



# Proportional variation and scaling in the hindlimbs of hopping mammals, including convergent evolution in argyrolagids and jerboas

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## Abstract

Bipedal hopping is a mode of locomotion seen today in four rodent lineages and one clade of marsupials. The Argyrolagidae, marsupials from the Oligocene to Pliocene of South America, have also been considered to be hoppers. These lineages all convergently evolved similar general morphologies, with elongated hindlimbs, reduced forelimbs, and elongated tails, and their similarities and variations may be informative in understanding the evolution of hopping in mammals. This study uses principal components analysis and log-log regressions to investigate variation in the hindlimb proportions of these hopping mammals and how this relates to body mass. We find that the distribution of hopping mammal masses is bimodal, divided at roughly 500 g. These two domains among hopping mammals may reflect optimisation for different forms of hopping locomotion; species under 500 g tend to have more elongated metatarsals relative to the rest of their hindlimbs, perhaps to facilitate rapid vertical jumps for predator evasion, a behaviour not seen in larger hoppers. Despite this bimodal distribution in body mass, hindlimb proportions cluster more by clade than mass, with some similarities among clades being especially noteworthy. The jerboas (Dipodidae, Rodentia) and Argyrolagidae share a particularly extreme degree of metatarsal elongation. The drivers of this convergence are unclear, but we hypothesise that the elongation may be related to the reduction/fusion of metatarsals in these groups, or a greater reliance on bipedality at slow speeds, as jerboas are known to utilise multiple bipedal gaits in addition to hopping.

**Keywords** Allometry · Argyrolagidae · Hopping locomotion · Jerboas · Mammals

## Introduction

### Hopping in mammals

Bipedal hopping, also known as saltation or ricochetal locomotion, is a relatively uncommon mode of locomotion in mammals, having five distinct origins among extant species (McGowan and Collins 2018). Among the rodents, hopping has arisen independently in four distinct clades:

the kangaroo rats (*Dipodomys*, Heteromyidae) from arid to semi-arid regions of North America (Donnelly et al. 2015); the Australian hopping mice (*Notomys*, Muridae) (Dawson 1976); the jerboas (Dipodidae) from arid regions of Eurasia and northern Africa (Zhang et al. 2013); and the springhares (Pedetidae) of southern and eastern Africa (Veiga et al. 2020). Meanwhile, hopping among marsupials is seen today only among the Macropodoidea (McGowan and Collins 2018), a clade including the kangaroos (Macropodidae), the rat-kangaroos (Potoroidae) and the musky rat-kangaroo, *Hypsiprymnodon moschatus* (Hypsiprymnodontidae). *H. moschatus* does not hop, but potoroids and macropodids likely share a hopping ancestry (Burk et al. 1998; Westerman et al. 2022). Within the Macropodidae are the extant subfamilies Lagostrophinae, which includes the banded hare wallaby *Lagostraphus fasciatus*, and Macropodinae, which includes the remaining extant members of Macropodidae (Prideaux and Warburton 2010).

Despite their disparate phylogenetic origins and body masses, hopping mammals have many convergently

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evolved similarities in their morphology. For example, all have elongated hindlimbs and reduced forelimbs, with a forelimb:hindlimb length ratio of  $<0.5$ . Long tails are another shared adaptation, likely for balance or control while hopping (McGowan and Collins 2018). Other shared features across hopping mammals include short necks, often with fused cervical vertebrae, which prevent whip-lash, and a robust lumbar region of the spine (Hildebrand and Goslow 2001).

Many hopping mammals also have reduced or lost pedal digits and/or fused metatarsals (McGowan and Collins 2018). Reduction in number and/or fusion of the metapodials is seen elsewhere among cursorial ungulates (Polly 2007: pp. 245–268; Clifford 2010), where it has been interpreted as a measure to reduce the mass of the distal segments of the limb, while maintaining the strength of those segments (Hildebrand 1960; Currey 2002: pp. 302–303). Lighter distal limb segments may then allow the limb to accelerate and decelerate more rapidly, resulting in the animal being able to achieve faster speeds (Gray 1968). Hopping mammals may derive some of these same benefits from the reduction in number of their digits, and/or fusion of their metatarsals.

Based on these common features of hopping mammals, the *Argyrolagidae*, an extinct marsupial clade from South America (Sánchez-Villagra 2001; Beck 2017; Abello and Candela 2020), may also have hopped bipedally. This family includes the genera *Argyrolagus* and *Microtragulus*, among others. *Argyrolagus* in particular has been remarked upon as having a similar general morphology to extant hopping rodents, with much longer hindlimbs than forelimbs, and all but two metatarsals on each foot being reduced or lost (Simpson 1970). A more detailed morpho-functional analysis of the fore- and hindlimbs of *Argyrolagus* by Abello and Candela (2020) further supports this idea, with many qualitative functional features, along with key quantitative indices such as intermembral indices, indicating adaptations to both hopping and digging.

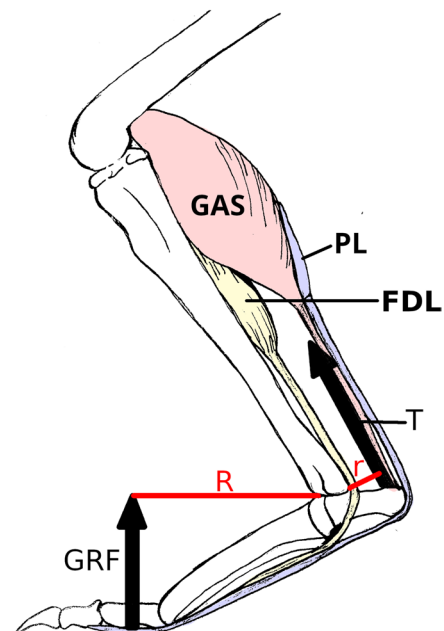
## Hopping and scaling

Extant hopping mammals cover a very wide range of body masses. Hopping rodents range from  $\sim 4$  g in the pygmy jerboa *Salpingotulus michaelis* (Boël et al. 2020) to  $\sim 3.5$  kg in the springhare *Pedetes capensis* (Webster and Dawson 2004). Meanwhile, hopping macropodoids range approximately from 1 to 90 kg (McGowan and Collins 2018).

Among terrestrial mammals, larger species generally adopt a less crouched stance, compensating for the increased stresses imposed on limb bones and joints by increasing the mechanical advantage of muscles acting on those joints (Biewener 1989). Hopping mammals cannot do this, as they must maintain a crouched posture in order to hop (Bennett

2000). Thus, the question of how hopping mammals adapt to increasing body sizes is an intriguing one.

One mass-related threshold affecting hopping mammals in particular, around 3 kg, has been widely discussed in the literature. The most widely held consensus is that in hoppers above  $\sim 3$  kg, the tendons of the ankle extensor muscle-tendon units (MTUs) (Fig. 1) (Alexander 1988) can store and return sufficient elastic energy that hopping becomes a more efficient gait for long-distance locomotion than the gaits of similarly-sized quadrupeds (Bennett and Taylor 1995; Bennett 2000; Schwaner et al. 2018). Meanwhile, hoppers under  $\sim 3$  kg—a mass category which encompasses all hopping rodents, except possibly the springhare, which has a body mass of around 3 kg (Veiga et al. 2020)—have ankle extensor tendons which are proportionally too thick, and thus too rigid, to store much elastic energy. Instead, these species use hopping primarily as a mechanism for escaping predation, rather than as an energetically efficient mode of locomotion (Thompson et al. 1980; Biewener and Blickhan 1988; Moore et al. 2017b). Some of the assumptions behind this hypothesis have been called into question: for example, one recent study found that kangaroo rat (*Dipodomys*) tendons are more pliant than previously assumed (Christensen et al. 2022) and are therefore able



**Fig. 1** Hindlimb of a macropod (based roughly on *M. giganteus*, but proportions are not exact), showing the key forces and muscle-tendon units acting around the distal segments of the hindlimb, focusing on the ankle extensors. Abbreviations: **FDL**, flexor digitorum longus; **GAS**, gastrocnemius; **GRF**, ground reaction force; **PL**, plantaris; **R**, lever arm of GRF; **r**, lever arm of tension in GAS and PL; **T**, tensional forces exerted by GAS and PL. Image by Megan Jones; based on Bennett and Taylor (1995), Biewener and Roberts (2000), McGowan et al. (2008)

to store more elastic energy than had been suggested. In general, however, the notion that the tendons of small hoppers store and return less elastic energy than those of their larger counterparts remains well supported.

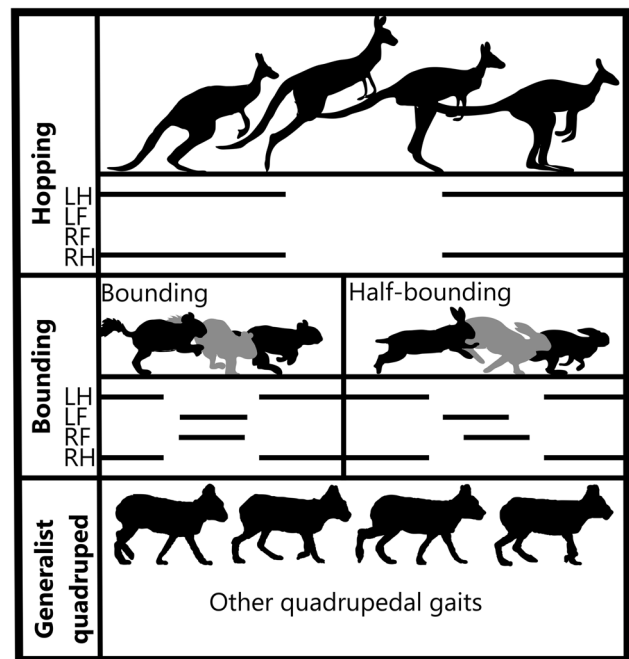
## Aims of the study

Despite fairly extensive research into the mechanics and scaling of the hindlimbs of hopping mammals, there has yet to be a comprehensive analysis of the variation in intra-hindlimb proportions among and between the hopping mammal clades. The absolute and relative lengths of the long bones in the hindlimbs have major implications for the function of those limbs, as they affect the lengths of key muscle-tendon units, and the lever arms and effective mechanical advantages of those units (Biewener and Patek 2018; Dunn 2018). Here, we focus on the proportions within the hindlimb, rather than absolute lengths. If hopping mammals have differences in their locomotion according to their size, or their clade, this may well be reflected in their intra-hindlimb proportions. In this study, we analyse the variation in intra-hindlimb proportions of hopping mammals, in order to further understand how different species have adapted their hindlimbs to a hopping mode of locomotion, and how body mass interacts with these adaptations.

## Materials and methods

### Materials and measurements

In total, 278 specimens were collected across 153 species. Of these, 136 were extant hopping mammals (60 rodents, 76 marsupials), including representatives from every extant lineage of hopping mammals, and two were representatives of the extinct, possibly hopping *Argyrolagidae*. The remaining specimens were composed of a variety of quadrupedally bounding and generalist quadrupedal mammal species, collected in order to provide a point of comparison to the hopping species. “Bipedal hopping”, “Quadrupedal bounding” and “Generalist quadrupedal” were defined as illustrated in Fig. 2. For the locomotor classifications of each species in the dataset, see Online Resource 1. Larger cursorial animals such as digitigrade carnivores and ungulates were excluded from the dataset, as this study focuses primarily on the smaller (< 10 kg) hopping mammals, and larger species, as well as unguligrade animals such as ungulates, may be less comparable. It is possible that some of these species may provide interesting points of comparison for the largest extant kangaroos, but this is outside the scope of the current study.



**Fig. 2** Definition of gaits used in this study, with lines indicating the time for which each limb is in contact with the ground (LF, left fore; LH, left hind; RF, right fore; RH, right hind). Terms on the lefthand side are the three locomotor classifications used in the study. Credits for silhouettes: Simons (1999), van der Weele and Banning (2001), Chagas et al. (2019), Wellcome Library, London (CC BY 4.0) via Wikimedia Commons

The materials used for this study included CT scans, photographs with scale bars, and measurements acquired through published literature or private correspondence. The sources and specimen numbers for each of these specimens are listed in Online Resource 1. For each specimen, the articular lengths of the femur, tibia, longest metatarsal, and associated proximal phalanx were measured. The photographs were measured in ImageJ 1.53 K (Schneider et al. 2012). All CT scans were accessed via MorphoSource.org (Duke University); for details on which scans were accessed, see Online Resource 1. These were imported into Amira-Avizo 3D 2021.1 (Thermo Fisher Scientific 2021), with voxels scaled according to x,y,z pixel spacing dimensions provided in the associated MorphoSource.com pages. The bones were then segmented from the CT scans, and measurements taken from the resulting surfaces, in Avizo.

For some specimens, certain bone lengths were unavailable, most frequently the proximal phalanx. These specimens had to be excluded from some of the analyses. A record of exactly which specimens were used in each analysis is provided in Online Resource 1.

An average mass for each species was obtained from the literature (Online Resource 1). In each case, if a mean mass

was available, this was used; if not, the median value of the published mass range was taken instead. The exception to this method was *Microtragulus bolivianus*, where a mass estimate was not available from the literature and had to be derived from available morphometric measurements (see below). A very few species appeared to have no recorded mass in the literature; these were excluded from those analyses that required a species mass (Online Resource 1).

The body mass estimate for *Microtragulus bolivianus* (22.8 g) was calculated using an equation from Zimincz (2011), who used dental allometry to calculate the body mass of various other argyrolagid species (including the value for *Argyrolagus scagliai* used in this study). The mean length of the third lower molar of three *M. bolivianus* specimens listed in table 1 of Babot and García-López (1.54 mm) was used to calculate the estimated body mass according to the allometric relationship described for m3L in table 1 of Zimincz (2011).

A rodent phylogeny was constructed from the consensus of Moore et al. (2015) and Fabre et al. (2012), while a marsupial phylogeny was taken from May-Collado et al. (2015). In each case, the phylogenies were pared down to include only the species included in the collected dataset. The Argyrolagidae were considered to be a member of the order Paucituberculata, following the analyses of Sánchez-Villagra (2001) and Beck (2017). The placement of Paucituberculata within the marsupials follows May-Collado et al. (2015).

Where mode of locomotion (generalist quadruped vs. bounding quadruped) for a taxon was uncertain, this was resolved with reference to the Animal Diversity Web (<https://animaldiversity.org>; University of Michigan Museum of Zoology 2020), Nowak (1999: pp. 1325–1663), and Nowak (2018: pp. 188–215). Here, we considered “bounding” locomotion to involve a leap (period of suspension) between the hindlimbs contacting the ground, and the forelimbs doing so—thus including what are generally described as both bounding and half-bounding gaits (Hildebrand 1980)—and here to be limited to those species which engage in cursorial bounding, as discussed by Lovegrove and Mowoe (2014). Only smaller species were considered here, so as to provide a good point of comparison to the hopping mammals, most of which are < 10 kg, and only one lineage of which (the macropods) exceeds ~3 kg.

## Analyses

All analyses in this study were performed in R version 4.1.2 (R Core Team 2021), unless otherwise specified.

In order to better contextualise any mass-related patterns found in the data, a histogram was produced of the body masses of all hopping taxa included in this study (excluding those for which body masses were unavailable, see Online

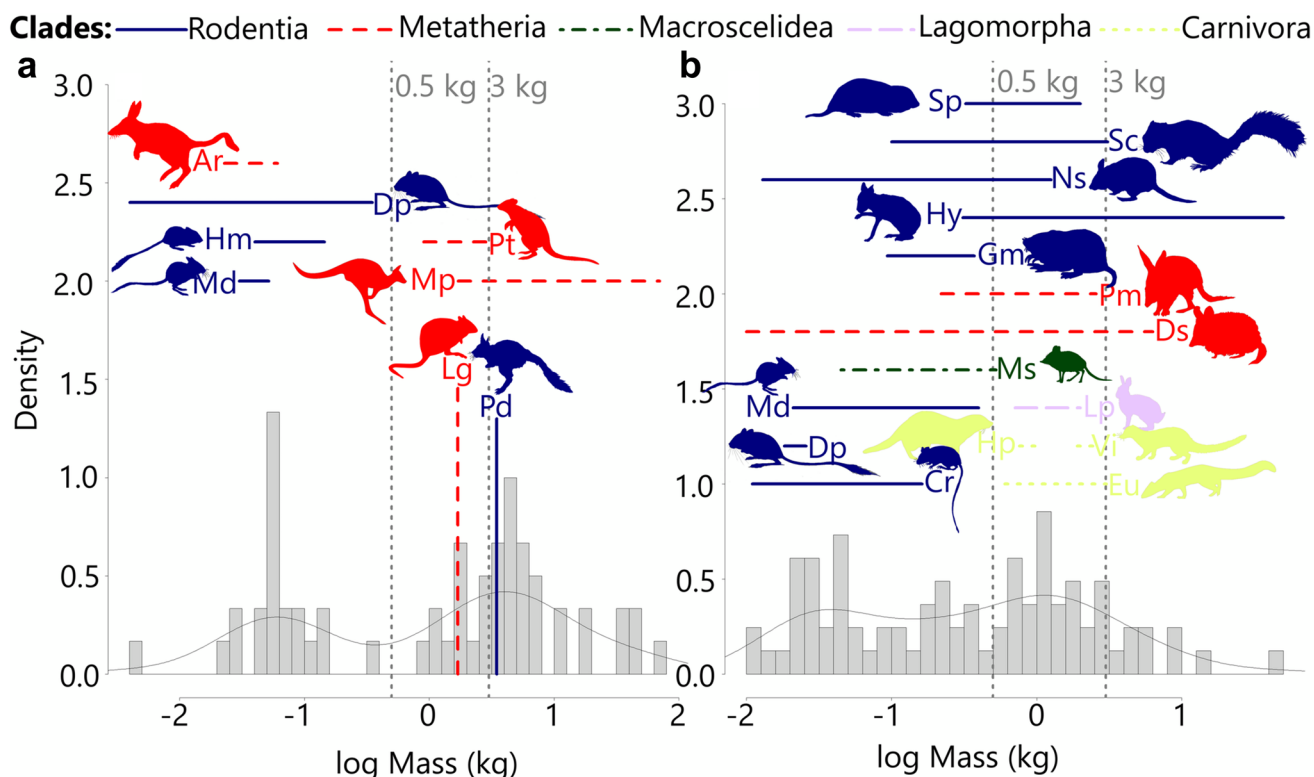
Resource 1), with the mass ranges of each family marked. For those species where multiple body mass estimates existed in the dataset, the mean value across all specimens in the dataset was taken. This was performed using the base R capabilities. The same process was then repeated for all quadrupedal taxa.

To identify patterns of hindlimb proportions by clade, a principal components analysis (PCA) was performed for all hopping and quadrupedal bounding specimens for which all four bone lengths were available. First, the length of each bone was normalised as a percentage of total leg length. In each case, total leg length was calculated as the sum of the four measured bone lengths. Then, the analysis was performed using the package FactoMineR (Lê et al. 2008). The red kangaroo *Osphranter rufus* was omitted from this data set, on the grounds that its extreme tibial elongation dominated the plot, making other patterns difficult to discern.

Next, we tested whether proposed key mass thresholds are reflected in the hindlimb proportions of hopping and bounding masses. The same dataset and normalised bone lengths used for the PCA were also run through a pairwise PERMANOVA (Anderson 2001), with the data categorised in three mass-based groups: < 0.5 kg, 0.5–3 kg, and > 3 kg. These thresholds reflect those discussed in the literature, and seen in the histogram of hopping mammal masses (see Results and Discussion for details). This procedure was repeated on three subsets of the data: all hoppers and bounders, all hoppers, and hoppers excluding the Dipodidae (whose position in the PCA was found to be notably different from other small hopping mammals, hence the exclusion). The analysis was performed using the package pairwiseAdonis (Martinez Arbizu 2017).

The above analyses highlighted metatarsal length as a key differentiating factor between some clades and mass groups, with particularly interesting patterns among the rodents. To investigate this further, a log-log plot of metatarsal length against mass for all hopping and bounding rodent species was constructed. Two linear regressions were then run on this dataset: one including the Dipodidae, the other excluding them. *Argyrolagus scagliai* and *Microtragulus bolivianus* were also plotted on this graph, but neither were included in the regressions. These regressions were repeated for the rest of the four measured long bones, as well as the total limb length. The same regressions were repeated for the generalist quadrupedal mammals. For the proximal phalanx and total limb length regressions, only those specimens with all four bone lengths available were used.

Finally, to further investigate how hopping correlates with hindlimb proportions in the context of non-hopping close relatives, the metatarsal:femur and tibia:femur ratios were calculated for all rodent and marsupial individuals where all three of these bone lengths were available. Heatmaps of the log<sub>10</sub> of these values were then plotted against the



**Fig. 3** Histogram of masses: **a**, all hopping taxa included in this study; **b**, all quadrupedal taxa included in this study for which masses were available. Horizontal lines show the range of masses in each family; vertical lines mark the mass of families for which only a single species was included. Narrow, grey dotted lines mark important mass thresholds discussed in the text. Abbreviations: **Ar**, Argyrolagidae; **Cr**, Cricetidae; **Dp**, Dipodidae; **Ds**, Dasyuridae; **Eu**, Eupleridae; **Gm**, Geomyidae; **Hm**, Heteromyidae; **Hp**, Herpestidae; **Hy**, Hystricognathi; **Lg**, Lagostrophinae; **Lp**, Leporidae; **Md**, Muridae; **Mp**, Macropodinae; **Ms**, Macroscelididae; **Ns**, Nesomyidae; **Pd**, Pedetidae; **Pm**, Peramelemorphia; **Pt**, Potoroidae; **Sc**, Sciuridae; **Sp**,

Spalacidae; **Vi**, Viverridae. Credits for silhouettes: McGowan and Collins (2018); Maija Karala (CC BY 3.0, <https://creativecommons.org/licenses/by/3.0/>), Sarah Werning (CC BY 3.0), Nina Skinner (CC BY 3.0), Margot Michaud (CC0 1.0), Xavier Jenkins (CC0 1.0), Birgit Lang (CC0 1.0), Ferran Sayol (CC0 1.0), T. Michael Keesey (Public Domain Mark 1.0) and C Monks (CC0 1.0), via phylopic.org; Bcexp, (CC BY-SA 4.0, <https://creativecommons.org/licenses/by-sa/4.0/>), Nobu Tamura (nobu.tamura@yahoo.com) (CC BY-SA 4.0), Chrumps (CC BY-SA 4.0), and John Gould (Public Domain) via Wikimedia Commons

previously obtained rodent and marsupial phylogenies using the package ggtree (Yu et al. 2017, 2018; Yu 2020). For those species for which multiple specimens had been measured, a single representative specimen was selected to be included in this plot (Online Resource 1).

## Results

### Body mass histogram

The histogram of the body masses of hopping species (Fig. 3a) shows a slightly skewed bimodal distribution, with a dip between the two peaks at around 400–500 g. There are no families which cross over the 500 g threshold. Within the < 500 g and > 500 g ranges, the mass ranges of families show a lot of overlap. However, only the Macropodinae reach masses significantly above 3 kg.

The histogram of the body masses of quadrupedal species (Fig. 3b) shows a much less pronounced bimodal distribution. Unlike in the case of the hopping species, there are no distinct boundaries limiting the size distribution of quadrupedal families. The 500 g line is crossed by seven of the fifteen families included in this study.

### Principal component analysis

In the PCA of percentage hindlimb bone lengths (Fig. 4), PC1 accounts for 48.46% of the total variation, and corresponds most closely to an axis of metatarsal length (negative values) vs. femur length (positive values), with some influence from the tibia (positive). Meanwhile, PC2 accounts for 38.51% of the total variation, and corresponds most closely to an axis of tibia length (negative) vs. proximal phalanx length (positive). The contributions of each measurement to the final principal components are summarised in Table 1.



**Table 1** Contributions of each bone length to the first two principal components of the PCA shown in Fig. 4. Each bone length has been normalised as a percentage of the entire leg length. The code for deriving these contributions was provided by Suresh Singh

	PC1	PC2
Femur	0.59	0.35
Tibia	0.39	-0.60
Metatarsal	-0.69	-0.15
Proximal phalanx	-0.11	0.70

This PCA does not distinguish hopping from bounding species, suggesting that the two groups do not have significantly different intra-hindlimb proportions. However, this PCA does not indicate the total length of the hindlimb relative to body mass, or the ratio of forelimb to hindlimb length (Howell 1944: pp. 205–206; McGowan and Collins 2018), both of which may be more reliable methods of distinguishing hoppers from bounders based on gross morphology.

This PCA reveals several patterns within the intra-hindlimb proportions of hopping and bounding mammals. First, the rodent families primarily separate along PC1, suggesting the main differences between these groups are in their metatarsal:femur proportions, with perhaps some influence from the tibia. The separation of rodents along this axis appears to be significantly related to phylogeny, as individuals within a single family tend to cluster together. The Dipodidae—both bipedal hopping and quadrupedal bounding species—are at the most extreme negative end of this axis, indicating extreme elongation of the metatarsals in this group. The Australian hopping mice (Muridae, *Notomys* spp.) are found towards the least extreme end of the PC1 range of the Dipodidae, although they are separated from this group along PC2. Meanwhile, the largest hopping rodent (the springhare *Pedetes capensis*) and the much smaller kangaroo rats (Heteromyidae, *Dipodomys* spp.) occupy a similar, more central PC1 range, with *P. capensis* separated slightly from *Dipodomys* along PC2. The most positive PC1 range occupied by the rodents is seen in the quadrupedally bounding Hystricognathi (Caviomorpha), consisting of the mara *Dolichotis patagonum* (Caviidae) and the viscachas *Lagidium peruanum* and *Lagostomus maximus* (Chinchillidae).

By contrast, the two main hopping marsupial families—the rat-kangaroos (Potoroidae) and the kangaroos, wallabies, and relatives (Macropodidae, including the subfamilies Macropodinae and Lagostrophinae)—separate primarily along PC2, reflecting differences in phalanx:tibia proportions. In general, the potoroids have higher PC2 values than the macropodids, indicating longer proximal phalanges and/or shorter tibiae in this group. This agrees with previous work which has shown that potoroids have longer proximal phalanges than macropodids (Janis et al. 2021).

Not all marsupial groups are primarily separated along PC2, however. The kultarr (Dasyuridae, *Antechinomys laniger*) is separated from the rest of the marsupials along PC1, plotting close to the Dipodidae and Muridae, though with a slightly more negative position on PC2 than either group. *A. laniger* is a small Australian marsupial previously described as similar in form to the Australian hopping mice, but which has been found to move through quadrupedal bounding, rather than bipedal hopping (Ride 1965; Marlow 1969; Baudinette et al. 1976). The argyrolagid *Argyrolagus scagliai* occupies a position between *Antechinomys laniger* and the Australian hopping mice (Muridae, *Notomys*). Meanwhile, the quadrupedal bounding Peramelemorphia (bandicoots and bilbies; Duszynski 2016) are mainly separated from the Potoroidae along PC1. The relative similarity of these two groups may be due to the fact that both use their hindlimbs in digging to some degree (Strahan 1984).

In general, there is a pattern of the smaller (<0.5 kg) taxa clustering more towards the negative end of PC1, regardless of phylogeny. However, this trend is not universal: the kangaroo rats (Heteromyidae, *Dipodomys* spp.) are the most notable exception, clustering towards the centre of the PCA graph, close to the ~3.5 kg springhare *Pedetes capensis*, despite having body masses in the range of 0.04–0.15 kg. Some of the Macroscelididae (sengis, quadrupedal bounding afrotheres also known as elephant shrews; Rathbun 2009) also approach a PC1 value of zero despite their low masses.

Within those taxa over 0.5 kg, there seems to be no significant or consistent separation of those species above the previously discussed 3 kg threshold from those below, particularly within families. There is also no consistent separation of bounding taxa from true bipedal hopping taxa in this PCA. This latter would likely change if forelimb measurements were included, since it has previously been shown that the ratio of forelimb to hindlimb length is a key, consistent difference between bipedal hoppers and quadrupedal species (Howell 1944: pp. 205–206; McGowan and Collins 2018), but our interest here is in the hindlimb. Some other potential influencing factors on the hindlimb proportions of these animals go unaddressed in this dataset, including stance (e.g., plantigrade vs. digitigrade). These factors are outside the scope of the current study but may be worthy of future investigation.

### Pairwise PERMANOVA

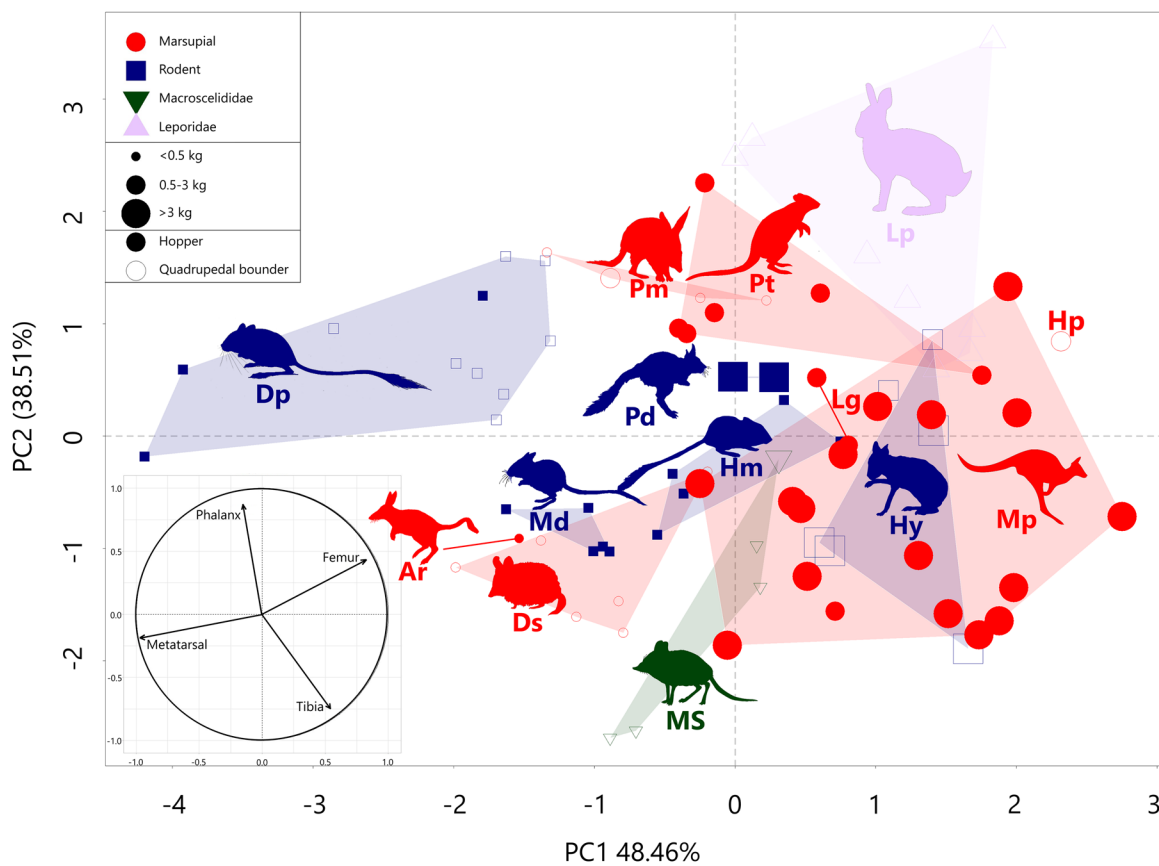
The pairwise PERMANOVA analyses (Table 2) compare species above and below two key mass thresholds: 500 g, the mass not crossed by any lineage of hopping mammal (Fig. 3a), and 3 kg, the previously suggested threshold above which significant elastic energy storage and return from tendons starts to occur. In these PERMANOVA analyses,

**Table 2** Results of the pairwise PERMANOVA analyses, comparing long bone lengths (normalised as a percentage of entire limb length) between size classes

Pairs	Df	Sum of squares	F-statistic	R <sup>2</sup>	P-value	Adjusted P-value
<b>Hoppers and bounders</b>						
<0.5 kg vs. 0.5-3 kg	1	0.043	38.342	0.411	0.001	0.003
<0.5 kg vs. > 3 kg	1	0.045	40.481	0.424	0.001	0.003
0.5-3 kg vs. > 3 kg	1	0.010	10.954	0.206	0.001	0.003
<b>Hoppers only</b>						
<0.5 kg vs. 0.5-3 kg	1	0.011	9.193	0.315	0.001	0.003
<0.5 kg vs. > 3 kg	1	0.025	20.002	0.408	0.001	0.003
0.5-3 kg vs. > 3 kg	1	0.004	4.234	0.145	0.021	0.063
<b>Hoppers, excluding Dipodidae</b>						
<0.5 kg vs. 0.5-3 kg	1	0.006	10.438	0.380	0.001	0.003
<0.5 kg vs. > 3 kg	1	0.011	13.044	0.334	0.001	0.003
0.5-3 kg vs. > 3 kg	1	0.004	4.234	0.145	0.020	0.060

a significant result indicates that the species in two of these categories have significantly different hindlimb proportions to one another. When bounding and hopping species were both included in the analysis, all three of these mass-based

categories were significantly different from one another. However, when only the hoppers were included in the analysis—with the outlier group Dipodidae either included or excluded—those species in the 0.5-3.0 kg and > 3.0 kg



**Fig. 4** PCA of hindlimb long bone lengths for hopping and bounding mammals. Each individual bone length was expressed as a percentage of the entire hindlimb length. Convex hulls group specimens by family. A version with numbers corresponding to key numbers in Online Resource 1 can be found in the supplementary material (Online Resource 2). The wheel in the lower left displays contributions of

each bone to PC1 and PC2. Abbreviations: **Ar**, Argyrolagidae; **Dp**, Dipodidae; **Ds**, Dasyuridae; **Hm**, Heteromyidae; **Hy**, Hystricognathi; **Lg**, Lagostrophinae; **Lp**, Leporidae; **Md**, Muridae; **Mp**, Macropodinae; **Ms**, Macroscelididae; **Pd**, Pedetidae; **Pm**, Peramelemorphia; **Pt**, Potoroidae. Credits for silhouettes as for Fig. 3. The code to produce the convex hulls was written by Tom Stubbs

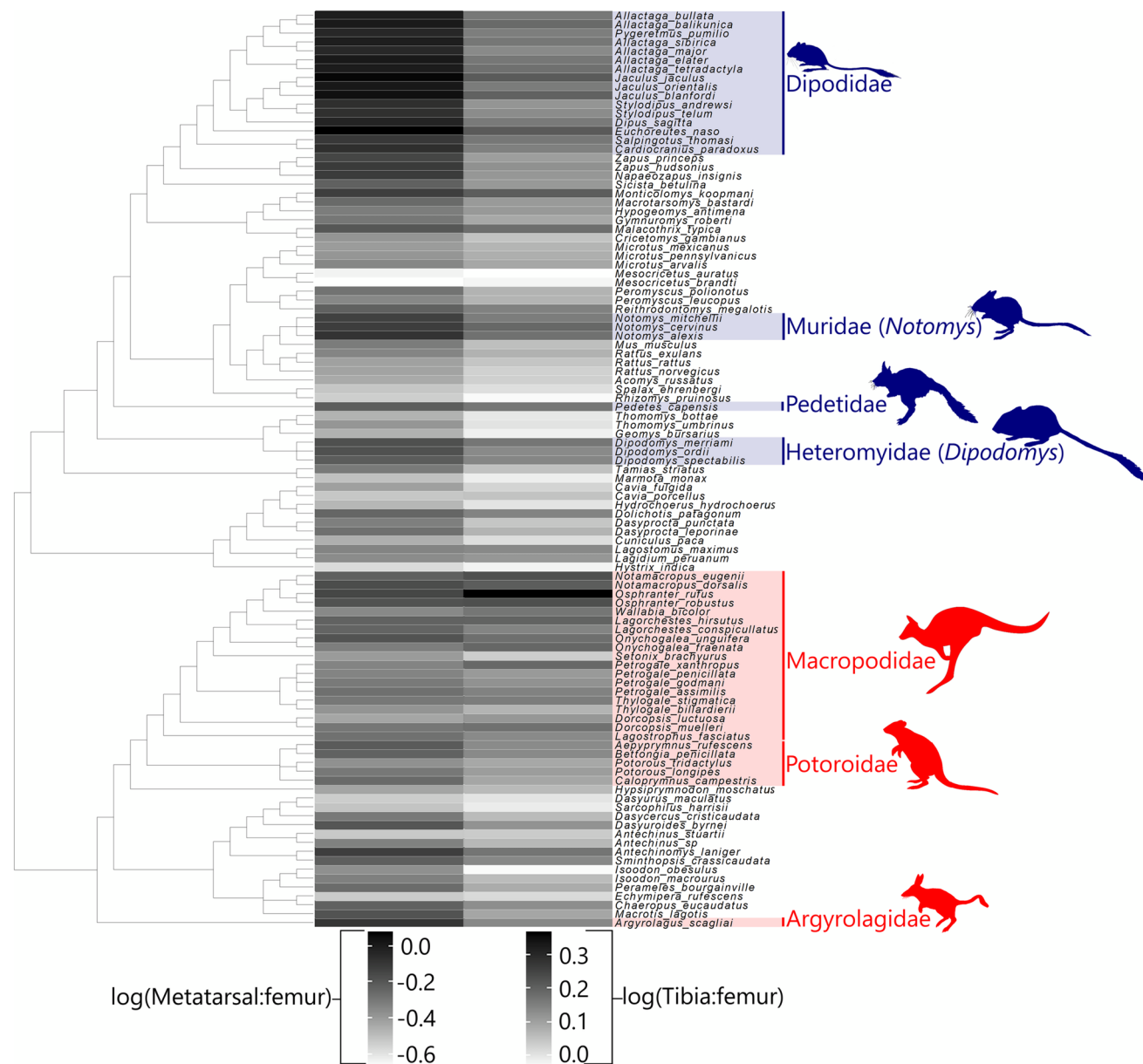
categories were no longer significantly different from one another. Meanwhile, those species below 500 g remained significantly different from all of the larger species.

### Phylogenetic heatmap of intra-hindlimb ratios

All four clades of bipedal hopping rodents have greater metatarsal:femur ratios than their close quadrupedal relatives, as well as greater tibia:femur ratios (Fig. 5). These two metrics vary in a very similar pattern across the Rodentia:

those species with longer metatarsals tend to also have longer tibiae.

The marsupials do also show metatarsal elongation among hopping species, but the pattern is less distinct than in the rodents. Tibial elongation in this group also tracks metatarsal elongation less precisely. While hopping species tend to have longer tibiae, particular extremes are reached in the larger macropodids, especially *Osphranter rufus*. *Argyrolagus* appears to show a combination of metatarsal:femur and tibia:femur ratios similar to that seen in many of the



**Fig. 5** Heatmap of metatarsal:femur and tibia:femur length ratios against phylogeny, for rodents and marsupials. Highlighted species are bipedal hoppers. All other species are bounders, or reasonably generalist quadrupeds. Code based on Griffin (2017). Credits for silhouettes: McGowan and Collins (2018); Maija Karala (CC

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hopping rodents, with the metatarsal elongation being particularly extreme. The kultarr *Antechinomys laniger* is also somewhat similar to the hopping rodents here, reflecting the traits that previously led some researchers to believe this to be a hopping species (Stannard and Old 2014).

### Linear regressions

In both cases, when the Dipodidae are either included in or excluded from the regression, metatarsal lengths of the hopping and bounding rodents show a significant pattern of negative allometry ( $L \propto M^{0.24 \pm 0.05}$  with Dipodidae included,  $L \propto M^{0.25 \pm 0.03}$  with Dipodidae excluded; Table 3). However, this is not significantly different from the degree of negative allometry seen in the quadrupeds included in this study ( $L \propto M^{0.26 \pm 0.04}$ ). With the Dipodidae excluded, the adjusted  $R^2$  value increases from 0.63 to 0.94, indicating a much better fit to the data. The bounding Dipodidae fall on this second regression line, while the hopping Dipodidae (excluding *Salpingotulus michaelis*) cluster above it (Fig. 6). *Notomys* specimens tend to place slightly above this regression line, and *Dipodomys* below, but both often fall within the 95% confidence interval of the line. Meanwhile, the argyrolagids *Argyrolagus scagliai* and *Microtragulus bolivianus* cluster with the hopping Dipodidae.

The remaining rodent hind limb bones scale with much less strong allometry than the metatarsals, although most do show some degree of negative allometry when the Dipodidae

are excluded. The length of the entire limb likewise shows slight negative allometry. The bone which scales closest to isometry is the femur, where  $L \propto M^{0.309 \pm 0.015}$ . The difference in the  $R^2$  value when the Dipodidae are excluded is also far less extreme in these regressions (Table 3). Among the generalist quadrupeds, the femur scales with isometry, while all other bones, and the hindlimb as a whole, scale with varying degrees of negative allometry. As such, the general allometric patterns of the hopping and bounding rodents do not tend to deviate from those of the generalist quadrupeds.

## Discussion

### Body mass in hopping mammals: two domains?

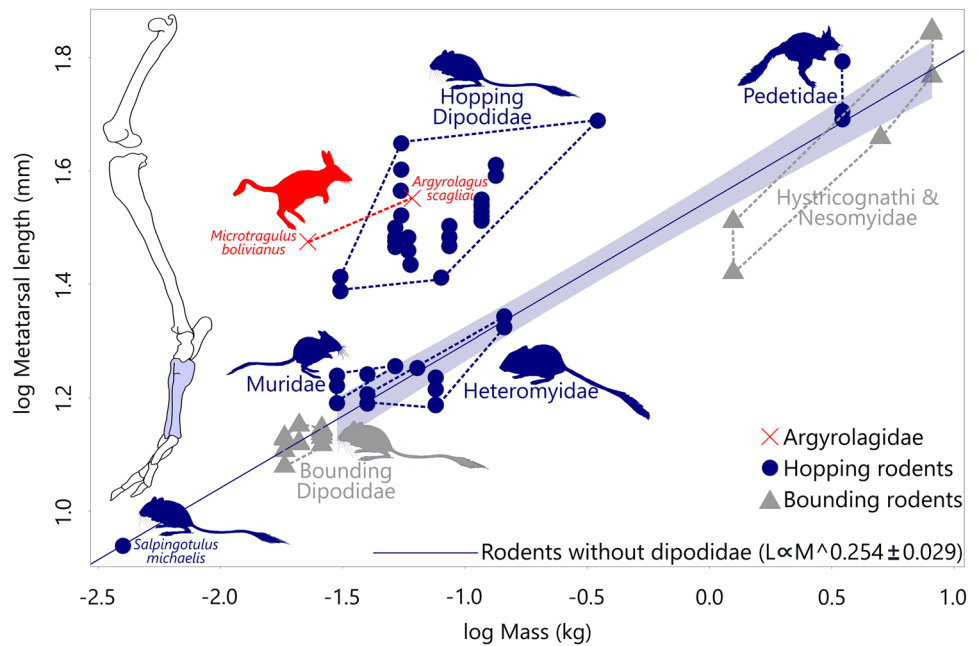
The histogram of hopping taxa body masses (Fig. 3a) suggests a dichotomy among the hopping mammals, with all taxa within a family falling either below or above ~500 g. Mass ranges found in the literature support this division. Dipodidae range from 4 g in *Salpingotulus michaelis* (Boël et al. 2020) to 350 g in *Allactaga major* (Vakhrusheva et al. 1994; Kurtén 1968). *Dipodomys* species cover roughly 40–150 g (Freymiller et al. 2021), while *Notomys* species span ~30 g in *N. alexis* to ~100 g in *N. amplus* and *N. longicaudatus* (Silva and Downing 1995). Meanwhile, the macropods (encompassing the Potoroidae and Macropodidae) have

**Table 3** Summary statistics of log-log regressions of bone length against body mass. Allometry is indicated by the slope value, with isometry being a slope of 0.33. Slopes significantly different from isometry are marked with an asterisk (\*) in the “specimens” column.

	Specimens	Intercept			Slope			Adjusted $R^2$	P-value
		Value	Upper 95% CI	Lower 95% CI	Value	Upper 95% CI	Lower 95% CI		
<b>Metatarsal</b>	BHR*	1.634	1.692	1.576	0.241	0.286	0.196	0.633	5.17E-16
	BHR-D*	1.548	1.579	1.517	0.254	0.283	0.224	0.937	2.72E-14
	GQ*	1.265	1.301	1.229	0.259	0.294	0.224	0.714	<2.2E-16
<b>Tibia</b>	BHR	1.962	1.994	1.930	0.312	0.337	0.288	0.905	<2.2E-16
	BHR-D*	1.932	1.954	1.911	0.296	0.316	0.276	0.977	<2.2E-16
	GQ*	1.747	1.769	1.725	0.302	0.324	0.280	0.891	<2.2E-16
<b>Femur</b>	BHR	1.813	1.838	1.787	0.314	0.334	0.294	0.937	<2.2E-16
	BHR-D*	1.787	1.804	1.771	0.309	0.325	0.294	0.988	<2.2E-16
	GQ	1.704	1.728	1.681	0.320	0.343	0.297	0.902	<2.2E-16
<b>Proximal phalanx</b>	BHR*	1.101	1.155	1.047	0.262	0.302	0.221	0.863	2.16E-13
	BHR-D*	1.090	1.147	1.034	0.278	0.329	0.227	0.886	3.56E-09
	GQ*	0.934	0.970	0.898	0.263	0.300	0.227	0.827	<2.2E-16
<b>Total limb</b>	BHR*	2.297	2.333	2.261	0.297	0.323	0.270	0.948	<2.2E-16
	BHR-D*	2.293	2.317	2.268	0.292	0.315	0.270	0.978	6.73E-15
	GQ*	2.151	2.177	2.126	0.290	0.312	0.260	0.918	<2.2E-16

Abbreviations: **BHR**, All bounding and hopping rodents; **BHR-D**, all bounding and hopping rodents, minus Dipodidae; **GQ**, generalist quadrupeds

**Fig. 6** Log-log regression of metatarsal length against body mass for hopping and bounding rodents, and Argyrolagidae. The solid line indicates the least squares regression line for all hopping and bounding rodents, excluding Dipodidae, while the shading indicates the 95% confidence interval of this line. Convex hulls (dotted lines) group points by family. The leg diagram shows a *Pedetes capensis* hindlimb and was drawn by Megan Jones from an unnumbered specimen in the private collection of Christine Janis (ex Harvard University Concord Field Station)



a mass range of around 1–90 kg (McGowan and Collins 2018). The Pedetidae only have one or two extant species (the exact taxonomy is debated; Pickford and Mein 2011) of body mass ~3.5 kg (Webster and Dawson 2004).

This dichotomy suggests that hopping mammals fall into one of two main domains. Interestingly, however, these domains do not line up with the widely-discussed 3 kg threshold for significant elastic energy storage in the hindlimb tendons (Bennett 2000). Instead, 3 kg lies close to the rightmost peak in the bimodal distribution.

The 3 kg threshold is worth briefly addressing before investigating the gap around 500 g further. While a 3 kg threshold is not reflected in the density curve on the histogram (Fig. 3a), nor is there a statistically significant change in intra-hindlimb proportions across this threshold (Table 2), it is notable that of all the families of hopping mammals above 500 g, the Macropodidae are the only family which has members much heavier than 3 kg. This may be random chance, an artefact of the fact that there are only four clades of hoppers above 500 g to begin with—the Potoroidae, two subfamilies within the Macropodidae (the Macropodinae, which include most kangaroos and wallabies, and the Lagostrophinae, or banded hare-wallaby) and the Pedetidae—three of which have a common hopping origin within the wider clade of the Macropodiformes. However, it may also suggest that there is a significant change in the factors and forces which govern hopping locomotion happening across this threshold, which only one family has managed to adapt to take advantage of. The main question this raises is whether there are any challenges that would prevent animals from crossing this threshold. So far, the suggested change at this threshold is an improvement of the energetic efficiency of

locomotion, which is unlikely to provide a barrier to animals attaining these sizes.

While today only the Macropodinae contains hoppers over a mass of 3 kg, other macropodid subfamilies also contained larger, likely hopping species. These include the lagostrophine (see Eldridge et al. 2019) *Troposodon bowensis* (see Flannery and Archer 1983), with molars of similar size to the agile wallaby *Notamacropus agilis*, indicating a body mass of around 12 kg. The extinct Sthenurinae (short-faced kangaroos, ~50–250 kg) contained Plio-Pleistocene giant species that may have been too big to hop (greater than ~160 kg), but also smaller Miocene ones such as *Rhizosthenurus flanneryi* (12–15 kg) that likely was a hopper (Janis et al. 2023). Thus, the 3 kg threshold of hopping mammals was crossed at least three times (Macropodinae, Sthenurinae and Lagostrophinae), implying that it does not reflect a biomechanical constraint, simply that most hopping mammals are, and have been, of smaller size.

Returning to the change in domains at ~500 g: the two different body mass groups also show some differences in intra-hindlimb proportions, as shown in the PCA (Fig. 4). Those species below 500 g tend to have more negative scores on PC1 in comparison to larger specimens, indicating proportionally longer metatarsals in these smaller species. Unlike in the histogram, this is not a completely clean separation—for example, the kangaroo rats (*Dipodomys*) cluster close to the much larger springhares (*Pedetes*) and overlap the range of the kangaroos (Macropodinae). However, the results of the pairwise PERMANOVAs (Table 2) confirm that those species above and below 500 g have significantly different limb bone proportions, even when the outlier group of the Dipodidae is excluded.

It can also be seen from the PCA (Fig. 4) and the mass histogram of quadrupedal taxa (Fig. 3b) quadrupedal mammals do not show the same gap at 500 g. In fact, roughly half of the quadrupedal families sampled in this study cross this boundary. This sample is not representative of global quadrupedal mammal diversity, but is sufficient to show that many families of quadrupedal mammals do cross over 500 g. Far more comprehensive studies of quadrupedal mammal mass distribution exist, such as Blackburn and Gaston (1998), which studied 2741 terrestrial mammal species, and found that their masses occur in a right-skewed distribution, with a single peak at roughly 30–100 g. Again, no gap at 500 g is seen here, suggesting that the gap seen among the hopping mammals is unique to this mode of locomotion.

The reasons behind this division of the hopping mammals are unclear. One possibility is that there are two divergent optima for hopping animal body size, with smaller hoppers optimised to escape predation, and larger hoppers optimised for sustained hopping as an efficient mode of locomotion. The main benefit of hopping which has been reported in smaller species, but not larger ones, is the ability to evade predation through sudden, extremely high vertical leaps (Moore et al. 2017b; McGowan et al. 2018; Schwaner et al. 2018), as seen in the kangaroo rats (Heteromyidae) (Schwaner et al. 2018) and the jerboas (Dipodidae) (Moore et al. 2017b). These vertical leaps are a very different mode of locomotion than sustained hopping and will require different functional adaptations. For example, the relatively thicker ankle extensor tendons seen in smaller species allow them to jump to great heights without risking tendon rupture (Biewener and Blickhan 1988). Thus, the same trait which makes energetically efficient hopping through elastic energy storage implausible in small species, becomes a beneficial adaptive feature when performing vertical leaps.

Adaptation for vertical leaps may also help to explain the observed tendency for species under 500 g to have elongated metatarsals in proportion to the rest of their hindlimb. Metatarsals function as the out-lever for the ankle extensor tendons. Elongating this lever arm will mean that for the same amount of contraction at the ankle, the tip of the foot will move much more rapidly, through a wider arc (Biewener and Patek 2018; Dunn 2018). Practically speaking, this means the body of the hopper will be propelled forward, or upwards, more rapidly, for the same degree of muscle contraction.

This hypothesis is not without issues, however. Springhares (Pedetidae, 3.5 kg) have reportedly been observed leaping vertically out of their burrows, perhaps to avoid predation (Butynski and Mattingly 1979), despite their relatively large size. Also, kangaroo rats (Heteromyidae) have similar intra-hindlimb proportions to the springhares (Fig. 4), which does not support the hypothesis that the metatarsal elongation of smaller hoppers is an adaptation

for rapid vertical jumps. In addition, the apparent metatarsal elongation among smaller hoppers may be at least partly due to a general pattern of allometry seen in all terrestrial mammals. Excluding the Dipodidae, the metatarsals of other small hoppers follow a line of negative allometry which is not significantly different in slope from the allometric pattern seen in the generalist quadrupedal specimens (Fig. 6; Table 3). Again, this dataset does not necessarily provide a representative sample of generalist quadrupedal mammals, so drawing conclusions from this regression should be done with caution. However, at least one previous study has also found negative metatarsal allometry to be present among larger (> 10 kg) terrestrial mammals (Janis and Wilhelm 1993). Christiansen (2002), meanwhile, found that the mass (not length) of mammalian metatarsals scales with isometry, but is overall poorly correlated with mass, and may be more reflective of locomotor mode.

Overall, the apparent existence of two mass-based domains of hoppers, with the smaller hoppers showing increased elongation of the metatarsals relative to the rest of the hindlimb, is an intriguing new observation. However, further study would be needed to determine what factors may be driving this division, and what, if any, significant differences exist between animals in the two domains.

## Rodents and metatarsal elongation

As shown in the PCA, the most important point of variance between hopping rodent families is in the degree of metatarsal elongation. There are two key patterns of metatarsal elongation which apply throughout the hopping and bounding rodents, regardless of phylogeny. First, a pattern of greater metatarsal elongation in hopping rodents than in their quadrupedal relatives; second, a pattern of negative metatarsal allometry among the hopping and bounding rodents.

## Metatarsal elongation in hoppers vs. quadrupeds

The heatmap phylogeny (Fig. 5) shows that across the rodents, regardless of their phylogenetic position, there is a clear pattern of greater metatarsal elongation relative to the femur in hopping species, compared to their quadrupedal relatives. The femur, as shown in Table 3, is the bone which scales closest to isometry in this dataset, so elongation of the metatarsal relative to the femur can be taken as a reasonably good proxy for metatarsal elongation relative to both the rest of the limb and body mass. This metatarsal elongation in hoppers is backed up by the results of the regressions, shown in Table 3, which show a significantly higher intercept for the hopping and bounding rodents than for the quadrupeds as a whole. This difference may partly be driven by the overall elongation of the hindlimbs of hoppers, but the difference

between the quadrupedal and hopper regression intercepts is greatest for the metatarsal regressions. This also agrees with and expands on the findings of Moore et al. (2015): that within the Dipodidae, there is a general pattern of metatarsal elongation being most extreme among hopping species. So, why do hoppers have such elongated metatarsals, in comparison to generalist quadrupeds?

It has previously been observed that both cursorial (Hildebrand 1960) and hopping (McGowan and Collins 2018) mammals tend to elongate the distal long bones of their limbs. Elongating any limb bone provides an overall elongation of the stride, increasing the speed at which the animal can travel without increasing stride frequency, which would be energetically costly (Hildebrand 1960; Gray 1968). Focusing this elongation in the distal portions of the limb allows the more massive parts of the limb (those where large, key muscles insert) to remain close to the body, so that the faster-moving distal parts of the limb are light, and take less energy to swing (Hildebrand 1960). The fact that some degree of tibial elongation relative to the femur is evident in the hopping rodents as well as cursors supports this interpretation of distal limb elongation as an adaptation to rapid, efficient movement.

As previously mentioned (see Sect. 4.1), elongating the metatarsals also increases the rapidity of movement which can be produced by the ankle extensors—although at the cost of the power of that movement (Biewener and Patek 2018; Dunn 2018). This increased rapidity of movement will help to produce the acceleration needed for an animal to leap, without requiring the ankle extensors to contract more strongly.

### Negative metatarsal allometry in rodents

There is a general pattern of negative metatarsal allometry among the hopping and bounding rodents, as seen in Fig. 6. The reason for this decrease in metatarsal length with size may be that, as body mass increases, the metatarsals will experience more stress. Particularly given the perpetually crouched stance of the hopping mammals, scaling with isometry would lead to increasing bending stresses in the long bones of the hindlimb with increasing size (Currey 2002: pp. 328–329). However, negative metatarsal allometry relative to the femur is a pattern common in a wide variety of mammals, not just among hopping rodents (Janis and Wilhelm 1993), and the slope of the hopping and bounding rodent regression is not significantly different from that of the generalist quadrupeds in this dataset (Table 3). So, this pattern may not be particularly informative about the hopping mammals specifically, and may instead reflect general mammalian patterns of allometry.

Alongside these general patterns of metatarsal allometry, there are also distinct differences between the families of

hopping rodents, indicating that not all lineages have adapted to the challenges of saltatory locomotion in exactly the same way. The most notable of these differences is in the Dipodidae, which have a particularly extreme degree of metatarsal elongation.

### The Dipodidae

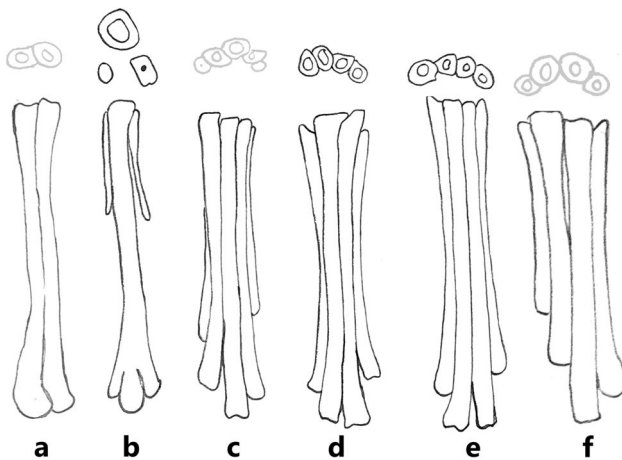
A consistent pattern throughout all of these analyses is that the jerboas and their relatives (Dipodidae), especially some of the later-diverging species such as *Allacta elater* and *Jaculus jaculus* (Moore et al. 2015), have the most extremely elongated metatarsals of any hopping mammals. In the PCA, all of the Dipodidae, bounding and hopping, occupy a region to the far negative end of PC1. However, in the regression of metatarsal length against mass, only the hopping Dipodidae (excluding *Salpingotulus michaelis*) have metapodials that are significantly elongated in comparison to the condition in other hopping rodents. Taken together, this suggests that all Dipodidae have unusually elongated metatarsals in comparison to their other hindlimb long bones, but extreme metatarsal elongation relative to body mass is only achieved in the hopping Dipodidae.

Why, then, are the jerboas so different from other hopping mammals in their metatarsal proportions?

One possibility is that the evolution of metatarsal fusion among the jerboas has facilitated their elongation. Metatarsal fusion is seen among the more derived jerboas, but is lacking in other hopping rodents (Moore et al. 2015; Villacís Núñez et al. 2022) (Fig. 7). These fused metatarsals form a cannon bone—a structure which can be made up of either an enlarged central metapodial, with the other digits being reduced or absent—as seen in equids (Currey 2002: pp. 302–303; Polly 2007: pp. 245–268)—or of two or more fused metapodials, as in the artiodactyls (Clifford 2010) and the jerboas. Cannon bones possess a greater second moment of area than the individual metatarsals would have, and so increase the limb segment's ability to resist bending forces, without having to increase the mass of the segment itself (Moore et al. 2015; Gutierrez et al. 2019; Currey 2002: pp. 302–303; Kaashoek et al. 2023). This increased resistance may allow for greater elongation of the metatarsal—producing the previously discussed benefits of faster movement of the foot—without risking fracture when hopping. However, this is not likely to be the only factor influencing metatarsal elongation in this family, since not all hopping Dipodidae show metatarsal fusion (Moore et al. 2015), yet all have significantly longer metatarsals than other hopping mammals of equivalent mass.

One possibility is that there is a difference in lifestyle between Dipodidae and the other hopping rodents that has driven this divergence in limb shape. However, jerboas, kangaroo rats, hopping mice and springhares have very similar general ecologies: they are all burrow-dwelling species,





**Fig. 7** Schematic sketches of metatarsals from six representatives of smaller hoppers and bounders, showing dorsal and cross-sectional views. These are not to scale, and are meant only to demonstrate variation in metatarsal fusion, reduction and digit loss. **a.** *Argyrolagus scagliai* (MMMP 7850-S); **b.** *Allactaga elater* (UF M30045); **c.** *Notomys cervinus* (NHMUK 1936.12.8.17); **d.** *Antechinomys laniger* (NHMUK 1932.2.11.23); **e.** *Dipodomys merriami* (UF M23955); **f.** *Pedetes capensis* (unnumbered specimen). *Argyrolagus scagliai* is based on Simpson (1970): fig. 15. The rest are drawn from direct observation of segmented CT scans or, in the case of *Pedetes capensis*, a physical specimen. Cross sections in black are directly drawn from CT scans; those in grey are conjecture, based on observation of the 3d structure. All diagrams drawn by Megan Jones. Institutional abbreviations: **MMMP**, Museo Municipal de Ciencias Naturales Lorenzo Scaglia (Mar del Plata, Argentina); **NHMUK**, Natural History Museum (London, UK); **UF**, Florida Museum of Natural History (University of Florida, Gainesville, FL, USA)

living in arid environments, with primarily herbivorous diets (Nowak 1999: pp.1325–1663). Substrate is another potential factor. However, Hall et al. (2022) found that the hopping of the kangaroo rat *Dipodomys ordii* was mostly unaffected by substrate, with little difference between a solid substrate and sand. They concluded that this was most likely down to the properties of the particular sand from the Mojave that they were using, the large toe-print area, and the low mass of the kangaroo rat combining to prevent the foot from penetrating far into the sand. Jerboa masses are generally not dissimilar to those of the kangaroo rats, so they too may not be much affected by changes in substrate. However, they may be found in areas with less penetration-resistant sand or have a smaller toe print area. This would result in more energy being lost to the substrate while hopping, requiring more work to be done for the same jump performance. The unusual metatarsals of the jerboas seem very unlikely to be a reaction to this, however. Adaptations to soft sand substrates usually involve a large contact area with the substrate, and an ability to spread the digits of the limb (Fornós et al. 2002), neither of which would be facilitated by elongating and fusing the metatarsals.

A more likely hypothesis is that the elongation of jerboa metatarsals is facilitated by a greater reliance on bipedal

locomotion than other hoppers. Moore et al. (2015) describe jerboas as obligate bipedal; meanwhile, kangaroo rats, hopping mice and springhares all use quadrupedal gaits at lower speeds (although kangaroo rats reportedly only use their forelimbs over short distances) (Nowak 1999: pp.1325–1663). Uniquely among hopping rodents, jerboas have multiple bipedal gaits: hopping, where the legs move in tandem, and skipping and running, where the legs are out of phase with one another by varying amounts. Jerboas can maintain lower speeds when skipping or running than when hopping (Moore et al. 2017a). By having these extra bipedal gaits, the jerboas may reduce the need to be able to use their forelimbs in locomotion comfortably. This would in turn allow their hindlimbs to elongate further without risking impeding movement at slow speeds.

### The Argyrolagidae

The proposed bipedal hopper *Argyrolagus scagliai* (Simpson 1970; Abello and Candela 2020) is most similar to the quadrupedal kultarr, *Antechinomys laniger*, in the PCA. However, this does not inform us as to whether *A. scagliai* was a bipedal hopper, as intra-hindlimb proportions do not clearly distinguish hopping from bounding mammals in our own analysis. A far more reliable indicator of bipedalism is the forelimb:hindlimb length ratio (Howell 1944: pp. 205–206; McGowan and Collins 2018), or a close proxy, the intermembral index (which excludes the pes and manus; Chen and Wilson 2015). Abello and Candela (2020) calculated the intermembral indices of *Argyrolagus*, and found that their hindlimbs were elongated relative to the forelimbs, to a degree that most resembles the proportions of extant bipedal hopping mammals. As the data collected in our study do not include forelimb measurements, these prior studies investigating intermembral relationships should be considered more reliable indicators of hopping ability. The present study aims instead to investigate variation and convergence within the hindlimbs of those species already known to or suspected to have engaged in bipedal hopping.

Most interestingly, the Argyrolagidae show a degree of extreme metatarsal elongation which is otherwise unique to the Dipodidae. In the regression of metatarsal length against body mass (Fig. 6), *A. scagliai* and another argyrolagid, *Microtragulus bolivianus*, cluster with the hopping Dipodidae. Meanwhile, all other hopping rodents, along with the kultarr (*Antechinomys laniger*), sit on or near the same line of negative allometry, with much shorter metatarsals in comparison to their body mass. Neither species of argyrolagid shows the metatarsal fusion seen in some Dipodidae (Simpson 1970; Babot and García-López 2016), but they have reduced all but two metatarsals (III and IV), with the remaining two being appressed, so that they may function as a single beam (Simpson 1970). This is an intriguing example



of an extinct marsupial evolving convergently with the most extreme morphology seen in hopping rodents seen today.

If the drivers behind extreme metatarsal elongation in the Dipodidae can be confidently identified, then the convergence between these two groups has the potential to provide additional clues to the ecology and locomotion of this extinct family of marsupials.

## Conclusion

Among the hopping mammals, there are a few overarching patterns in the allometry of hindlimb proportions. Species under around 500 g tend to have longer metatarsals in proportion to the rest of their hindlimbs than larger species, potentially correlating with a dichotomy around 500 g, which is crossed by no known clade of hopping mammals. The exact cause and implications of this gap at 500 g, and how biomechanically significant it may be, is as yet unknown. We also found that potoroids and macropodids are primarily distinguished by the relative lengths of their phalanges and tibiae, with longer phalanges in the potoroids, and longer tibiae in the macropodids.

The most extreme adaptations of intra-hindlimb proportions are limited to specific clades, such as the elongated metatarsals of the hopping Dipodidae (a valid clade; see Villacís Núñez et al. 2022) and the Argyrolagidae. This elongation seems unrelated to body mass, and its causes require further investigation. Greater reliance on bipedalism, and the development of multiple bipedal gaits beyond hopping, may be a driving factor; metatarsal fusion and loss may also have aided the development of these more extreme forms. Whatever the cause, the convergence of the Dipodidae and Argyrolagidae in this feature is an intriguing new observation.

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**Author contributions** The study was conceived by C.J., designed by C.J. and M.J. Data collection was performed by M.J., C.J. and K.T. Analyses were performed by M.J. The first draft of the manuscript was written by M.J., and C.J. and K.T. commented on previous versions of the manuscript. All authors read and approved the final manuscript.

**Data availability** All data generated and analysed during this study are included in this published article, and its supplementary information files.

## Declarations

**Ethics approval** This study did not require ethics approval.

**Competing interests** The authors declare no competing interests.

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