

Ecological and evolutionary significance of sizes of giant extinct kangaroos

Kristofer M. Helgen^{A,B,C}, Rod T. Wells^D, Benjamin P. Kear^{B,C}, Wayne R. Gerdtz^E
and Timothy F. Flannery^{B,F}

^ADivision of Mammals, National Museum of Natural History, Smithsonian Institution, NHB 390, MRC 108, PO Box 37012, Washington, DC 20013-7012, USA.

^BSouth Australian Museum, North Terrace, Adelaide, SA 5000, Australia.

^CSchool of Earth and Environmental Sciences, University of Adelaide, Adelaide, SA 5005, Australia.

^DSchool of Biological Sciences, Flinders University of South Australia, Adelaide, SA 5001, Australia.

^ESchool of Ecology and Environment, Deakin University, Melbourne Campus, Burwood, Vic. 3125, Australia.

^FCorresponding author. Email: flannery.tim@saugov.sa.gov.au

Abstract. A method, based on femoral circumference, allowed us to develop body mass estimates for 11 extinct Pleistocene megafaunal species of macropodids (*Protemnodon anak*, *P. brehus*, *P. hopei*, *P. roechus*, *Procoptodon goliah*, *P. gilli*, *Simosthenurus maddocki*, *S. occidentalis*, *Sthenurus andersoni*, *S. stirlingi* and *S. tindalei*) and three fossil populations of the extant eastern grey kangaroo (*Macropus giganteus*). With the possible exception of *P. goliah*, the extinct taxa were browsers, among which sympatric, congeneric species sort into size classes separated by body mass increments of 20–75%. None show evidence of size variation through time, and only the smallest (*P. gilli*) exhibits evidence suggestive of marked sexual dimorphism. The largest surviving macropodids (five species of *Macropus*) are grazers which, although sympatric, do not differ greatly in body mass today, but at least one species (*M. giganteus*) fluctuated markedly in body size over the course of the Pleistocene. Sexual dimorphism in these species is marked, and may have varied through time. There is some mass overlap between the extinct and surviving macropodid taxa. With a mean estimated body mass of 232 kg, *Procoptodon goliah* was the largest hopping mammal ever to exist.

Introduction

Body mass is among the most critical determinants of an organism's ecology (Brown *et al.* 2004; Jetz *et al.* 2004; Smith *et al.* 2004), and palaeoecology is thus heavily reliant on accurate estimates of the body mass of extinct species (e.g. Damuth and MacFadden 1990; Alexander 1998; Stiner *et al.* 1998; Smith 2002). Hitherto, studies of Australia's Pleistocene environments have been hampered by the absence of accurate body mass estimates for many extinct species. The lack of such data is, in Australia's case, particularly acute, for before 46 000 years ago (46 kybp) Australia supported a diverse array of megafaunal vertebrates >40 kg in mass, most of which are now extinct and whose ecology remains obscure (Roberts *et al.* 2001; Miller *et al.* 2005; cf. Trueman *et al.* 2005). Rigorous body mass estimates have been attempted for only a handful of these taxa, principally the reptilian carnivore *Megalania prisca*, the marsupial carnivore *Thylacoleo carnifex*, and the large marsupial browser *Diprotodon optatum* (Wroe *et al.* 1999, 2003, 2004; Wroe 2002). *Megalania* was a gigantic varanid whose rarity in fossil deposits and propensity to grow throughout life (i.e. judging from surviving varanids) pose particular challenges

to accurately estimating its body size (Erickson *et al.* 2003; Molnar 2004). Estimating body mass for *T. carnifex* and *D. optatum* is also difficult, as both are morphologically isolated vombatiform marsupials with no living analogues. It is hardly surprising that in each of these cases different approaches have yielded widely varying estimates (Murray 1991; Wroe *et al.* 1999, 2003, 2004; Burness *et al.* 2001; Wroe 2002; Erickson *et al.* 2003; Molnar 2004).

Obtaining accurate body mass estimates for Australian megafaunal species whose remains are abundant and which have many living relatives should, in theory, be easier. The kangaroos and wallabies (family Macropodidae, taxonomy following Kear and Cooke 2001; Long *et al.* 2002; Prideaux 2004) offer such an opportunity. More than three-quarters of megafaunal marsupial herbivores from the Australian Pleistocene were macropodids (27 of 34 species), and the remains of many species are moderately common to abundant in Pleistocene fossil deposits. Four genera of large-bodied macropodids (*Procoptodon*, *Sthenurus*, *Simosthenurus* and *Protemnodon*) became completely extinct before ~46 kybp; along with the surviving species of *Macropus*, these macropodid genera dominated medium-

sized herbivore niches in Pleistocene Australia. With one exception drawing from comparisons of endocranial volume (concentrating mainly on non-macropodids: Wroe *et al.* 2003), only ‘rule of thumb’ or ‘best guess’ body mass estimates exist for any of these fossil species (Johnson and Prideaux 2004). For example, on the basis of extrapolations from linear measurements, Murray (1991) estimated a mass of <150 kg for the largest Pleistocene kangaroo, *Procoptodon goliah*, and 25–80 kg for most other sthenurines.

The oldest macropodid fossils are estimated to be Late Oligocene in age, at which time all species appear to have been small terrestrial or scansorial herbivores (Long *et al.* 2002). By the Late Miocene, species as large as the extant red and grey kangaroos had evolved, and by the Early Pliocene the macropodids had become the dominant herbivores in Australasia, with most extant genera appearing in the fossil record for the first time. Today there are ~65 living species of macropodids, an ecomorphologically diverse taxonomic assemblage comprising shallow burrowers and plains-dwellers to rock-dwelling specialists and arboreal denizens of tropical rainforests (Flannery 1995; Strahan 1995). Despite this variability, all living macropodids locomote terrestrially by hopping bipedally at medium to high speeds (Baudinette 1989; Webster and Dawson 2004), and with the exception of the New Guinean *Protemnodon tumbuna* (Flannery *et al.* 1983) all extinct species are also thought to have been bipedal hoppers (Flannery 1989, 2004).

On the basis of a regression of femoral circumference and body mass data derived from a large number of extant macropodids, here we estimate body mass for four Late Pleistocene species of *Protemnodon*, three of *Sthenurus*, two of *Simosthenurus* and two of *Procoptodon* (including *P. goliah* and ‘*P. gilli*’, the largest and smallest of the megafaunal kangaroos, respectively), as well as multiple, temporally separated Quaternary samples of the eastern grey kangaroo (*Macropus giganteus*).

Materials and Methods

Previous estimates of body mass for megafaunal kangaroos generally derive from extrapolations based on univariate skull and dental measurements (Flannery 1980; Murray 1991), but these types of comparisons are potentially unreliable (Myers 2001; Wroe *et al.* 2003, 2004). Cranial metrics may be determined and/or tightly constrained by feeding requirements, and dental dimensions are particularly problematic for macropodids, in which molars erupt continually and are successively shed. In contrast, load-bearing long bones (such as the femur or humerus) exhibit similar scaling relationships across unrelated taxa and over a wide range of body sizes and are considered more appropriate for body mass extrapolations (Anderson *et al.* 1985; Anyonge 1993; Reynolds 2002). Predictions based on mid-shaft circumferences of load-bearing long bones are particularly powerful (Anderson *et al.* 1985; Wroe *et al.* 2004), and because kangaroos are bipedal, femoral dimensions are especially appropriate. For this study, we measured the least femoral circumference (*c*), i.e. the circumference of the femur immediately distal to the third trochanter (Fig. 1), in 107 wild-collected macropodid museum specimens with associated body mass data (see Appendix 1). These femoral and body mass data relate to adult,

subadult and juvenile animals representing 26 extant species in nine genera, and span the full spectrum of lifestyle and body size variation among living macropodids (Appendix 1). Captive-living animals (potentially overweight and poorly mobile) and very young pouch young (those too young to hop) were excluded from our analyses. The maturity of specimens was evaluated by comparative size, degree of ephiphyseal fusion, and by comparing the ossification and dental development of associated crania when available.

We \log_{10} -transformed these data for extant macropodids to generate a regression equation that describes the relationship between actual body mass (M_{obs}) and *c* for our dataset of extant macropodid specimens (Fig. 2):

$$\log_{10}(M_{obs}) = 2.5932[\log_{10}(c)] - 3.2842. \quad (1)$$

In retransforming these logarithmic values to actual values for body mass, we corrected for the effects of logarithmic transformation bias by multiplying all predicted values by a ‘smearing estimator’ (Smith 1993), in this case corresponding to a value of 1.0146. We have used the resulting equation to derive estimated body masses (M_{est}) of megafaunal kangaroo specimens for which femora are available (Appendix 2):

$$M_{est} = 1.0146 * 10^{[2.5932 \log_{10}(c) - 3.2842]}. \quad (2)$$

In using this equation for extrapolative estimations, we have made the assumption that limb–body postures of extinct kangaroos were similar to those of extant kangaroos, and that cross-sectional geometry of the femur scales at a similar rate in all taxa examined.

Results

The genus *Protemnodon*

Protemnodon includes approximately a dozen species of large ‘wallabies’ spanning the Early Pliocene to Late Pleistocene, and is the only Late Pleistocene megafaunal

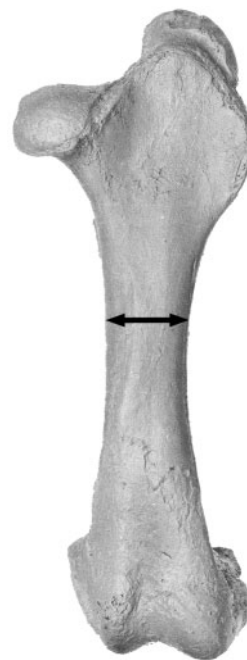


Fig. 1. Measurement of femoral circumference employed here, as described in the text. Figured is a femur of *Sthenurus stirlingi* (SAM P22533, adapted from Wells and Tedford 1995).

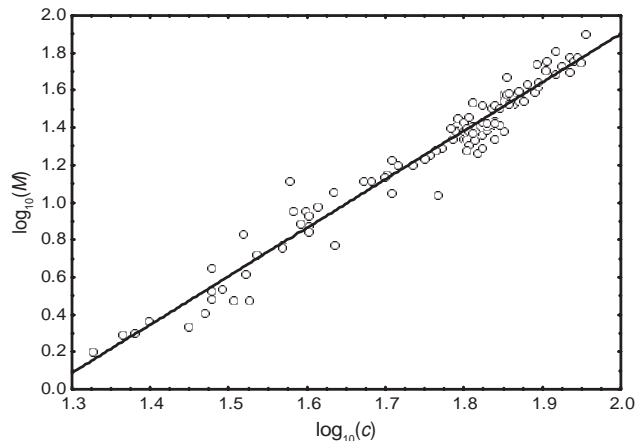


Fig. 2. Regression of measured body mass (M) against femoral circumference (c) in 107 museum specimens representing extant macropodid species (Appendix 1): $\log_{10}(M) = 2.5932 \log_{10}(c) - 3.2842$; $r^2 = 0.9579$.

genus of macropodid shared between Australia and New Guinea (Long *et al.* 2002). Though they are represented by small samples, our analyses include all three species known from the Late Pleistocene of Australia and one Late Pleistocene species from New Guinea (Table 1).

Protemnodon anak (mean $M_{est} = 131$ kg) is known from a large number of localities in more mesic parts of eastern Australia. Our sample of four individuals is drawn from the Early Pleistocene Morwell fire-hole deposits (Flannery 1980) and the Late Pleistocene Green Waterhole of South Australia (Pledge 1980). Although separated geographically by ~400 km and temporally by up to 2 million years, this sample is relatively homogeneous in predicted body size (Table 1).

On the basis of cranial dimensions, *Protemnodon brehus* was thought to be slightly larger than *P. anak* (Bartholomai 1973), yet femoral measurements indicate that it was slightly

smaller in body mass. Two femoral measurements for adults were obtained (both from deposits poorly constrained temporally), giving a mean estimated body mass of 111 kg. A femur from a large subadult was similar in size to those of adults (109 kg) and is included in Table 1.

A single specimen of *Protemnodon roechus* (thought to be the largest *Protemnodon* species on the basis of dental dimensions) is included in our study. This femur (which is cracked and may have been expanded by calcite wedging) yielded a mass estimate of 166 kg, which should be regarded as a maximum value. Although *P. brehus* and *P. roechus* apparently occurred predominantly in drier regions than *P. anak*, all three species were regionally sympatric in south-eastern Australia. Body masses of these species increase progressively by 20–25% from smallest to largest, and we suspect that their sympatry was facilitated by a combination of differential habitat preferences and differences in body mass.

The only New Guinean *Protemnodon* for which a femur is available is *P. hopei*, a Late Pleistocene inhabitant of alpine grasslands in the west of the island. The single available femur for *P. hopei* yields an estimated body mass of 45 kg, making this species probably the smallest of the New Guinean megafauna.

The genus *Sthenurus*

Species of *Sthenurus* were browsers of the Australian Pliocene to Late Pleistocene. Their fossils occur predominantly in regions that are arid to semi-arid today. We obtained body mass estimates from three of the six currently recognised species (Prideaux 2004).

Our samples of *S. stirlingi*, *S. tindalei* and *S. andersoni* are all derived from the Middle to Late Pleistocene sediments of Lake Callabonna, northern South Australia (Tedford and Wells 1990; Wells and Tedford 1995). With a mean estimated mass of 72 kg, *S. andersoni* was only ~60% as heavy as *S. tindalei*, which in turn was probably ~30–40% smaller than *S. stirlingi* (Table 1). On the basis of these small

Table 1. Femoral and estimated body mass metrics for fully mature specimens of late Pleistocene megafaunal kangaroos from Australia and New Guinea (Appendix 2), in increasing order of size. Shown for each species are sample size (n), mean femoral circumference (c), the coefficient of variation for c (CV), the mean estimated body mass \pm s.d. (M), range of estimated body mass, and a previous estimate (PE), here based on a review of recently published estimates of body mass (Johnson and Prideaux 2004)

Species	n	c (mm)	CV (%)	M (kg)	Range (kg)	PE (kg)
<i>Protemnodon hopei</i>	1	79.5	–	45	–	50
<i>'Procoptodon' gilli</i>	4	85.0	10.6	54 \pm 15.6	43–77	30
<i>Sthenurus andersoni</i>	4	95.3	4.1	72 \pm 7.5	63–79	50
<i>Simosthenurus maddocki</i>	2	98.0	–	78	74–82	50
<i>Protemnodon brehus</i>	3	112.7	0.5	110 \pm 1.5	109–111	100
<i>Simosthenurus occidentalis</i>	5	115.0	5.5	118 \pm 14.3	97–136	50
<i>Sthenurus tindalei</i>	3	118.9	5.2	127 \pm 17.0	110–144	100
<i>Protemnodon anak</i>	4	120.1	4.6	131 \pm 15.8	122–153	100
<i>Protemnodon roechus</i>	1	132.0	–	166	–	100
<i>Sthenurus stirlingi</i>	4	133.6	6.0	173 \pm 26.8	151–205	150
<i>Procoptodon goliah</i>	3	150.0	1.76	232 \pm 10.7	224–244	250

samples, we suggest that niche separation in these three sympatric congeners was at least partly mass-based.

The genus *Simosthenurus*

The most recent revision of *Simosthenurus* (Prideaux 2004) provisionally recognises eight species, which range in age from Pliocene to Late Pleistocene. Of these, we have representatives of two Late Pleistocene species, *S. maddocki* and *S. occidentalis*. Our sample of *S. maddocki* consists of one subadult and two adults, all from Green Waterhole Cave, South Australia. The subadult (presumably a very young animal) has an estimated mass of 30 kg, the adults 74 and 82 kg. Our sample of *S. occidentalis*, also drawn from Green Waterhole Cave, comprises a subadult ($M_{est} = 56.5$ kg) and five adults (mean $M_{est} = 118$ kg). These two sympatric species of *Simosthenurus* appear to have differed in mass by a factor of ~50%.

The genus *Procoptodon*

A recent taxonomic revision (Prideaux 2004) considerably widened the generic concept of *Procoptodon*, provisionally including within it eight species, all Pleistocene in age, including several species previously assigned to *Simosthenurus*.

The genus includes the largest (*P. goliath*) and smallest (*P. gilli*) of the Pleistocene megafaunal kangaroos. Our sample of *P. gilli* is drawn from Green Waterhole Cave and Naracoorte Caves, and consists of one subadult ($M_{est} = 22.5$ kg) and four adults (mean $M_{est} = 54$ kg). Our sample of *Procoptodon goliath*, the largest hopping animal that ever lived, consists of three adults from localities in South Australia and western New South Wales (mean $M_{est} = 232$ kg).

Size variation in *Macropus giganteus*

The extant eastern grey kangaroo (*Macropus giganteus*) is one of the most abundant large herbivores represented in Pleistocene deposits in eastern Australia, in some instances

comprising more than 90% of individuals in a site (Flannery and Gott 1985). We obtained body mass estimates for three fossil and one extant sample of *M. giganteus*.

The mammalian fauna from the Early Pleistocene Morwell fire-hole deposits of west Gippsland consists entirely of *Macropus* (two species) and *Protemnodon anak* (Flannery 1980). All are represented by articulated skeletons, in some cases accompanied by traces of soft tissue. A second, large sample (41 mature individuals) was obtained from the Lancefield swamp deposits near Melbourne. This sample dates to ~70–80 kybp (J. Dortch, *in litt.*). Bones in the deposit are disarticulated, but *M. giganteus* comprises 95% of all individuals. A third sample comes from Green Waterhole Cave, South Australia. The deposit is considered to be Late Pleistocene in age, but is poorly constrained temporally. Our final sample consists of 30 subadults and adults drawn from an extant population of *M. giganteus* near Hay, western New South Wales (Table 2).

Our body mass estimates for Pleistocene populations of *M. giganteus*, especially from Lancefield, are surprisingly large. On the basis of dental dimensions, Flannery (1980) previously estimated Pleistocene *M. giganteus* (= *M. g. titan*) to have been about twice the mean mass of extant specimens. Judging from femoral circumference, the mean mass of Lancefield *M. giganteus* appears to have been nearly four times that of living *M. giganteus* (at which time it would have been larger than most contemporary megafaunal kangaroos: Table 1), while the Late Pleistocene specimens from Green Waterhole are here estimated to have weighed twice as much as extant specimens. These temporal ‘snapshots’ reveal drastic fluctuations in body size in *M. giganteus* during the late Quaternary.

Discussion

For the first time, our dataset for extant macropodid specimens allows for rigorous estimates of body mass for

Table 2. Femoral and measured body mass metrics for fully mature modern *Macropus* specimens, and estimated body mass metrics for fully mature specimens of Pleistocene *Macropus giganteus*

Shown for each species are sample size (n), mean femoral circumference \pm s.d. (c), observed range of c (Range_c), the coefficient of variation for c (CV), the mean (observed or predicted) body mass \pm s.d. (M), the range of (measured or estimated) body mass (range_m)

Specimen	n	c (mm)	Range _c (mm)	CV (%)	M (kg)	Range _m (kg)
Modern <i>M. rufus</i>						
<i>M. rufus</i> females	14	67 \pm 3.0	63–74	4.6	26 \pm 4.8	19–35
<i>M. rufus</i> males	11	81 \pm 5.7	72–89	7.1	52 \pm 7.9	40–65
<i>M. rufus</i> all	25	73 \pm 8.4	63–89	11.6	37 \pm 14.6	19–65
Modern <i>M. giganteus</i>						
<i>M. giganteus</i> females	6	69 \pm 4.5	62–75	6.5	31 \pm 4.8	26–36
<i>M. giganteus</i> males	5	82 \pm 8.5	68–88	10.3	50 \pm 14.6	25–60
<i>M. giganteus</i> all	11	74 \pm 8.8	62–88	11.9	39 \pm 13.8	25–60
Pleistocene <i>M. giganteus</i>						
Morwell	8	107 \pm 9.4	91–115	8.8	99 \pm 22.5	63–116
Lancefield	41	124 \pm 7.2	107–136	5.8	143 \pm 20.8	97–180
Green Waterhole	5	91 \pm 4.1	86–96	4.5	65 \pm 7.3	55–73

Pleistocene megafaunal kangaroos from Australia and New Guinea, and provides a method for estimating the body mass of additional museum specimens and of fossil taxa discovered in the future. In this case, the estimates are based on a well supported relationship between femoral and body mass data from 26 species of extant macropodids of varying sizes and ages that span the ecological and morphological diversity of the family. These include small desert dwellers, small rainforest dwellers, large species from xeromorphic and mesic environments, rock-dwellers, arboreal herbivores, and secondarily terrestrial descendants of arboreally adapted species. Though body mass estimates for the larger extinct species are almost four times as large as the heaviest specimens included in our database of extant macropodids, our regression demonstrates a uniform relationship between femoral circumference and mass across a more than 40-fold increase in body mass among living taxa. While it is possible that this apparent scaling pattern differs fundamentally from scaling relationships that characterised the body plans of the largest kangaroos, our data for *M. giganteus* demonstrate that the postcranial dimensions of this species formerly approached those of the very largest Pleistocene kangaroos (Tables 1, 2). This intraspecific size fluctuation suggests that a radically different kangaroo body plan is not required for the attainment of very large size. Ultimately, the best way to validate these predictions might be through volumetric, rather than linear, dimensional comparisons, i.e. through the production of plasticine reconstructions based on detailed analyses of comparative macropodoid anatomy, but this goes well beyond the scope of the present work.

Our estimates of body mass permit several lines of preliminary inquiry. Was there overlap in body mass between macropodids that became extinct in the Late Pleistocene and those that survived? Could our estimates help explain the survival of some species and the extinction of others? How does the Australian Pleistocene macropodid fauna compare with assemblages of large mammalian herbivores on other continents? Can anything be said of the palaeoecology of the species involved? We begin with the question of body mass overlap, crucial in past discussions of megafaunal extinction.

With the exception of some previous estimates for *P. goliath*, our estimated body masses for megafaunal kangaroos are generally greater than previous authors have suggested (Murray 1984, 1991; Johnson and Prideaux 2004). The estimated mass of all 10 extinct Australian species examined in this study exceed the mean body masses of all surviving marsupial herbivores (Strahan 1995). Yet to evaluate whether there was size overlap between currently extant and extinct species during the Late Pleistocene, we must estimate body masses from Pleistocene populations of surviving species because many Australian animals have dwarfed significantly during the late Quaternary (Marshall and Corruccini 1978).

The eastern grey kangaroo (*Macropus giganteus*) is among the largest of surviving marsupials. A Late Pleistocene sample of *M. giganteus* from Green Waterhole, South Australia co-occurs with fossils of '*P. gilli*', *S. occidentalis*, *S. maddocki* and *P. anak*, and was presumably contemporary with them. Our mean body mass estimate for the Green Waterhole sample of *M. giganteus* is 65 kg, slightly larger than that of '*P. gilli*'. Among extant macropodids, only the red kangaroo (*M. rufus*) and the western grey kangaroo (*M. f. fuliginosus*) are larger than *M. giganteus* today, and these species have probably also declined in body size during the late Quaternary. On the basis of dental measurements, Marshall and Corruccini (1978) estimated a size decrease of 30–35% in *M. rufus* since the Late Pleistocene. (However, *M. rufus* is rare in Pleistocene deposits, and we cannot relocate the specimens on which this estimate was based.) Nevertheless, judging from data for *M. giganteus* alone, there was clearly overlap in body mass between at least one surviving Australian macropodid and species that became extinct in the Late Pleistocene (Tables 1, 2). In New Guinea, the delineation in body mass between species that became extinct in the Late Pleistocene and those that survived is more clear-cut: *Protemnodon hopei* was the smallest of the New Guinean megafauna but, with an estimated body mass of 45 kg, it was about twice the mass of *Macropus agilis*, the largest surviving Melanesian marsupial.

The extant species of *Macropus* contrast with the extinct megafaunal kangaroos on several counts. First, the extreme fluctuation in body mass through time that we document for *Macropus giganteus* is unique. We suspect that geographic variation is unlikely to be contributing significantly, both because there is little evidence for significant geographic variation in body mass for *M. giganteus* today, and because all of our populations are from a limited geographical region, within a radius of ~300 km from Melbourne. The Early Pleistocene Morwell sample has a mean estimated body mass of 99 kg. The Lancefield sample (~70–80 kybp) is more than 40% larger (mean M_{est} = 143 kg), while that from Green Waterhole Cave (Late Pleistocene, but poorly constrained in age) is much smaller (mean M_{est} = 65 kg) than either the Morwell or Lancefield samples. Modern specimens average about one-half the mass of the Green Waterhole Cave series (Table 2). The full significance of the size fluctuations that occurred before megafaunal extinction (which in Australia is dated to ~46 kybp: Roberts *et al.* 2001) will become apparent only with better dating and more samples. Postmegafaunal extinction dwarfing similar to that seen in *M. giganteus*, however, is recorded for various large mammals on other continents (Hooijer 1950; Kurtén 1968), including the American bison (*Bison bison*), Bighorn sheep (*Ovis canadensis*) and jaguar (*Panthera onca*) (Schultz *et al.* 1972; Marshall and Corruccini 1978).

It is striking that there is no evidence of Pleistocene body size fluctuations in any of the now-extinct megafaunal

kangaroos. For example, *Sthenurus andersoni*, a common species that persisted for 3.5 million years over a broad geographic range in south-eastern Australia, seemingly exhibited no significant temporal variation in dental measurements (Prideaux 2004). This matter deserves further investigation, as we suspect it will shed light on the unique survival of *Macropus* species among the larger Australian marsupials.

A second striking aspect of body mass in *Macropus* is that, though some species are certainly larger-bodied than others on average, extant populations of the five largest extant species of the genus (*M. rufus*, *M. fuliginosus*, *M. giganteus*, *M. antilopinus* and *M. robustus*) are broadly similar in body mass, with mature males averaging 30–40 kg. All of these species are grazers with broadly similar dietary requirements, and three or four of them can occur in regional sympatry in inland eastern and north-eastern Australia (McAlpine *et al.* 1998; McCullough and McCullough 2000). This sympatric occurrence seems to be facilitated more by local habitat preferences, predicated on rainfall patterns, vegetation type, slope, rockiness, and other factors, than by body size or diet. In contrast, among the large extinct browsers of the genera *Protemnodon*, *Sthenurus* and *Simosthenurus*, sympatric congeners appear to have fallen into discrete size classes. The three species of *Sthenurus* occurring together in the Lake Callabonna deposits of South Australia differed markedly in body size: our estimates suggest that *S. stirlingi* was ~40% larger than *S. tindalei*, which in turn was almost twice the size of *S. andersoni*. The two species of *Simosthenurus* that occurred together at Green Waterhole (*S. occidentalis* and *S. maddocki*) also differed in mean body mass by ~50%, and '*P. gilli*' (also found at Green Waterhole), until recently also classified in *Simosthenurus* (Prideaux 2004), is nearly 50% smaller again than *S. maddocki*. These size relationships may indicate that body mass differences were a fundamental mechanism for providing niche separation in these otherwise broadly similar browsing kangaroos; their different body sizes presumably allowed them to browse at different vertical heights, for example.

In species richness and ecological diversity, the Quaternary macropodid fauna of Australia and New Guinea (~90 species) rivals other great continental assemblages of herbivorous mammals, such as the ecomorphologically diverse modern bovid radiations of Africa. In addition to small, medium and large terrestrial herbivores of forests and open habitats, the Australo-Papuan macropodid radiation also includes arboreal, burrowing and alpine representatives, arguably spanning a greater range of ecological versatility than seen in the African bovids. Nevertheless, the African Bovidae span a greater range of body sizes. Our data suggest that Quaternary macropodids ranged in adult body mass from 800 g (the modern species *Lagorchestes hirsutus*) to ~230 kg (in *Procoptodon goliath*) – a 300-fold span, com-

pared to a 600-fold span among African bovids (1.5–940 kg: Kingdon 1997). Interestingly, the apparent lesser importance of size-mediated sympatry in large macropodid grazers (*Macropus*) versus browsers (*Sthenurus*, *Simosthenurus*) is seemingly paralleled within African bovid tribes. For example, within grazing antelope lineages, such as the Reduncini (e.g. *Kobus*, *Redunca*) and Hippotragini (e.g. *Hippotragus*), size distinctions among sympatric congeners are less striking than in sympatric congeneric browsing antelopes of the genus *Tragelaphus* (including *Taurotragus*: Willows-Munro *et al.* 2005), in which four or five size-differentiated species can co-occur locally (Kingdon 1997). Wider-reaching and more detailed analyses are required to assess whether this analogy betrays a more general ecological pattern among closely related, large-bodied herbivorous mammals in areas of geographic overlap.

The larger extant species of *Macropus* are strongly sexually dimorphic, with adult males averaging 1.5–2 times larger than adult females (McCullough and McCullough 2000). Rensch's rule, a common scaling relationship in mammals (e.g. Rensch 1960; Fairbairn 1997), would predict that the larger kangaroos of the Pleistocene should exhibit even greater sexual dimorphism. So far our data do not support this proposition. With the possible exception of '*P. gilli*', which is similar in size to the modern *Macropus* species, in all Pleistocene kangaroo taxa that we have studied (including Pleistocene *M. giganteus*), values of the coefficient of variation (CV) for *c* (and M_{est}) are comparable with intrasexual but not intersexual CV values for *c* (and M_{obs}) in modern *Macropus rufus* and *M. giganteus* (Tables 1, 2). This suggests that these larger kangaroos may not have been as sexually dimorphic as modern *Macropus* spp. In the case of *S. stirlingi* and *S. tindalei*, individual skeletons from Lake Callabonna have been allocated to sex on the basis of the relative robustness of the forearm (Wells and Tedford 1995). Relevant sexed samples are small (two males and two females for *S. stirlingi*, one of each sex for *S. tindalei*), but our predictions suggest that in *S. stirlingi* males were ~25% larger (195 kg) than females (151 kg), while in *S. tindalei* there was no significant difference between the sexes. Almost all megafaunal kangaroos are currently known by few intact adult femora, so additional sampling for each species will clearly shed further light on this point. Nevertheless, the lack of clear dimorphism in our present samples of most megafaunal kangaroos, especially within the large sample of *M. giganteus* from Lancefield ($n = 41$), is an unexpected result.

True bipedal hopping is a distinctive but relatively rare method of locomotion that has arisen independently several times in vertebrates, including in passerine birds and various rodent lineages (Thompson *et al.* 1980; Hayes and Alexander 1983), but macropodids are the only large-bodied animals that locomote in this way (Alexander and Vernon 1975; Webster and Dawson 2004). Previous comparative studies of

limb scaling in kangaroos have suggested that 50–60 kg is the optimal mass for a macropodid, with larger-bodied animals apparently at risk of tendon breakage during hopping (Bennett and Taylor 1995; Bennett 2000). Our study supports certain previous suggestions that *Procoptodon goliath* weighed more than 200 kg, and that several other Pleistocene kangaroos weighed well over 100 kg. These results suggest a need for renewed investigations into the scaling relationships and functional adaptations that enabled bipedal hopping in such large mammals.

Acknowledgments

This paper is dedicated to the memory of the late Russell V. Baudinette. We thank Dick Tedford, Bert Roberts, Jared Diamond, Craig McGowan, Gavin Prideaux, Tomasz Owerkowicz, Phillip Matthews, Mike Bennett and two anonymous reviewers for insightful discussion and other contributions to this manuscript. We especially thank S. Ingelby and T. Ennis (Australian Museum), W. Longmore (Museum Victoria), and C. Kemper and D. Stemmer (South Australian Museum) for access to specimens under their care. John Kelly of Kangaroo Industry Australia and the staff of Southern Game Meats facilitated the acquisition of femora of red and grey kangaroos of known bodyweight. KMH was supported by fellowships from NSF and the Australian IPRS program.

References

- Alexander, R. M. (1998). All-time giants: the largest animals and their problems. *Palaeontology* **41**, 1231–1245.
- Alexander, R. M., and Vernon, A. (1975). The mechanics of hopping in kangaroos (Macropodidae). *Journal of Zoology* **177**, 265–303.
- Anderson, J. F., Hall-Martin, A., and Russell, D. A. (1985). Long-bone circumference and mass in mammals, birds, and dinosaurs. *Journal of Zoology* **207**, 53–61.
- Anyonge, W. (1993). Body mass in large extant and extinct carnivores. *Journal of Zoology* **231**, 339–350.
- Bartholomai, A. (1973). The genus *Protomnodon* Owen (Marsupialia, Macropodidae) in the upper Cainozoic deposits of Queensland. *Memoirs of the Queensland Museum* **16**, 309–363.
- Baudinette, R. V. (1989). The biomechanics and energetics of locomotion in Macropoidea. In 'Kangaroos, Wallabies and Rat-kangaroos'. (Eds G. Grigg, P. Jarman and I. Hume.) pp. 245–253. (Surrey Beatty: Sydney.)
- Bennett, M. B. (2000). Unifying principles in terrestrial locomotion: do hopping Australian marsupials fit in? *Physiological and Biochemical Zoology* **73**, 726–735. doi:10.1086/318110
- Bennett, M. B., and Taylor, G. C. (1995). Scaling of elastic strain energy in kangaroos and the benefits of being big. *Nature* **378**, 56–59. doi:10.1038/378056a0
- Brown, J. H., Gillooly, J. F., Allen, A. P., Savage, V. M., and West, G. B. (2004). Toward a metabolic theory of ecology. *Ecology* **85**, 1771–1789.
- Burness, G. P., Diamond, J., and Flannery, T. (2001). Dinosaurs, dragons, and dwarfs: the evolution of maximal body size. *Proceedings of the National Academy of Sciences of the United States of America* **98**, 14518–14523. doi:10.1073/pnas.251548698
- Damuth, J., and MacFadden, B. J. (1990). 'Body Size in Mammalian Paleobiology: Estimation and Biological Implications.' (Cambridge University Press: Cambridge.)
- Erickson, G. M., De Ricqlès, A., De Buffrenil, V., Molnar, R. E., and Bayless, M. K. (2003). Vermiform bones and the evolution of gigantism in *Megalania*: how a reptilian fox became a lion. *Journal of Vertebrate Paleontology* **23**, 966–970.
- Fairbairn, D. J. (1997). Allometry for sexual size dimorphism: pattern and process in the coevolution of body size in males and females. *Annual Review of Ecology and Systematics* **28**, 659–687. doi:10.1146/annurev.ecolsys.28.1.659
- 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. (1989). Phylogeny of the Macropodoidea: a study in convergence. In 'Kangaroos, Wallabies and Rat-kangaroos'. (Eds G. Grigg, P. Jarman and I. Hume.) pp. 1–46. (Surrey Beatty: Sydney.)
- Flannery, T. F. (1995). 'Mammals of New Guinea.' Revised edn. (Reed Publishing: Sydney.)
- Flannery, T. F. (2004). 'Country.' (Text Publishing: Melbourne.)
- Flannery, T. F., and Gott, B. (1985). The Spring Creek locality: a late Pleistocene megafaunal site from southwestern Victoria. *Australian Zoologist* **21**, 385–422.
- Flannery, T. F., Mountain, M.-J., and Aplin, K. (1983). Quaternary kangaroos (Macropodidae, Marsupialia) from Nombe rock shelter, Papua New Guinea, with comments on the nature of the megafaunal extinction in the New Guinea highlands. *Proceedings of the Linnean Society of New South Wales* **107**, 75–98.
- Hayes, G., and Alexander, R. M. (1983). The hopping gaits of crows (Corvidae) and other bipeds. *Journal of Zoology* **200**, 205–213.
- Hooijer, D. A. (1950). The study of subspecific advance in the Quaternary. *Evolution* **4**, 360–361. doi:10.2307/2405604
- Jetz, W., Carbone, C., Fulford, J., and Brown, J. H. (2004). The scaling of animal space use. *Science* **306**, 266–268. doi:10.1126/science.1102138
- Johnson, C. N., and Prideaux, G. J. (2004). Extinctions of herbivorous mammals in the late Pleistocene of Australia in relation to their feeding ecology: no evidence for environmental change as cause of extinction. *Australian Ecology* **29**, 553–557. doi:10.1111/j.1442-9993.2004.01389.x
- Kear, B. P., and 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.
- Kingdon, J. (1997). 'The Kingdon Field Guide to African Mammals.' (Academic Press: London.)
- Kurtén, B. (1968). 'Pleistocene Mammals of Europe.' (Aldine Publications: Chicago.)
- Long, J., Archer, M., Flannery, T., and Hand, S. (2002). 'Prehistoric Mammals of Australia and New Guinea.' (University of New South Wales Press: Sydney.)
- Marshall, L. G., and Corruccini, R. S. (1978). Variability, evolutionary rates, and allometry in dwarfing lineages. *Paleobiology* **4**, 101–118.
- McAlpine, C. A., Mott, J. J., Grigg, G. C., and Sharman, P. (1998). The influence of landscape structure on kangaroo abundance in a disturbed semi-arid woodland. *The Rangeland Journal* **21**, 104–134. doi:10.1071/RJ9990104
- McCullough, D. R., and McCullough, Y. (2000). 'Kangaroos in Outback Australia: Comparative Ecology and Behaviour of Three Coexisting Species.' (Columbia University Press: New York.)
- Miller, G. H., Fogel, M. L., Magee, J. W., Gagan, M. K., Clarke, S. J., and Johnson, B. J. (2005). Ecosystem collapse in Pleistocene Australia and a human role in megafaunal extinction. *Science* **309**, 287–290. doi:10.1126/science.1111288

- Molnar, R. E. (2004). 'Dragons in the Dust: The Paleobiology of the Giant Monitor Lizard *Megalania*.' (Indiana University Press: Bloomington, IL.)
- Murray, P. (1984). Extinctions Downunder: a bestiary of extinct Australian late Pleistocene monotremes and marsupials. In 'Quaternary Extinctions'. (Eds P. S. Martin and R. G. Klein.) pp. 600–628. (University of Arizona Press: Tucson, AZ.)
- Murray, P. (1991). The Pleistocene megafauna of Australia. In 'Vertebrate Palaeontology of Australasia'. (Eds P. V. Rich, J. M. Monghan, R. Baird and T. H. Rich.) pp. 1071–1164. (Pioneer Design Studio, Monash University: Melbourne.)
- Myers, T. J. (2001). Marsupial body mass prediction. *Australian Journal of Zoology* **49**, 99–118. doi:10.1071/ZO01009
- Pledge, N. S. (1980). Macropodid skeletons, including *Simosthenurus* Tedford, from an unusual "drowned cave" deposit in the southeast of South Australia. *Records of the South Australian Museum* **18**, 131–141.
- Prideaux, G. J. (2004). Systematics and evolution of the sthenurine kangaroos. *University of California Publications in Geological Sciences* **146**, 1–623.
- Rensch, B. (1960). 'Evolution above the Species Level.' (Columbia University Press: New York.)
- Reynolds, P. S. (2002). How big is a giant? The importance of method in estimating body size of extinct mammals. *Journal of Mammalogy* **83**, 321–332. doi:10.1644/1545-1542(2002)083<0321:HBIAGT>2.0.CO;2
- Roberts, R., Flannery, T., Ayliff, L., Yoshida, H., Olley, J., *et al.* (2001). New ages for the last Australian megafauna: continent-wide extinction about 46,000 years ago. *Science* **292**, 1888–1892. doi:10.1126/science.1060264
- Schultz, C. B., Tanner, L. G., and Martin, L. D. (1972). Phyletic trends in certain lineages of Quaternary mammals. *Bulletin of the University of Nebraska State Museum* **9**, 183–195.
- Smith, R. J. (1993). Logarithmic transformation bias in allometry. *American Journal of Physical Anthropology* **90**, 215–228. doi:10.1002/ajpa.1330900208
- Smith, R. J. (2002). Estimation of body mass in paleontology. *Journal of Human Evolution* **43**, 271–287. doi:10.1006/jhev.2002.0573
- Smith, F. A., Brown, J. H., Haskell, J. P., Lyons, S. K., Alroy, J., *et al.* (2004). Similarity of mammalian body size across the taxonomic hierarchy and across space and time. *American Naturalist* **163**, 672–691. doi:10.1086/382898
- Stiner, M. C., Achyuthan, H., Arsebuk, G., Howell, F. C., Josephson, S. C., Juell, K. E., Pigati, J., and Quade, J. (1998). Reconstructing cave bear paleoecology from skeletons: a cross-disciplinary study of middle Pleistocene bears from Yarimburgaz Cave, Turkey. *Paleobiology* **24**, 74–98.
- Strahan, R. (1995). 'Mammals of Australia.' (Smithsonian Institution Press: Washington, DC.)
- Tedford, R. H., and Wells, R. T. (1990). Pleistocene deposits and fossil vertebrates from the "Dead Heart of Australia". *Memoirs of the Queensland Museum* **28**, 263–284.
- Thompson, S. D., MacMillen, R. E., Burke, E. M., and Taylor, C. R. (1980). The energetic cost of bipedal hopping in small mammals. *Nature* **287**, 223–224. doi:10.1038/287223a0
- Trueman, C. N. G., Field, J. H., Dortch, J., Charles, B., and Wroe, S. (2005). Prolonged coexistence of humans and megafauna in Pleistocene Australia. *Proceedings of the National Academy of Sciences of the United States of America* **102**, 8381–8385. doi:10.1073/pnas.0408975102
- Webster, K. N., and Dawson, T. J. (2004). Is the energetics of mammalian hopping locomotion advantageous in arid environments? *Australian Mammalogy* **26**, 153–160.
- Wells, R. T., and 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.
- Willows-Munro, S., Robinson, T. J., and Matthee, C. A. (2005). Utility of nuclear DNA intron markers at lower taxonomic levels: phylogenetic resolution among nine *Tragelaphus* spp. *Molecular Phylogenetics and Evolution* **35**, 624–636. doi:10.1016/j.ympev.2005.01.018
- Wroe, S. (2002). A review of terrestrial mammalian and reptilian carnivore ecology in Australian fossil faunas, and factors influencing their biodiversity: the myth of reptilian domination and its broader ramifications. *Australian Journal of Zoology* **50**, 1–24. doi:10.1071/ZO01053
- Wroe, S., Myers, T., Wells, R. T., and Gillespie, A. (1999). Estimating the mass of the Pleistocene marsupial lion, *Thylacoleo carnifex* (Thylacoleonidae: Marsupialia): implications for the ecomorphology of a marsupial super-predator and hypothesis of impoverishment of Australian marsupial carnivore faunas. *Australian Journal of Zoology* **47**, 489–498. doi:10.1071/ZO99006
- Wroe, S., Myers, T., Seebacher, F., Kear, B., and Gillespie, A. (2003). An alternative method for predicting body mass: the case of the Pleistocene marsupial lion. *Paleobiology* **29**, 403–411.
- Wroe, S., Crowther, M., Dortch, J., and Chong, J. (2004). The size of the largest marsupial and why it matters. *Proceedings of the Royal Society of London. Series B. Biological Sciences* **271**(Suppl.), S34–S36.

Appendix 1. Specimens of extant macropodid species included in the regression analysis

AM M = Australian Museum (Sydney); C = Museum Victoria (Melbourne);

SAM M = South Australian Museum (Adelaide)

Species	Museum accession no.	<i>c</i>	<i>M_{obs}</i>	Sex
<i>Dendrolagus dorianus</i>	AM M30720	39.5	9	Male
	AM M30753	40.0	8.5	Male
<i>Dendrolagus inustus</i>	AM M25390	51.0	17	Male
<i>Dendrolagus mbaiso</i>	AM M30749	38.1	9	Female
<i>Dendrolagus scottae</i>	AM M24424	43	11.5	Female
	AM M25397	41.0	9.5	Male
<i>Dorcopsis atrata</i>	AM M19461	40.0	7.5	Male
<i>Dorcopsis</i> sp. (probably <i>luctuosa</i>)	C.31632	33.2	4.1	Female
<i>Dorcopsis muelleri</i>	AM M32341	47.0	13	Male
	AM M32339	37.0	5.9	Female
<i>Dorcopsulus vanheurni</i>	AM M30727	24.0	2	Male
<i>Macropus agilis</i>	AM M9146	58.5	11	Unknown
<i>Macropus eugenii</i>	C.17532	32.9	6.8	Male
<i>Macropus fuliginosus</i>	AM M21497	90.0	80	Female
	AM M21438	71.0	24	Female
<i>Macropus giganteus</i>	AM M33374	71.0	35	Male
	SAM (EGF1)	66.5	27.0	Female
	SAM (EGF2)	65	24.0	Female
	SAM (EGF3)	63.5	21.5	Female
	SAM (EGF4)	61	22.0	Female
	SAM (EGF5)	59	19.5	Female
	SAM (EGF6)	61.5	24.0	Female
	SAM (EGF7)	64.5	25.5	Female
	SAM (EGF8)	58	19.0	Female
	SAM (EGF9)	62	26.5	Female
	SAM (EGF10)	63	22.0	Female
	SAM (EGF11)	62	28.0	Female
	SAM (EGF12)	69	26.0	Female
	SAM (EGF13)	74.5	36.0	Female
	SAM (EGF14)	70	26.0	Female
	SAM (EGF15)	73	36.0	Female
	C.5533	66.5	33.1	Female
	SAM (EGM1)	68.5	32.0	Male
	SAM (EGM2)	66.5	23.0	Male
	SAM (EGM3)	88	57.0	Male
	SAM (EGM4)	73	34.0	Male
	SAM (EGM5)	77.5	39.0	Male
	SAM (EGM6)	67.5	24.5	Male
	SAM (EGM7)	71	38.0	Male
	SAM (EGM8)	73	36.0	Male
	SAM (EGM9)	71.5	38.0	Male
	SAM (EGM10)	63.5	22.0	Male
SAM (EGM11)	72	34.0	Male	
SAM (EGM12)	69	33.5	Male	
SAM (EGM13)	70	32.0	Male	
SAM (EGM14)	86	60.0	Male	
SAM (EGM15)	82.5	49.0	Male	
AM M33373	87.0	57	Male	
C.31633	63.0	24.0	Male	
C.5534	43.1	5.9	Male	
C.5535	54.2	15.9	Male	
<i>Macropus parma</i>	C.10716	30.0	3.4	Female
	C.10717	31.0	3.5	Female
	C.10718	25.0	2.3	Female
	C.9592	23.1	2.0	intersex
	AM M37053	30.0	3.035	Unknown
<i>Macropus parryi</i>	AM M14103	52.0	15.7	Female
<i>Macropus robustus</i>	C.11592	60.5	25.3	Male

(continued next page)

Appendix 1. (Continued)

Species	Museum accession no.	<i>c</i>	<i>M</i> _{obs}	Sex
<i>Macropus rufogriseus</i>	C.8728	48.0	13.0	Female
	C.22286	40.0	7.0	Female
	C.26504	50.3	14.1	Male
	C.8727	50.0	13.8	Male
<i>Macropus rufus</i>	SAM (RF1)	63	27.0	Female
	SAM (RF2)	67.5	25.5	Female
	SAM (RF3)	64	20.5	Female
	SAM (RF4)	64	28.5	Female
	SAM (RF5)	65.5	18.5	Female
	SAM (RF6)	63.5	25.0	Female
	SAM (RF7)	69	22.0	Female
	SAM (RF8)	74	35.0	Female
	SAM (RF9)	65	21.5	Female
	SAM (RF10)	64	24.0	Female
	SAM (RF11)	67.5	26.5	Female
	SAM (RF12)	69	27.5	Female
	SAM (RF13)	69	26.5	Female
	SAM (RF14)	64.5	34.5	Female
	SAM (RF15)	64.5	23.5	Female
	SAM (RM1)	78	55.0	Male
	SAM (RM2)	66.5	19.5	Male
	SAM (RM3)	78.5	41.5	Male
	SAM (RM4)	80	51.0	Male
	SAM (RM5)	86	50.5	Male
	SAM (RM6)	75	35.0	Male
	SAM (RM7)	80.5	57.0	Male
	SAM (RM8)	82.5	64.5	Male
	SAM (RM9)	63.5	19.0	Male
	SAM (RM10)	71.5	47.0	Male
SAM (RM11)	74	39.5	Male	
SAM (RM12)	88	60.0	Male	
SAM (RM13)	84	54.0	Male	
SAM (RM14)	78.5	44.0	Male	
SAM (RM15)	72	38.5	Male	
AM M33372	89.0	56	Male	
AM S14103	76.0	43	Male	
AM M37128	33.5	3	Male	
AM M21593	37.0	5.75	Male	
<i>Petrogale brachyotis</i>	C.11593	34.3	5.3	Male
<i>Petrogale cf. godmani</i>	C.26530	37.7	13.0	Male
<i>Petrogale mareeba</i>	AM M9187	29.5	2.562	Male
<i>Setonix brachyurus</i>	AM M14102	32.0	3	Male
<i>Thylogale billardieri</i>	C.7995	21.2	1.6	Unknown
<i>Thylogale stigmatica</i>	AM M37152	30.0	4.45	Male
<i>Wallabia bicolor</i>	C.16117	28.0	2.2	Female
	C.8334	51.1	11.3	Female
	AM M21355	57.0	18	Male
	C.27027	39.0	7.7	Male
	C.16148	56.1	17.2	Male

Appendix 2. Registration numbers and femoral circumferences (c) for fossil specimens studied

(sa) = subadult (distal epiphysis of femur unfused); AM F = Australian Museum vertebrate palaeontology collection (Sydney); AMNH = American Museum of Natural History paleontology collection (New York); FUCN = Flinders University palaeontology collection (Adelaide); NMV P = Museum of Victoria palaeontology collection (Melbourne); SA = South Australia; SAM P = South Australian Museum palaeontology collection (Adelaide); UCMP = University of California Museum of Paleontology collection (Berkeley)

<i>Macropus giganteus titan</i>	Lancefield Swamp NMV P(unregistered) 93 (sa), 93 (sa), 96 (sa), 108 (sa), 106.5 (sa), 107, 108, 111, 113, 113, 117, 117, 117, 118, 119, 119, 119, 120, 120, 122, 123, 123, 123, 123, 123, 123, 123, 125, 125, 126, 127, 127, 127, 128, 128, 128, 128, 129, 129, 130, 132, 132, 133, 133, 134, 135, 136. Green Waterhole SAM P17532 (sa), 75; SAM P18297 (sa), 89; SAM P17525, 96; SAM P17270, 94; SAM P17270, 93; SAM P17312, 86; FUCN 4005, 89. Morwell NMV P194574, 94.8; NMV P(unregistered), 90.9; NMV P(unregistered), 107.5; NMV P39112, 110; NMV P39113, 112.1; NMV P42533, 114.5; NMV P39101, 114.8; NMV P42533, 115.1.
<i>Protemnodon anak</i>	Morwell NMV P39101, 117; NMV P159917, 119.2; Green Waterhole FUCN 400111, 116; SAM P27272, 128.
<i>Protemnodon brehus</i>	Spring Creek NMV P173087, 113; Alt Creek Normanville, SA. SAM P (unregistered), 113; Blanche Cave Naracoorte SAM P(unregistered) (sa), 112.
<i>Protemnodon hopei</i>	Kwiyawagi, West Papua AM F88924, 79.5.
<i>Protemnodon roechus</i>	Lake Victoria NMV P26570, 132.
<i>Procoptodon goliah</i>	Lake Menindee UCMP 45475, 149; Henschke's Cave SAM P17357, 153; Haystack Cave SAM P(unregistered) 148.
<i>'Procoptodon' gilli</i>	Green Waterhole SAM P17503, 80; SAM P17268, 78; Naracoorte Caves SAM P(unregistered), 84; FUCN1403 (sa), 61; S123 0703, 98.
<i>Simosthenurus maddocki</i>	Green Waterhole SAM P18311, 100; FUCN 1403, 96; SAM S123 07, 68 (sa).
<i>Simosthenurus occidentalis</i>	Green Waterhole SAM P17259, 122; SAM P18298, 117; SAM P17282, 117; SAM P17474, 114; SAM P17301 (sa), 87; SAM P20820, 107.
<i>Sthenurus andersoni</i>	Lake Callabonna SAM P13673, 91; Narrina, SA. SAM P(unregistered), 99; Cheese and Putty Cave, SA. SAM P40054, 98; SAM P13673, 93.
<i>Sthenurus stirlingi</i>	Lake Callabonna SAM P22533, 143; SAM P139340, 130.4., AMNH 117495 (sa), 104; AMNH 117496, 127; AMNH 117497, 127; AMNH 117498, 137.5
<i>Sthenurus tindalei</i>	Lake Callabonna AMNH 117493, 125; AMNH 117499, 112.7.
