD	QM F31549
Cookeroo hortusensis	F23	Macropodidae Bulungamayinae	Wayne's Wok	Riversleigh FZB	Early Miocene	QLD	QM F19813
Bulungamaya sp. A	F24	Macropodidae Bulungamayinae	Leaf	Wipajiri	Early Miocene	SA	SAM P17896
Bulungamaya sp. B	F25	Macropodidae Bulungamayinae	Leaf	Wipajiri	Early Miocene	SA	AR 3265
Bulungamaya delicata (CS)	F26	Macropodidae Bulungamayinae	Camel Sputum	Riversleigh FZB	Early Miocene	QLD	QM F30390
Bulungamaya delicata (WW)	F27	Macropodidae Bulungamayinae	Wayne's Wok	Riversleigh FZB	Early Miocene	QLD	QM F56988
Ganguroo bilamina	F28	Macropodidae Bulungamayinae	Leaf	Wipajiri	Early Miocene	SA	UCMP 88221
Ganguroo bilamina (WW1)	F29	Macropodidae Bulungamayinae	Wayne's Wok	Riversleigh FZB	Early Miocene	QLD	QM F56265
Ganguroo bilamina (WW2)	F30	Macropodinae Bulungamayinae	Wayne's Wok	Riversleigh FZB	Early Miocene	QLD	QM F56998
Ganguroo bilamina	F31	Macropodinae Bulungamayinae	Judith's Horizontals	Riversleigh FZB	Early Miocene	QLD	QM F36351
Ganguroo robustiter #1	F32	Macropodidae Bulungamayinae	AL 90	Riversleigh FZC	Middle Miocene	QLD	AR 19598
Ganguroo robustiter #2	F33	Macropodidae Bulungamayinae	AL 90	Riversleigh FZC	Middle Miocene	QLD	QM F411237
Ganguroo robustiter #3	F34	Macropodidae Bulungamayinae	AL 90	Riversleigh FZC	Middle Miocene	QLD	QM F40114
Wanburoo hilarus (G)	F35	Macropodidae Sthenurinae	Gag	Riversleigh FZC	Middle Miocene	QLD	QM F20525
Wanburoo hilarus (HH)	F36	Macropodidae Sthenurinae	Henk's Hollow	Riversleigh FZC	Middle Miocene	QLD	QM F19839
Rhizosthenurus flanneryi	F37	Macropodidae Sthenurinae	Encore	Riversleigh FZD	Early-late Miocene	QLD	QM F31456

Key to museum acronyms: AR = Palaeontological collections, University of New South Wales. QM = Queensland Museum. NT = Northern Territory Museum. SAM = South Australian Museum. UCMP = University of California, Museum of Paleontology (Berkeley).

Table A3. Extant taxa measured in calcaneal analyses.

Taxon	Key	Common Name	Family/ Subfamily	Loc.	Specimen number
Hypsiprymnodon moschatus	1	Musky Rat-kangaroo	Hypsiprymno-dontidae	NH	SAM M11940
Aepyprymnus rufescens	2	Rufous Bettong	Macropodidae/Potoroinae	RH	AMNH 22788
Aepyprymnus rufescens	3	Rufous Bettong	Macropodidae/Potoroinae	RH	QM J5580
Bettongia gaimardi	4	Tasmanian Bettong	Macropodidae/Potoroinae	RH	AMNH 65268
Bettongia penicillata	5	Brush-tailed Bettong /Woylie	Macropodidae/Potoroinae	RH	SAM M22661
Potorous tridactylus	6	Long-Nosed Potoroo	Macropodidae/Potoroinae	RH	SAM M7381
Potorous tridactylus	7	Long-Nosed Potoroo	Macropodidae/Potoroinae	RH	AMNH 65328
Dendrolagus bennettianus	8	Bennett's Tree- kangaroo	Macropodidae/Macropodinae	NH	WAM M5530
Dendrolagus dorianus	9	Doria's Tree- kangaroo	Macropodidae/Macropodinae	NH	AM M9109
Dendrolagus lumholtzi	10	Lumholtz's Tree- kangaroo	Macropodidae/Macropodinae	NH	AMNH 65258
Dendrolagus lumholtzi	11	Lumholtz's Tree- kangaroo	Macropodidae/Macropodinae	NH	AMNH 65263
Dendrolagus matschiei	12	Matschie's Tree- kangaroo	Macropodidae/Macropodinae	NH	AMNH 194793
Dendrolagus scotti	13	Scott's Tree- kangaroo	Macropodidae/Macropodinae	NH	AM M24424
Dorcopsis luctosa	14	Grey Dorcopsis	Macropodidae/Macropodinae	RH	SAM M15178
Dorcopsis muelleri	15	Brown Dorcopsis	Macropodidae/Macropodinae	RH	AM 194790
Dorcopsulus vanheurni	16	Lesser Forest Wallaby	Macropodidae/Macropodinae	RH	AMNH 109664
Lagorchestes conspicillatus	17	Spectacled Hare- wallaby	Macropodidae/Macropodinae	RH	AMNH 197695
Lagorchestes hirsutus	18	Rufus Hare- wallaby /Mala	Macropodidae/Macropodinae	RH	AM M40038
Lagostrophus fasciatus	19	Banded Hare- wallaby	Macropodidae/Lagostrophinae	RH	AM M40303
Macropus agilis	20	Agile Wallaby	Macropodidae/Macropodinae	SH	AMNH 184582
Macropus agilis	21	Agile Wallaby	Macropodidae/Macropodinae	SH	AMNH 35621
Macropus eugenii	22	Tammar Wallaby	Macropodidae/Macropodinae	SH	AMNH 193974
Macropus fuliginosus	23	Western Grey Kangaroo	Macropodidae/Macropodinae	SH	AMNH 200826
Macropus giganteus	24	Eastern Grey Kangaroo	Macropodidae/Macropodinae	SH	AMNH 35747
Macropus giganteus	25	Eastern Grey Kangaroo	Macropodidae/Macropodinae	SH	QM J11525
Macropus giganteus	26	Eastern Grey Kangaroo	Macropodidae/Macropodinae	SH	AMNH 90136
Macropus giganteus	27	Eastern Grey Kangaroo	Macropodidae/Macropodinae	SH	AMNH 42904
Macropus irma	28	Western Brush Wallaby	Macropodidae/Macropodinae	SH	AMNH 150319
Macropus robustus	29	Common Wallaroo/Euro	Macropodidae/Macropodinae	SH	AMNH 65036
Macropus rufogriseus	30	Red-necked Wallaby	Macropodidae/Macropodinae	SH	AMNH 14154
Macropus rufogriseus	31	Red-necked Wallaby	Macropodidae/Macropodinae	SH	AMNH 273247
Macropus rufus	32	Red Kangaroo	Macropodidae/Macropodinae	SH	AMNH 200473
Macropus rufus	33	Red Kangaroo	Macropodidae/Macropodinae	SH	AMNH 70284
Macropus rufus	34	Red Kangaroo	Macropodidae/Macropodinae	SH	QM J22115
Onychogalea fraenata	35	Brindled Nail-Tail Wallaby	Macropodidae/Macropodinae	RH	AMNH 43959
Onychogalea fraenata	36	Brindled Nail-Tail wallaby	Macropodidae/Macropodinae	RH	NMV C6500
Petrogale assimilis	37	Allied Rock- wallaby	Macropodidae/Macropodinae	RH	QM J4470
Petrogale lateralis	38	Black Footed Rock- wallaby	Macropodidae/Macropodinae	RH	AM 24183
Petrogale pencillata	39	Brush-Tailed Rock- wallaby	Macropodidae/Macropodinae	RH	AMNH 35758
Setonix brachyurus	40	Quokka	Macropodidae/Macropodinae	RH	AMNH 160043
Thylogale billardierii	41	Tasmanian Pademelon	Macropodidae/Macropodinae	RH	AMNH 65215
Thylogale stigmatica	42	Red-Legged Pademelon	Macropodidae/Macropodinae	RH	AM M51512
Thylogale thetis	43	Red-Necked Pademelon	Macropodidae/Macropodinae	RH	AMNH 106127
Wallabia bicolor	44	Swamp Wallaby	Macropodidae/Macropodinae	RH	AMNH 65722

Key to locomotor mode (= Loc.): NH = non-hopper or rare hopper; RH = regular hopper; SH = specialized hopper.
Key to museum acronyms: AM = Australian Museum. AMNH = American Museum of Natural History. QM = Queensland Museum. NMV = Museum Victoria. SAM= South Australian Museum. WAM = Western Australian Museum.

Table A4. Extinct macropodoids measured for calcaneal data.

Taxon	Key	Family/ Subfamily	Locality/ Site	Formation	Locality age	State	Specimen number
Ngamaroo archeri	F1	Macropodidae incertae sedis	Mammalon Hill	Etadunna FZD	Late Oligocene	SA	SAM P23821
Nambaroo sp.	F2	Balbaridae	Lake Pitikanta	Etadunna FZC	Late Oligocene	SA	UCR 22357
Nambaroo gillespieae	F3	Balbaridae	Quantum Leap	Riversleigh FZB	Early Miocene	QLD	QM F34532
Balbaroo sp 1	F4	Balbaridae	Leaf	Wipajiri Formation	Early Miocene	SA	UCR 21985
Balbaroo sp. 2	F5	Balbaridae	Leaf	Wipajiri Formation	Early Miocene	SA	UCMP 88303
Balbaroo sp. 3	F6	Balbaridae	Leaf	Wipajiri Formation	Early Miocene	SA	UCMP 88306
Balbaroo nalima	F7	Balbaridae	AL90	Riversleigh FZC	Middle Miocene	QLD	QM F41234
Balbaroo camfieldensis	F8	Balbaridae	Bullock Creek	Camfield Beds	Middle Miocene	NT	NTM P907-59
"Genus P sp. A"	F9	Macropodidae/ ? Macropodinae	Lake Pitikanta	Etadunna FZC	Late Oligocene	SA	UCMP 88452
Rhizosthenurus flanneryi	F10	Macropodidae/ Sthenurinae	Encore	Riversleigh FZD	Late middle to early late Miocene	QLD	QM F31456
Dorcopsoides fossilis	F11	Macropodidae Macropodinae	Alcoota	Waite Formation	Late Miocene	NT	NTM P878-6

Key to museum acronyms: QM = Queensland Museum. NTM = Northern Territory Museum. SAM= South Australian Museum. UCMP = University of California, Museum of Paleontology (Berkeley). UCR = University of California, Riverside.

Table A5. Discriminant functions for Stepwise Discriminant Analyses. The third function was not statistically significant in any analysis.

Analysis	Function 1	Function 2
Craniodental analysis with complete set of measurements	4.057+0.183(JMB) - 0.268(LPRL) + 0.733(M3-M1)	-6.141+0.135(JMB) - 0.619(LPRL) - 0.742(M3-M1)]
Craniodental analysis with reduced set of measurements	-3.021+0.095(JD) - 0.475(LPRL) + 0.108(LMRL) + 0.210(M4H2) + 0.682(M3-M1)	-6.263 + 0.180(JD) - 0.469(LPRL) + 0.057(LMRL) + 0.0880(M4H2) - 0.533(M3-M1)]
Calcaneal analysis	-2.180 - 0.533(C11) + 0.14(C13) – 0.615(C5) + 0.933(C21)	-3.327 + 0.239(C11) + 0.586(C13) - 0.111(C5) – 0.641(C21)

Table A6. Probabilities for group assignment: Craniodental data, complete set of variables.
Group 1 = omnivore. Group 2 = browser. Group 3 = mixed feeder. Group 4 = grazer.

Taxon	Group Assigned	Group Predicted	Prob. I	Prob. II	Prob. III	Prob. IV
H. moschatus	1	1	0.9965	0.0000	0.0035	0.0000
A. rufescens	1	1	0.9024	0.0145	0.0831	0.0000
B. gaimardi	1	1	0.9956	0.0021	0.0023	0.0000
B. lesueuri	1	1	0.6903	0.2372	0.0725	0.0000
B. penicillata	1	3	0.4276	0.0071	0.5653	0.0000
P. tridactylus	1	1	0.9966	0.0009	0.0026	0.0000
D. bennetianus	2	2	0.0001	0.9994	0.0004	0.0000
D. dorianus	2	2	0.0000	0.9994	0.0006	0.0000
D. inustus	2	2	0.0002	0.9995	0.0004	0.0000
D. lumholtzi	2	2	0.0005	0.9975	0.0020	0.0000
D. matschiei	2	2	0.0062	0.9315	0.0623	0.0000
Do. atrata	2	2	0.0004	0.9995	0.0001	0.0000
Do. hageni	2	2	0.0000	0.9999	0.0000	0.0000
Do. muelleri	2	2	0.0005	0.9995	0.0000	0.0000
Dor. macleayi	2	1	0.6747	0.2511	0.0742	0.0000
Dor. vanheurni	2	1	0.9517	0.0371	0.0112	0.0000
L. conspicillatus	3	3	0.0352	0.1686	0.7962	0.0000
L. hirsutus	3	3	0.4843	0.0044	0.5113	0.0000
La. fasciatus	3	1	0.6248	0.0069	0.3683	0.0000
M. agilis	3	3	0.0021	0.0961	0.9019	0.0000
M. antilopinus	4	4	0.0000	0.0000	0.0000	1.0000
M. dorsalis	3	3	0.0066	0.0004	0.9930	0.0000
M. eugenii	3	3	0.0236	0.0009	0.9756	0.0000
M. irma	3	3	0.0017	0.0019	0.9964	0.0000
M. fuliginosus	4	4	0.0000	0.0000	0.0000	1.0000
M. giganteus	4	4	0.0000	0.0000	0.0000	1.0000
M. robustus	4	4	0.0000	0.0000	0.0000	1.0000
M. rufus	4	4	0.0000	0.0000	0.0000	1.0000
M. rufogriseus	3	3	0.0002	0.0024	0.9969	0.0006
M. parryi	3	3	0.0003	0.0040	0.9955	0.0002
O. unguifera	3	3	0.0011	0.0001	0.9988	0.0000
P. brachyotis	3	3	0.0471	0.0538	0.8991	0.0000
P. godmani	3	3	0.2826	0.0284	0.6891	0.0000
P. inornata	3	3	0.0324	0.0022	0.9654	0.0000
P. lateralis	3	3	0.0785	0.0144	0.9072	0.0000
S. brachyurus	2	3	0.1874	0.0329	0.7797	0.0000
T. billardierii	3	3	0.0788	0.0158	0.9054	0.0000
T. browni	3	3	0.1185	0.0111	0.8704	0.0000
T. brunii	3	3	0.0362	0.0721	0.8917	0.0000
T. stigmatica	3	3	0.1445	0.0138	0.8418	0.0000
T. thetis	3	3	0.0314	0.0054	0.9633	0.0000
W. bicolor	2	3	0.0002	0.0396	0.9597	0.0004
Ganguroo robustiter		1	0.9143	0.0719	0.0138	0.0000
"Genus P sp. A'		1	0.8406	0.0293	0.1302	0.0000
Rhizosthenurus flanneryi		2	0.0000	1.0000	0.0000	0.0000

Table A7. Probabilities for group assignment: Craniodental data, reduced set of variables.
Group 1 = omnivore. Group 2 = browser. Group 3 = mixed feeder. Group 4 = grazer.

Taxon	Group Assigned	Group Predicted	Prob. I	Prob. II	Prob. III	Prob. IV
Extant taxa						
H. moschatus	1	1	0.9841	0.0010	0.0149	0.0000
A. rufescens	1	3	0.2345	0.1802	0.5853	0.0000
B. gaimardi	1	1	0.9681	0.0267	0.0052	0.0000
B. lesueuri	1	1	0.9748	0.0243	0.0009	0.0000
B. penicillata	1	1	0.9924	0.0007	0.0069	0.0000
P. tridactylus	1	1	0.9732	0.0175	0.0094	0.0000
D. bennetianus	2	2	0.0019	0.9977	0.0004	0.0000
D. dorianus	2	2	0.0000	0.9987	0.0012	0.0000
D. inustus	2	2	0.0004	0.9991	0.0004	0.0000
D. lumholtzi	2	2	0.0064	0.9926	0.0011	0.0000
D. matschiei	2	2	0.0067	0.9562	0.0370	0.0000
Do. atrata	2	2	0.0020	0.9979	0.0001	0.0000
Do. hageni	2	2	0.0003	0.9997	0.0000	0.0000
Do. muelleri	2	2	0.0009	0.9991	0.0000	0.0000
Dor. macleayi	2	1	0.8445	0.1433	0.0122	0.0000
Dor. vanheurni	2	1	0.9150	0.0777	0.0074	0.0000
L. conspicillatus	3	3	0.1852	0.1709	0.6439	0.0000
L. hirsutus	3	3	0.4624	0.0099	0.5277	0.0000
La. fasciatus	3	3	0.3635	0.0159	0.6207	0.0000
M. agilis	3	3	0.0001	0.0125	0.9852	0.0022
M. antilopinus	4	4	0.0000	0.0000	0.0000	1.0000
M. dorsalis	3	3	0.0019	0.0003	0.9978	0.0001
M. eugenii	3	3	0.0188	0.0008	0.9804	0.0000
M. irma	3	3	0.0015	0.0028	0.9956	0.0001
M. fuliginosus	4	4	0.0000	0.0000	0.0000	1.0000
M. giganteus	4	4	0.0000	0.0000	0.0000	1.0000
M. robustus	4	4	0.0000	0.0000	0.0000	1.0000
M. rufus	4	4	0.0000	0.0000	0.0000	1.0000
M. rufogriseus	3	3	0.0001	0.0004	0.9945	0.0050
M. parryi	3	3	0.0002	0.0014	0.9968	0.0016
O. unguifera	3	3	0.0006	0.0001	0.9990	0.0004
P. brachyotis	3	3	0.0988	0.0346	0.8667	0.0000
P. godmani	3	3	0.0455	0.0231	0.9315	0.0000
P. inornata	3	3	0.0096	0.0023	0.9881	0.0000
P. lateralis	3	3	0.0147	0.0098	0.9756	0.0000
S. brachyurus	2	1	0.4999	0.0484	0.4516	0.0000
T. billardierii	3	3	0.1120	0.0214	0.8667	0.0000
T. browni	3	3	0.0198	0.0156	0.9647	0.0000
T. brunii	3	3	0.1150	0.1095	0.7755	0.0000
T. stigmatica	3	3	0.1546	0.0194	0.8260	0.0000
T. thetis	3	3	0.0460	0.0075	0.9465	0.0000
W. bicolor	2	3	0.0008	0.0089	0.9899	0.0004

Taxon	Group Assigned	Group Predicted	Prob. I	Prob. II	Prob. III	Prob. IV
South Australia taxa						
Balbaroo sp. A #1		2	0.0011	0.9885	0.0104	0.0000
Balbaroo sp. A #2		2	0.0020	0.7768	0.2212	0.0000
Balbaroo sp. A #3		2	0.0157	0.8676	0.1166	0.0000
Balbaroo sp. B #1		3	0.0335	0.2755	0.6910	0.0000
Balbaroo sp. B #2		2	0.0013	0.9374	0.0613	0.0000
Balbaroo (?*Nambaroo*)		2	0.0458	0.8799	0.0743	0.0000
Bulungamaya sp. A		1	0.8663	0.0891	0.0446	0.0000
Bulungamaya sp. B		1	0.8663	0.0891	0.0446	0.0000
Ganguroo bilamina		1	0.9362	0.0477	0.0162	0.0000
"Genus P sp. A"		1	0.5312	0.1227	0.3462	0.0000
"*Kyeema mahonyi*"		1	0.9780	0.0023	0.0197	0.0000
Nambaroo sp. A		1	0.8462	0.0113	0.1425	0.0000
Nambaroo sp.		1	0.5003	0.4986	0.0011	0.0000
Ngamaroo archeri #1		2	0.2041	0.7571	0.0389	0.0000
Ngamaroo archeri #2		2	0.1791	0.8118	0.0091	0.0000
Queensland taxa						
Balbaroo fangaroo		2	0.0021	0.9922	0.0058	0.0000
Balbaroo nalima		2	0.0060	0.9934	0.0006	0.0000
Bulungamaya delicata (CS)		1	0.9155	0.0798	0.0048	0.0000
Bulungamaya delicata (WW)		1	0.9147	0.0771	0.0082	0.0000
Galanarla tessellata		3	0.0642	0.0052	0.9306	0.0000
Ganawanamaya acris		2	0.1971	0.6750	0.1279	0.0000
Ganawanamaya aediculus		2	0.1971	0.6750	0.1279	0.0000
Ganguroo bilamina (JH)		1	0.9444	0.0455	0.0102	0.0000
Ganguroo bilamina (WW1)		1	0.9147	0.0771	0.0082	0.0000
Ganguroo bilamina (WW2)		1	0.8447	0.1522	0.0032	0.0000
Ganguroo robustiter #1		1	0.4864	0.4857	0.0280	0.0000
Ganguroo robustiter #2		1	0.8184	0.0178	0.1637	0.0000
Ganguroo robustiter #3		1	0.8184	0.0178	0.1637	0.0000
Gumardee springae		2	0.0448	0.9537	0.0015	0.0000
Cookeroo hortusensis		2	0.0018	0.9976	0.0006	0.0000
Nambaroo couperi		1	0.6029	0.1181	0.2789	0.0000
Nambaroo gillespieae		2	0.0352	0.7880	0.1768	0.0000
Rhizosthenurus flanneryi		2	0.0000	1.0000	0.0000	0.0000
Wabularoo naughtoni		2	0.0003	0.9939	0.0059	0.0000
Wanburoo hilarus (G)		2	0.0002	0.9998	0.0000	0.0000
Wanburoo hilarus (HH)		2	0.0000	1.0000	0.0000	0.0000
Wururoo dayamayi		2	0.0037	0.9941	0.0022	0.0000

Table A8. Probabilities for group assignment: Calcaneal data
Group 1 = non-hopper or rare hopper. Group 2 = regular hopper. Group 3 = specialized hopper.

Taxon	Group Assigned	Group Predicted	Prob. I	Prob. II	Prob. III
Extant taxa					
H. moschatus	1	2	0.0015	0.9985	0.0000
A. rufescens #1	2	2	0.0002	0.9913	0.0085
A. rufescens #2	2	2	0.0001	0.9948	0.0051
B. giamardi	2	2	0.0000	0.9978	0.0022
B. penicillata	2	2	0.0071	0.9928	0.0001
P. tridactylus #1	2	2	0.0013	0.9984	0.0003
P. tridactylus #2	2	2	1.0000	0.0000	0.0000
D. bennettianus	1	1	0.9993	0.0007	0.0000
D. dorianus	1	1	0.9993	0.0007	0.0000
D. lumholtzi #1	1	1	1.0000	0.0000	0.0000
D. lumholtzi #2	1	1	1.0000	0.0000	0.0000
D. matschiei	1	1	0.9231	0.0769	0.0001
D. scottae	1	1	0.9996	0.0004	0.0000
Do. muelleri	2	2	0.0208	0.9710	0.0082
Do. luctosa	2	2	0.0659	0.9339	0.0002
Dor. vanheuri	2	2	0.0014	0.9982	0.0004
L. hirsutus	2	2	0.0061	0.9921	0.0019
L. conspicillatus	2	2	0.0000	0.9895	0.0105
La. fasiciatus	2	2	0.0319	0.9681	0.0001
M. agilis #1	3	3	0.0000	0.0097	0.9903
M. agilis #2	3	3	0.0005	0.0938	0.9057
M. eugenii	3	2	0.0018	0.9583	0.0400
M. irma	3	2	0.0002	0.7676	0.2321
M. fuliginosis	3	3	0.0000	0.0001	0.9999
M. giganteus #1	3	3	0.0000	0.0000	1.0000
M. giganteus #2	3	3	0.0000	0.0001	1.0000
M. giganteus #3	3	3	0.0000	0.0004	0.9996
M. giganteus #4	3	3	0.0000	0.0009	0.9991
M. robustus	3	3	0.0000	0.0467	0.9533
M. rufogriseus #1	3	3	0.0000	0.1641	0.8359
M. rufogriseus #2	3	3	0.0000	0.0055	0.9945
M. rufus #1	3	3	0.0000	0.0000	1.0000
M. rufus #2	3	3	0.0000	0.0001	1.0000
M. rufus #3	3	3	0.0000	0.0017	0.9983
O. freanata #1	2	2	0.0006	0.9881	0.0114
O. freanata #2	2	2	0.0004	0.9428	0.0568
P. assimilis	2	2	0.0057	0.9936	0.0007
P. lateralis	2	2	0.0004	0.9984	0.0013
P. penicillata	2	2	0.0132	0.9859	0.0009
S. brachyurus	2	2	0.0397	0.9602	0.0001
T. billardierii	2	2	0.0038	0.8995	0.0967
T. stigmatica	2	2	0.0003	0.9932	0.0065
T. thetis	2	2	0.0016	0.9909	0.0075
W. bicolor	2	2	0.0095	0.8496	0.1410

Taxon	Group Assigned	Group Predicted	Prob. I	Prob. II	Prob. III
South Australia taxa					
Balbaroo sp. #1		2	0.0080	0.9918	0.0002
Balbaroo sp. #2		1	0.7902	0.2097	0.0000
Balbaroo sp. #3		1	0.9999	0.0001	0.0000
"Genus P sp. A"		2	0.0080	0.9920	0.0001
Nambaroo sp.		2	0.0006	0.9986	0.0008
Ngamaroo archeri		2	0.0006	0.9979	0.0015
Queensland taxa					
Balbaroo nalima		3	0.0000	0.0300	0.9700
Nambaroo gillespieae		2	0.0001	0.9087	0.0912
Rhizosthenurus flanneryi		3	0.0001	0.0223	0.9776
Northern Territory taxa					
Balbaroo canfieldensis		2	0.0001	0.9861	0.0138
Dorcopsoides fossilis		2	0.0005	0.6051	0.3945