The relationship between calcaneum dimension ratios and body mass

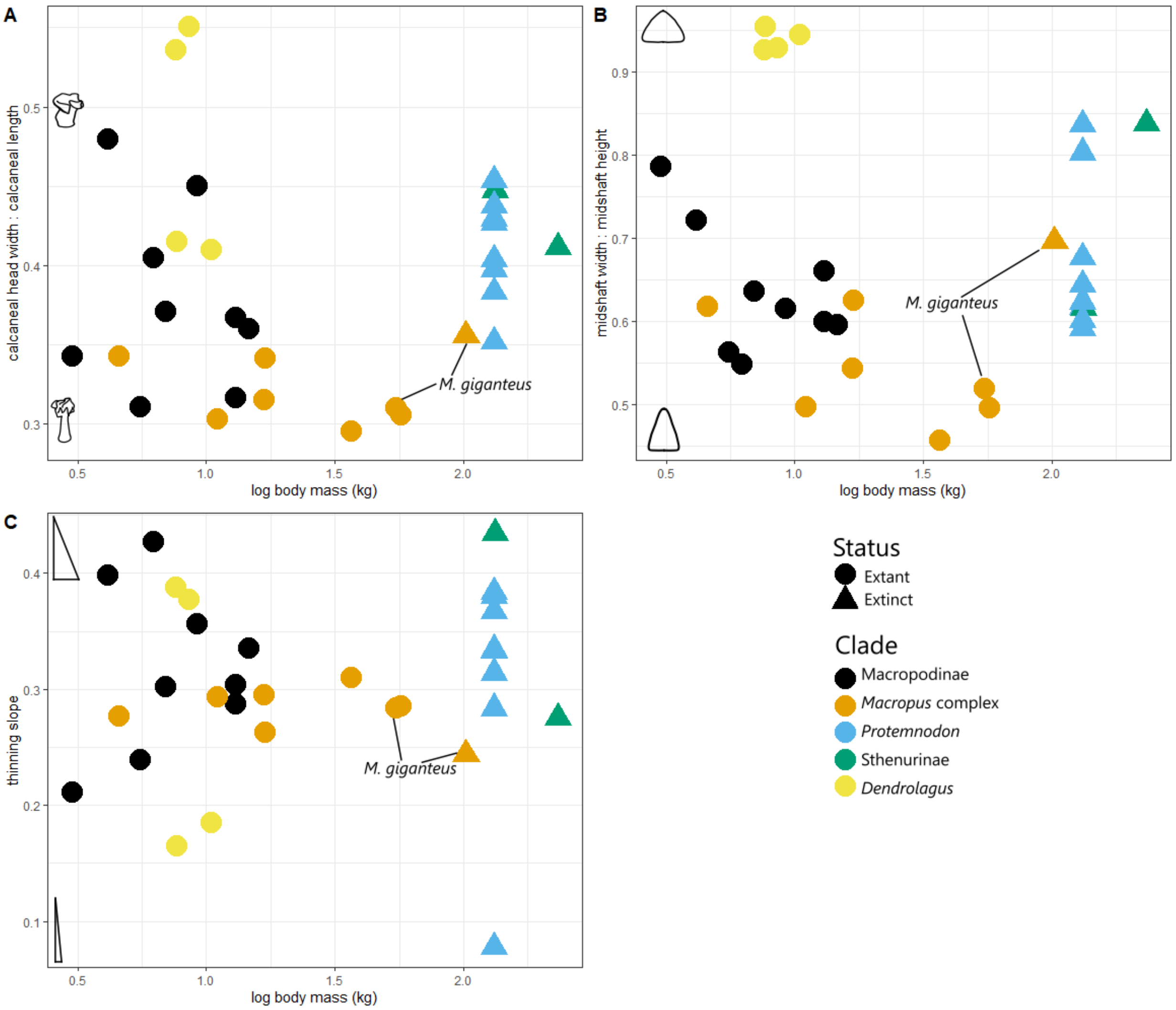

Fig. S1 Calcaneum dimension ratios against log-transformed body mass. (a) Calcaneal head width to calcaneal length; (b) midshaft width to midshaft height; (c) slope of calcaneal head width to midshaft width ("thinning slope"). Points are coloured by clade. *n* = 31.

Methods

Three indices were calculated for the calcaneal dataset collected in the NMV (Museums Victoria), and plotted against mass. These were: ratio of calcaneal head width to total calcaneal length; ratio of mediolateral width at midshaft to dorsoventral width at midshaft; and the slope of mediolateral width from the calcaneal head to the midshaft (calculated as the difference between the two mediolateral widths, divided by half the total calcaneal length). Together, these indices help us to broadly characterise calcaneal morphology, and to see if there are any adaptations of the insertion point of the gastrocnemius tendon which should be taken into consideration when interpreting results from the main study.

Results

The calcanea of giant extinct kangaroo species were shorter relative to calcaneal head width (Fig. S1a), and less mediolaterally compressed at the midshaft (Fig. S1b) than in smaller extant species. This is a departure from a general pattern among extant species of longer, narrower calcanea with increasing size. The third index, the rate at which the calcaneum narrows from the tuber calcanei to the midshaft (Fig. S1c), seems less informative, with no clear trend over size or between clade groups (including in the extinct species).

Discussion

While the thinning slope (Fig. S1c) seems relatively uninformative, the other two indices both indicate a departure from allometric patterns in the calcanea of extinct giant kangaroos. In living species, the calcanea grow relatively longer and mediolaterally narrower with size. Meanwhile, the relative dimensions of the extinct species' calcanea resemble those of small macropodines, and even some tree kangaroos, far more than large extant kangaroos. The calcaneal morphology of large extant kangaroos is surely strongly influenced by the high forces exerted on the tuber calcanei by the gastrocnemius tendon when hopping. The large kangaroos face a trade-off in their ankle extensor tendon dimensions. A narrower tendon is able to store and return more elastic energy, but is less able to withstand high forces (McGowan et al., 2008; Bennett and Taylor, 1995). Thus, a kangaroo adapted to optimise efficient hopping would be expected to have a tendon (and corresponding tuber calcanei) with the narrowest width possible without risking tendon rupture. A relatively longer calcaneum may also be advantageous, providing the gastrocnemius tendon with a greater in-lever, and resulting in the tendon being stretched over a longer distance at the mid-stance of a hop, increasing elastic strain energy storage. The changing dimensions of calcanea from small to large Macropodinae seem to reflect this adaptation to maximum efficiency, with increased relative length and a more narrow shaft, and no particularly great flaring of the shaft towards the tuber calcanei (Fig. S1). The fact that the sthenurines and *Protemnodon* depart from this, seemingly more than would be demanded by allometry, and adopt proportions more comparable to small macropodines, may suggest a shift away from prioritising efficiency in hopping.

Unusually, *Macropus giganteus* is a megafaunal species which became smaller after the Pleistocene, rather than becoming extinct (Helgen et al., 2006). Today, the species has a body mass on a par with other large extant kangaroos. Our calcaneal dataset includes one *M. giganteus* specimen from the Pleistocene, and one modern specimen. Very interestingly, the Pleistocene *M. giganteus* specimen follows the pattern of other giant species, possessing a relatively shorter, broader calcaneum. Meanwhile, the smaller modern member of the species possesses a longer, narrower calcaneum, similar to that of the red kangaroo *Osphranter rufus*. This suggests that this pattern is at primarily related to body size, rather than being driven by phylogeny.

Wagstaffe et al. (2022) studied the second moments of area and cortical bone distribution of sthenurine and macropodine calcanea. They found that sthenurine calcanea are less resistant to bending than macropodine calcanea, and suggest that the broader heads of sthenurine calcanea reflect a movement away from optimising the elastic energy storage capacity of the gastrocnemius tendon. Their findings do suggest that sthenurine species were not optimally adapted for hopping, but also seem to indicate that this correlates more with phylogeny than body mass, as the paper compares sthenurines and macropodines of similar body masses, and finds these differences throughout. The largest specimen they studied, *Macropus* cf. *M. titan* (estimated at 176 kg), retained a strengthened calcaneum with high resistance to bending, and the authors predicted that this species would still have hopped, despite its size. Unfortunately, no *M. titan* specimens are included in our own dataset. However, the single giant extinct macropodine we did measure, *Macropus giganteus*, shows deviations in shape from the smaller macropodines, closer to the ranges of the even larger sthenurine and *Protemnodon* specimens. So, in contrast to the findings of Wagstaffe et al. (2022), we do find that giant macropodines may show physical adaptations which suggest a move away from optimisation for hopping locomotion.

The intra-hindlimb proportions of Macropodiformes

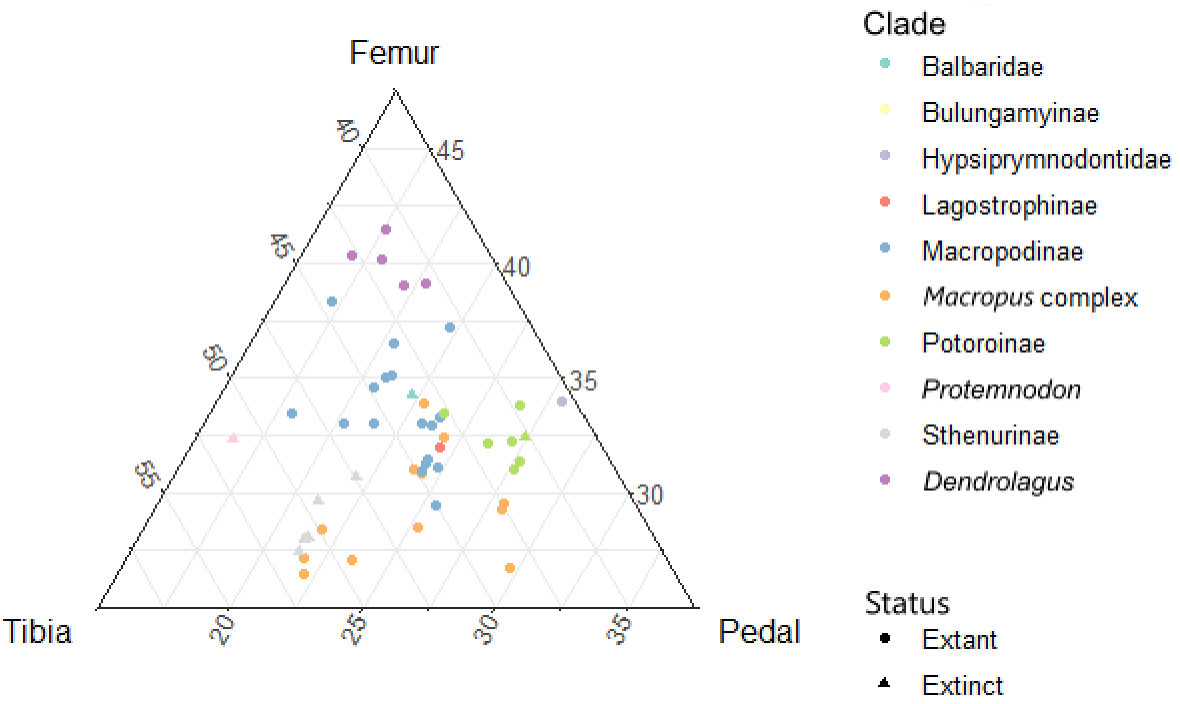

Fig. S2 Ternary diagram of the length of the tibia, femur, and pedal bones (fourth metatarsal + associated proximal phalanx) of macropods. Each value is the length of the segment as a proportion of the entire leg. Each point is the species mean. The colours of the points denote clades within the Macropodiformes, while shape denotes whether a species is extant or extinct. *n* = 116 specimens, 50 species means.

Methods

A ternary diagram using species means of bone lengths was produced in R, showing the relative proportions of the femur, tibia, and foot bones (metatarsal + proximal phalanx) for each species.

Results

The ternary diagram (Fig. S2) shows that relative hindlimb proportions among macropodiforms generally cluster by taxon. The tree-kangaroos are the most distinct group, with short tibiae and feet, reflecting their unique mode of locomotion among extant macropodiforms. Among the extinct groups, the balbarid *Ganawamaya gillespieae* clusters in the centre of the space occupied by extant macropodiforms, closest to the non-*Macropus*-complex Macropodinae. *Protemnodon* has short feet, much like the tree-kangaroos, but has a similarly elongated tibia to the *Macropus* complex. Finally, the Sthenurinae occupy the leftmost side of the range of the *Macropus* complex, indicating similar general hindlimb proportions to that group, although they tend to have somewhat shorter feet than many members of the *Macropus* complex.

Linear regressions of macropodiform hindlimb long bones against body mass

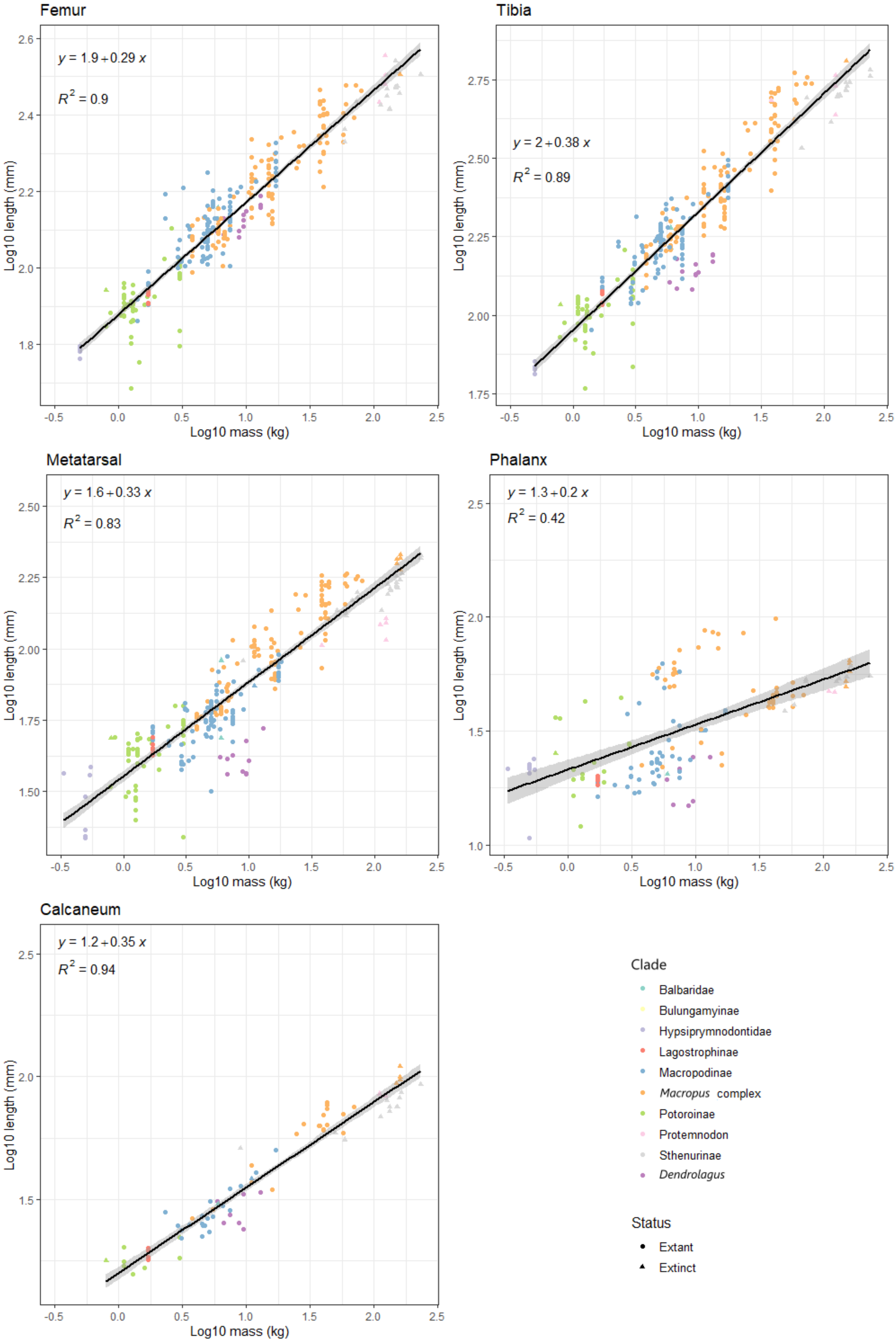

Fig. S3 Least squares regressions of log-transformed hind limb bone length against log-transformed body mass. The colours of the points denote clades within the Macropodiformes, while shape denotes whether a species is extant or extinct. Shading indicates 95% confidence intervals. *n* = 303 (femur), 300 (tibia), 298 (metatarsal), 149 (phalanx), and 82 (calcaneum). For methods and results see under Table S2, below.

Table S2: Results of linear OLS regressions of log-transformed bone length against log-transformed body mass. Entries highlighted in pale grey show significant negative allometry, while those in dark grey show significant positive allometry. Entries with no highlighting (white background) are not significantly different from isometry.

			95% CI			
Bone	**Group (*n*)**	**Exponent**	**Lower**	**Upper**	**Adjusted R^2**	**P-value**
Femur	All (303)	0.29	0.28	0.30	0.90	<2.2E-16
	Macropus complex excluded (197)	0.29	0.27	0.30	0.90	<2.2E-16
Tibia	All (300)	0.38	0.36	0.39	0.89	<2.2E-16
	Macropus complex excluded (194)	0.35	0.33	0.36	0.89	<2.2E-16
Metatarsal	All (298)	0.33	0.31	0.35	0.83	<2.2E-16
	Macropus complex excluded (197)	0.29	0.27	0.31	0.80	<2.2E-16
Proximal phalanx	All (149)	0.20	0.16	0.24	0.41	<2.2E-16
	Macropus complex excluded (102)	0.18	0.14	0.21	0.44	<2.2E-16
Calcaneum	All (82)	0.35	0.33	0.37	0.94	<2.2E-16
	Macropus complex excluded (59)	0.33	0.31	0.35	0.94	<2.2E-16

Methods

A linear (OLS) regression was run on log-transformed bone lengths against log-transformed body masses for each bone. This was repeated in each case with and without members of the *Macropus* complex included, since it has been argued that the *Macropus* complex are likely anomalous (Janis et al., 2014), with their hindlimb long bone lengths not reflecting general allometric patterns. Only regressions including the *Macropus* complex are illustrated in Fig. S4; the statistics for all regressions can be seen in Table S2.

Results

The only bone which shows significant positive allometry is the tibia, and that allometry becomes non-significant when the *Macropus* complex is excluded, suggesting that the exceedingly long tibiae of the largest extant kangaroos may be a quirk of that particular group, rather than a general allometric pattern across the macropodiforms. The femur and proximal phalanx scale with negative allometry regardless of the inclusion of the *Macropus* complex, while the metatarsal scales with negative allometry only when the Macropus complex is excluded. The calcaneum scales with isometry. The proximal phalanx length is by far the least linked to body mass, as shown by its much lower R^2 value (0.42, vs. >0.8 in all other bones).

References

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