

# A horse walks into a bar: an explanation for the long face

Christine M. Janis<sup>1,2,\*</sup>, William Richardson<sup>1</sup>, Nuria Melisa Morales-García<sup>1</sup> & C. Nicolas Baird<sup>3,4</sup>

<sup>1</sup> Bristol Palaeobiology Group, School of Earth Sciences, University of Bristol, Wills Memorial Building, Queens Road, Bristol, BS8 1RJ, UK

<sup>2</sup> Department of Ecology, Evolution and Organismal Biology, Brown University, Providence, RI 02912, USA (\*corresponding author's e-mail: christine\_janis@brown.edu)

<sup>3</sup> Division of Paleontology, American Museum of Natural History, New York, NY 10024, USA

<sup>4</sup> Lamont-Doherty Earth Observatory, Columbia University, Palisades, NY 10968, USA

Received 20 Feb. 2024, final version received 20 May 2024, accepted 21 May 2024

Janis, C. M., Richardson, W., Morales-García, N. M. & Baird, C. N. 2024: A horse walks into a bar: an explanation for the long face. — *Ann. Zool. Fennici* 61: 503–529.

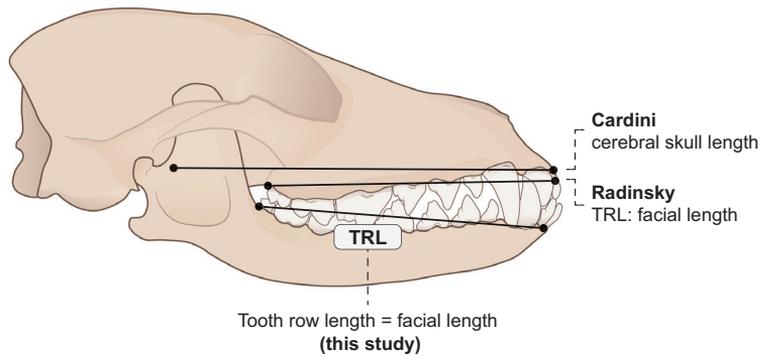
It is a common observation that most larger (over around 5–10 kg) herbivorous mammals have longer faces than carnivorous ones. A horse has a relatively longer face than a lion, or even than a wolf. This difference in face length is not the case for smaller mammals: rabbits and ferrets have similarly short faces. A shorter face bestows a mechanical advantage at the front of the jaw, advantageous for cropping forage as well as killing prey. Why is this ability sacrificed in long-faced larger herbivores? We propose that longer faces relate to the ability to use the forelimbs in feeding; for reasons of allometric scaling and locomotor specialization, forelimb mobility becomes restricted in larger animals, and a longer face becomes important for food prehension. We test this hypothesis with a large dataset of face lengths and anatomical assessment of forelimb mobility in extant mammals (including a few extinct equids).

## Introduction

“A horse walks into a bar”. Everybody knows the punchline to that joke, “Why the long face?”. This punchline, or variants thereof, is familiar enough to be used in the titles of scientific papers (e.g. Cardini *et al.* 2015, Evans *et al.* 2019, Heck *et al.* 2019, Richardson *et al.* 2024). Long facial portions of the skull are familiar to us in large herbivores such as horses, antelope, deer, giraffe, camels, etc. In contrast, large carnivores, especially felids, usually have relatively shorter faces. Why is this the case?

Mammalian face length (i.e. the length of the rostral part of the skull, excluding the basicra-

nium; *see* Emerson & Bramble 1993) has been a matter of scientific interest for the past several decades. Most studies focus on the allometry of facial length both within species (intraspecific or static allometry) and among taxa (interspecific or evolutionary allometry), while others consider changes in relative cranial proportions over the development of individuals (ontogenetic allometry). Earlier studies of relative face lengths in mammals (interspecific allometry; e.g. Radinsky 1985, Emerson & Bramble 1993) used linear measurements for their investigations, while more recent studies use scans of skulls, and complex morphometric explorations such as CREA (Craniofacial Evolutionary Allometry) (Cardini



**Fig. 1.** Measurement taken to estimate facial length (TRL), in comparison with those of other authors. Drawing based on a specimen of *Canis aureus*, from the University of Michigan Museum of Zoology (specimen number 101191), photographed by Phil Myers, Animal Diversity Web, Creative Commons Attribution-Noncommercial-Share Alike 3.0 Unported License. Figure by Science Graphic Design (sciencegraphicdesign.com).

& Polly 2013, Cardini 2019). CREA investigates the length of the face relative to the basicranium, finding that in most mammalian taxa face length scales with positive allometry. However, note that Radinsky (1985) considered that the apparently longer faces in larger species in a lineage is mainly the result of the negative allometry of the basicranium, and his measure of facial length shows isometric scaling in most cases. Mitchell *et al.* (2024) provide an extensive review of current issues in mammalian facial length and allometry.

However, our interest here is not so much in facial allometry but in the absolute differences in relative face length among different mammalian lineages. That is, we are concerned with the elevation (intercepts) of the regression lines when comparing different taxa in regressions of facial length on body mass, not the slope. Few researchers have addressed this issue, perhaps because long-faced large herbivores are just simply so familiar to us.

Our thinking about this issue stemmed from the study by Morales-García *et al.* (2021) investigating jaw shape in Mesozoic mammals in comparison with a diversity of extant small mammals (< 5 kg) of known diets. One of the components of jaw shape is the length of the jaw corpus, essentially the tooth-bearing portion of the jaw, from the back of the last molar to the base of the first incisor. This portion of the jaw is essentially the same as Radinsky's measure of facial length, measured on the skull (tooth row

length or TRL *see* Fig. 1): animals with longer rostral portions of the skull perform have longer mandibles to match them. This study (Morales-García *et al.* 2021) showed that among small mammals, both carnivores and herbivores have short jaws while insectivores have long jaws. This was explained as relating to the mechanical advantage of the jaw; short jaws have a high mechanical advantage at the incisors/canines at the front of the jaw, best for power, while long jaws have low mechanical advantage, good for speed (Maynard Smith & Savage 1959).

Bite forces are at a maximum at about the level of the first or second molar, close to the insertion of the jaw adductor muscles, and then decrease anteriorly along the jaw (Laird *et al.* 2024); thus, a long-faced animal will have a weaker anterior bite than a shorter-faced one with similar jaw musculature. Long jaws not only provide a faster closing speed, good for rapidly snapping small fast prey like insects (*see* Gill *et al.* 2014), but may also be useful for mammals that poke their snouts into holes to gain access to food sources. Bite force and gape are inversely correlated (*see* Laird *et al.* 2024 and references therein). In terms of simple skull geometry, a longer face would be expected to yield a larger gape at the incisors and canines — but in reality, nature is not that simple, and issues of gape are further discussed below, at the end of this section.

Note that herbivorous and carnivorous mammals differ in how their facial elongation relates

to their dentition. Long-faced herbivores have lost or greatly reduced their canines, often have reduced their premolars, and usually have a gap (diastema) between the incisors and postcanine teeth. In contrast, a long-faced carnivore may have some smaller gaps, but usually the entire space along the jaw is taken up with the dentition (*see* Fig. 1).

This relationship of jaw length to diet raises a question about larger mammals (i.e. over around 10 kg). If short jaws provide better mechanical advantage for biting and ingesting food, then why do larger mammals sacrifice this advantage? A horse does not need a speedy bite to catch grass, nor does it have to poke its face into crevices to obtain forage. In contrast, some large herbivores have short faces and a powerful incisor bite, most notably great apes. However, these herbivores use their hands to select food and to bring it to their mouths, something a horse is unable to do, and great apes are able to retain more mobile limbs because of their primarily arboreal mode of locomotion. Smaller mammals can, and do, use their forelimbs to aid in food selection (a squirrel being a familiar example; *see* Iwaniuk *et al.* 1998). Some small, long-faced ungulates do exist (long-faced in comparison with most mammals of that size); e.g. deer such as the southern pudu (*Pudu puda*, 10 kg), antelope such as Kirk's dik-dik (*Madoqua kirki*, 5 kg) and tragulids such as the Java mouse deer (*Tragulus javanicus*, 1.5 kg). However, these mammals all have a highly cursorial morphology with an unguligrade foot posture (*see* below). In contrast hyraxes (Procaviidae, Hyracoidea, Afrotheria), so-called “sub-ungulates” (and not considered here), have shorter faces than these true ungulates and much less derived postcranial morphologies, although hyraxes do not use their forelimbs to any great extent for food manipulation (first author's personal observation from many years of keeping pet hyraxes).

We propose that the relatively longer faces of large herbivores (and also some large carnivores, such as canids) relate to the use of the face for food prehension and initial ingestion: a longer face will provide a greater ability to use the anterior dentition toprehend food if the hands cannot be used to help. To understand this, one has only to think of the difficulty that humans have with

the Halloween “apple-bobbing” contest, where the use of hands is not allowed to help grab an apple floating on the surface of the water in a bucket — this must be done only using the mouth. A cat would likely also have problems doing this, a dog or a horse much less so.

Larger mammals, especially if specialized for cursorial locomotion, have limbs that become highly specialized for terrestrial support, which limits the extent of limb mobility in anything other than the parasagittal plane (*see* discussion in Janis & Martín-Serra 2020). This relates to issues of allometry; larger animals do not show much of an increase in long bone diameter with increasing size, at least up to a body mass of around 300 kg, past which slight positive allometry can be observed (Biewener 2005, Dick & Clemente 2017). Thicker bones would render larger animals too heavy to move. Instead, larger animals adjust their posture (their limb joints becoming less flexed), and they also adjust their behaviour, being more reserved in their movements.

Terrestrially-specialized large mammals also have greater restriction of the range of motion in their joints than arboreal or semi-arboreal ones, especially in the forelimb at the elbow (Figueirido *et al.* 2016, Jones & Janis 2022) and the shoulder (Janis *et al.* 2020) (*see* also Janis & Martín-Serra 2020, for similar, but less extreme, differences in morphologies between terrestrial and arboreal taxa in smaller mammals). The hands and feet become more modified, especially in cursorial forms (in the mainly bipedal kangaroos this applies to the hindlimbs only). While the basal mammalian condition is for a plantigrade foot posture with little modification of the hands and feet, many larger extant terrestrial mammals have a foot posture that is at least digitigrade (bears being an obvious exception, but their plantigrade foot posture may be a secondary specialization; *see* Panciroli *et al.* 2017), and all extant ungulates have a posture that is unguligrade, or at least subunguligrade (Tapiriidae, Rhinocerotidae, Hippopotamidae, and also Elephantidae) (Polly 2007). Kubo *et al.* (2019) note that smaller mammals are usually plantigrade, while larger mammals are usually digitigrade or unguligrade. These more derived foot postures entail specializations of the hands

and feet, with elongated metapodials and the loss and/or compression of the digits.

Other authors have investigated the issue of forelimb dexterity in mammals, although these studies have mainly considered within-ordinal differences (e.g. Bishop 1964 [primates], Iwaniuk 1996 [macropodoids], Iwaniuk *et al.* 2000 [carnivorans], Wishaw *et al.* 1998 [rodents]). Iwaniuk *et al.* (1999) devised an index of forelimb dexterity for carnivorans based on observed patterns of limb mobility. Below we describe the Forelimb Mobility Index devised from limb bone morphology. Note that the proximal (forelimb) mobility that Iwaniuk *et al.* (1999) describe relates to our descriptions of shoulder rotation (proximal humerus) and ability for supination (distal humerus), while their distal (forepaw) mobility relates to our descriptions of limb posture and metacarpal length and compression.

The above-listed studies have been concerned with small to medium-sized mammals with moderate degrees of manual dexterity and, in general (felid and canid carnivorans are the exception) consider mammals that have not modified the bones of their hands to any great extent and retain a plantigrade foot posture. Our study is concerned with a broader size and locomotor range of mammals, mainly comparing ungulate mammals with relatively limited forelimb movement with other mammals with varying degrees of forelimb movement.

Digitigrade mammals (mainly canid and felid carnivorans), with elongated and compressed metacarpals, have limited ability to use their hands for manipulation of objects, and little ability to supinate the hand, while unguligrade mammals (ungulates) have no ability for manipulation and their hands are restricted to a prone position. This is not to say that such mammals are unable to use their forelimbs for other functions than locomotion — dogs can grip a bone between their paws and horses can use their forelimbs to paw the ground and dig — but this is not the same as being able to pick up objects with their hands. Thus, larger and, especially, more cursorially adapted mammals will be increasingly unable to use their hands to help in feeding, and will be expected to have longer faces to aid in food prehension. We investigate this hypothesis here.

To return to the issue of gape. Large gapes serve different functions in carnivores and herbivores; a large gape permits the seizing of larger prey items for carnivores, and is associated with active engagement of the jaw adductor muscles, while in herbivores a large gape is mainly used for display, and is associated with passive stretch of the jaw adductors (Herring & Herring 1974). Moreover, whether or not a large gape can be permitted by the amount of stretch possible in the adductor muscles, especially the masseter muscle, varies greatly between carnivores and herbivores. Carnivorous mammals retain the generalized condition of a jaw adductor musculature dominated by the temporalis muscle, while herbivores have a reduced temporalis but a greatly enlarged masseter muscle (especially the superficial masseter), reflecting the need for transverse jaw movements and prolonged mastication by the molars (Scapino 1993). To accommodate this large masseter muscle, the geometry of the skull between carnivores and herbivores is very different. In particular, the angle between the craniomandibular joint (which is now elevated) and the points of origin and insertion of the masseter is much more acute in herbivores. Herbivores also have a greatly deepened angle of the mandible to accommodate the enlarged masseter, which may have a pinnate architecture that results in a lesser ability to stretch (Herring & Herring 1974, *see* especially their fig. 3). While the bony and muscular architecture of the jaw in carnivores permits a large gape, in herbivores it restricts the gape. Herbivores with a wide-gape threat display, such as hippos and hyraxes, have modified their mandibular anatomy to allow for a greater degree of stretch in the masseter muscle (Herring 1975).

Canids and felids make an interesting contrast in terms of the trade-offs between gape and jaw length, and how this relates to prey prehension. Many larger canids are pack-hunting, cursorial predators while most larger felids are solitary, ambush predators. Their prey-capture techniques also differ: canids deliver multiple, swift shallow bites while felids employ deep and prolonged bites, and these differences are reflected in both the shapes of their incisor arcade and the strength of the incisors and canines (Biknevicius *et al.* 1996). Canids have less robust canines than

felids, but more robust incisors, which appear to reinforce the canines during biting by limiting the motion of the prey, much as felids can limit prey motion with their forelimbs (Biknevics *et al.* 1996). The longer face of canids would here be an essential prehension mechanism to compensate for the lack of forelimb dexterity (a necessary morphology for a highly cursorial mammal that chased after its prey), as well as affording a larger gape.

In tandem with this, the scaling of facial lengths differs between canids and felids, manifesting especially in larger species that take large-sized prey. Canids have relatively longer faces than felids. Larger canid species that take relatively small prey have proportionally very long faces, e.g. the Ethiopian wolf (*Canis simensis*), where the long narrow jaws allow for rapid jaw closure at the expense of bite force. However, the slightly larger (~22 kg *versus* 14 kg) hunting dog (*Lycaon pictus*) hunts large ungulate prey in packs, and its snout is relatively short and broad for a canid, enabling a relatively greater bite force at the canines, but at the expense of a wide gape (Slater *et al.* 2008). The opposite pattern is seen in larger felids, where the felid shorter face results in a lesser capacity for a large gape. Large felids like the lion (*Panthera leo*) have proportionally longer faces than smaller ones: here a relatively weaker bite at the canines is a trade-off for the ability to have a larger gape to handle relatively larger prey (Slater & Van Valkenburgh 2009).

## Material and methods

We estimated facial lengths by taking measurements of the lower jaw, an osteological element that is more available in museum collections than skulls, and less likely to break. For example, skulls of ruminant artiodactyls, which lack upper incisors, have often lost the premaxilla, while the lower jaw (retaining the incisors) is more likely to remain intact. We used Radinsky's (1985) measurement of Tooth Row Length (TRL) from the back of the last molar to the alveolus of the first incisors, although measured along the lower jaw rather than on the skull (*see* Fig. 1). This measure was adapted for kangaroos, where the

procumbent lower (first) incisors match up with a considerable portion of the overlying cranium, and in this instance we measured TRL to the tip of the lower incisors. Note that this measure of facial length avoids problems of long-appearing faces due to posterior movement of the orbit (Mitchell *et al.* 2024). While all ungulates considered here have long faces, many of them (e.g. horses, grazing bovids) may appear to have an exceptionally long face because of the posterior orbit position.

Photographs of the taxa were obtained from museum online resources (or supplied by the first author from museum collections) and were measured using ImageJ. Lineages included were those with body masses mostly over 5 kg (i.e. canids but not mustelids) and a large enough number of extant (or available extinct) species to accurately estimate a regression line spanning a range of body masses (i.e. canids but not hyaenids).

We measured only extant taxa, except for the equids, where in order to obtain a size range of species comparable with other ungulates (especially as extant equids are all of a similar size) we also included a number of extinct taxa (as was also done by Radinsky 1985). Note that including only extant equids results in a similar, but truncated, regression line (Richardson 2021). We measured TRL for a total of 196 taxa: 45 bovids (Bovidae), 19 cervids (Cervidae), 27 equids (Equidae, including 23 extinct taxa), 18 canids (Canidae), 25 felids (Felidae), 14 arctoid carnivores (Ursidae, Ailuridae and Procyonidae), 15 cercopithecids (Primates, Cercopithecidae), and 33 kangaroos (Macropodidae).

Arctoid carnivores, as considered here, do not form a clade, but including these families together allows for a size range comparable to that of the other taxa studied. We did not include mustelids as we were primarily interested in including a comparable number of smaller taxa with the ursids, with similar diets (mostly omnivorous) and locomotion (mostly scansorial). The coatimundis (Procyonidae; genera *Nasua* and *Nasuella*) were not included as they have an elongated snout associated with burrowing in ground litter for food — we do not consider that their inclusion would have had much effect on the arctoid slope or intercept. We expected kangaroos to be especially interesting;

while their hind legs are specialized for ricochet locomotion, their forelimbs are less specialized, although they are employed at slower gaits than hopping. Body masses for extant taxa were obtained mainly from the Animal Diversity website (<https://animaldiversity.org>). All measurement data, including the specimen numbers of the taxa measured and the source of the body masses, are given in Appendix 1.

The individual taxa were also assigned a value of forelimb mobility, as the “Forelimb Mobility Index” (FMI). This was done in a qualitative fashion by assessing foot posture (unguligrade, digitigrade or plantigrade), metapodial length and compression, and shoulder and elbow mobility (detailed in Appendix 2). The limb mobility was assessed from the anatomy of the proximal and distal humeral articulations, sourced from publications that had performed geometric morphometric studies on these articular surfaces in correlation with locomotor mode (Figueirido *et al.* 2016, Janis & Martín-Serra 2020, Janis *et al.* 2020, Jones & Janis 2022). None of these papers considered ungulates, which are well known to have little or no ability to abduct the shoulder and supinate the hand. In the case of the extinct equids, many of which have less derived limb anatomies than extant ones (*see below*), humeral mobility was assessed from photographs taken at the American Museum of Natural History (New York) by the first author.

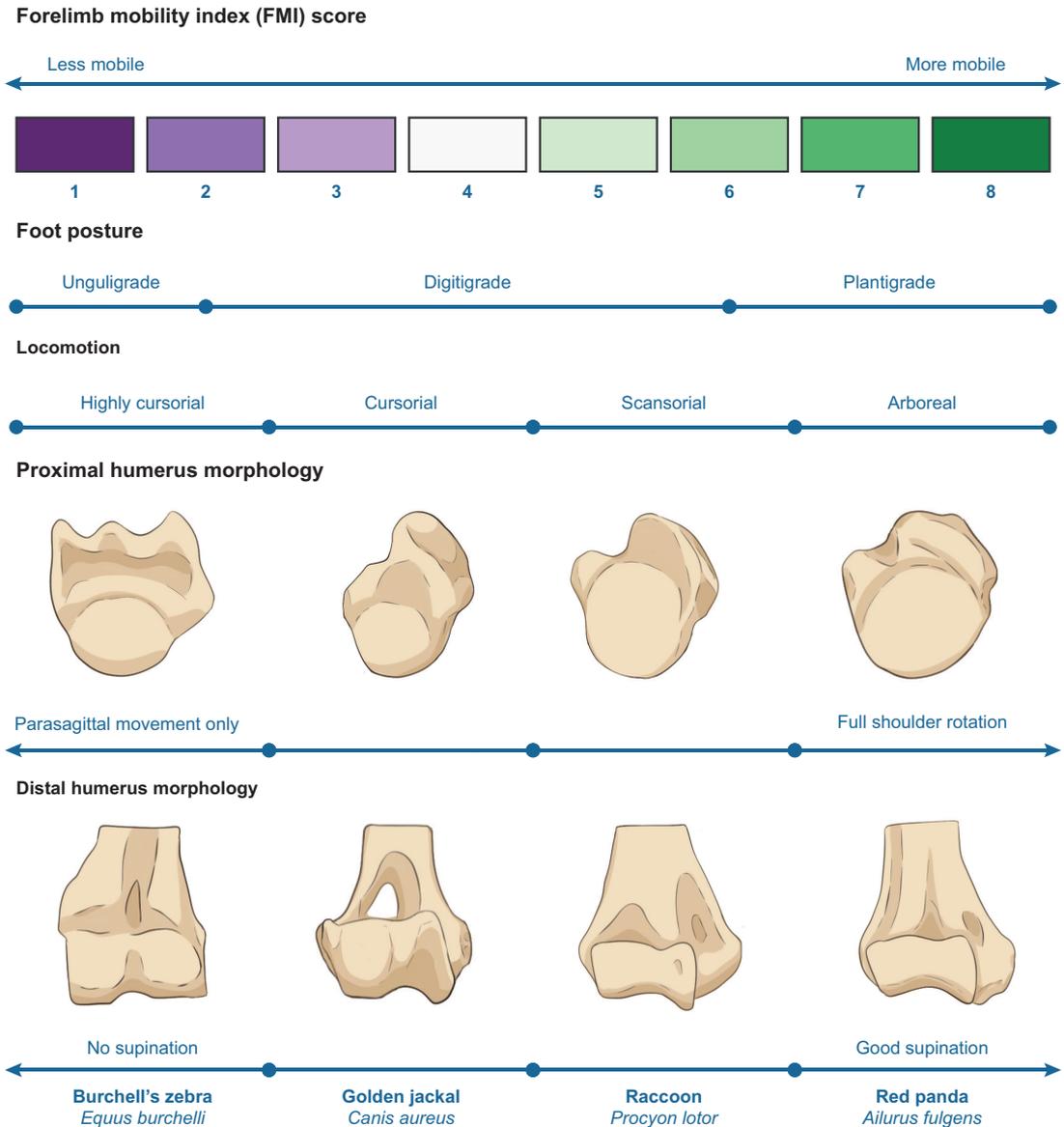
The FMI ranged from 1 (least mobile: unguigrade ungulates) to 8 (most mobile: arboreal taxa). In general, mammals with an FMI 6–8 can pluck food with their hands and bring it to their mouths to eat; mammals with an FMI of 4–5 have some ability to use their forelimbs for food prehension, such as grappling with prey; mammals with an FMI of 1–3 have more limited forelimb mobility, but those with an FMI of 2–3 (mainly canids) can still manipulate food to a certain extent (e.g. a dog eating a bone) (*see Figueirido et al.* 2016). The features used in devising the index for each taxon are listed in Appendix 2 and shown in Fig. 2.

All extant ungulates were assigned an FMI of 1. For the extinct equids, members of the family Equinae and derived members of the Anchitheriinae that shared the spring foot and unguigrade

foot posture of the Equinae (*see Janis & Bernor 2019*) were assigned an FMI of 1. Other anchitheriines that lacked a spring foot, likely retained a foot pad, and had some morphological features indicative of less immobile forelimbs (e.g. the ulna was not fused to the radius) were assigned an FMI of 2. Members of the Hyracotheriinae, which had a four-digit manus (one or three in all other equids), with relatively short metacarpals and a more spreading hand, likely with a tapir-like foot pad (*see Wood et al.* 2011), were assigned an FMI of 3 (similar to that of most canids).

Most canids were assigned an FMI of 3 (digitigrade, cursorial, mostly pounce-pursuit predators); the specialized pack-hunting pursuit predators, with longer and more compressed metapodials and more restricted forearm motion (wolves, *Canis lupus*, *Canis rufus*; hunting dog, *Lycaon pictus*; dhole, *Cuon alpinus*: *see Figueirido et al.* 2015) were assigned an FMI of 2. Felids, digitigrade forms but with generally more mobile forelimbs than canids, were assigned an FMI of 5 (more scansorial forms, e.g. the ocelot, *Leopardus pardalis*) or 4 (more terrestrial forms, e.g. the lynxes, *Lynx* spp.) and the highly cursorial cheetah (*Acinonyx jubatus*) was assigned an FMI of 3 (*see Panciroli et al.* 2017). Among the arctoid carnivores: all taxa are plantigrade but vary in their degree of arboreal/scansorial versus terrestrial behaviour and adaptations. Procyonids and ailurids, with morphological adaptations for considerable forelimb mobility, were assigned an FMI of 7. Arboreal ursids (e.g. the sun bear, *Helarctos malayanus*) were assigned an FMI of 7, and more strictly terrestrial forms (e.g. the grizzly bear, *Ursus arctos*) an FMI of 6.

The cercopithecoid primates are mostly plantigrade, but some highly terrestrial species (the ones assigned a lower FMI below) have digitigrade forelimbs (Patel 2009). Those that are arboreal or scansorial were assigned an FMI of 8, but the larger, more specialized terrestrial baboons (*Papio* spp., *Theropithecus gelada*) were assigned an FMI of 7, as was the smaller, highly terrestrial patas monkey (*Erythrocebus patas*). Baboons do manipulate food with their forelimbs, but they have modifications of their forelimbs for terrestrial life (e.g., longer metacarpals) that may restrict forelimb mobility. Kan-



**Fig. 2.** Forelimb mobility index among different mammals, and some anatomical correlates. Drawings of bones (by Emily Green from Science Graphic Design) from photographs taken by the first author. All elements right hand side; proximal humerus in superior view, anterior to top, medial to left; distal humerus in anterior (cranial) view, medial to right. Source of taxa photographed: Burchell's zebra, *Equus burchelli*, MCZ 5003; Golden jackal, *Canis aureus*, MCZ 9342; Raccoon, *Procyon lotor*, MCZ 61037; Red panda, *Ailurus fulgens*, MCZ 64643. MCZ = Museum of Comparative Zoology, Harvard University, USA. Figure by Science Graphic Design (sciencegraphicdesign.com).

garoos all have a palmigrade forelimb posture, with a degree of forelimb mobility comparable to scansorial (semi-arboreal) mammals; they were assigned an FMI of 7, except for tree-kangaroos (*Dendrolagus* spp.), which were assigned a value of 8. Tree-kangaroos have a more highly mobile

humeral morphology (Janis *et al.* 2020, Jones & Janis 2022), and also show more extensive upper arm movement in reaching and grasping than other macropodoids (Iwaniuk *et al.* 1998).

We performed standard major axis (SMA) analyses to test for significant differences in

slopes, elevations, and shifts along best-fit lines for tooth row length (TRL) and body mass pairwise between families, using the package *smatr* (<https://cran.r-project.org/web/packages/smatr/index.html>; Warton *et al.* 2012) in R ver. 3.2.0 (R Core Team 2023) and R Studio ver. 2023.09.1+494 (RStudio Team 2023). Using the standard workflow of the *smatr* package, we estimated a common slope across all clades, then compared this to the slopes calculated for each clade to determine whether any significantly differed from the common slope. In the event that there were no significant differences from the common slope, we carried out pairwise comparisons between each clade. Both TRL and body mass were  $\log_{10}$ -transformed. Differences were considered significant at  $p < 0.05$ , and  $p$  values for multiple comparisons were adjusted using the Šidák correction. (For more detailed discussion of SMA see Warton *et al.* 2006 and Taskinen & Warton 2011, for a comparison of SMA with ordinary least squares analyses using allometric data see Benoit 2010.) While our statistics may be considered rather simplistic, we consider them to be appropriate for this study, especially as our data consist of single data points without within-species replication.

We did not attempt to phylogenetically correct the data, nor apply a methodology such as PGLS. Mitchell *et al.* (2024) have shown that phylogenetic correction may be counterproductive in studies of allometry as size often varies directly with phylogeny. That is, larger animals within a lineage are usually the most derived ones, as would be suspected from Cope's Rule. Thus, in removing the effects of phylogeny one is removing the effects of body size, the relevant variable for comparison of any morphology.

Scatterplots were used to visualize the data. They were created in R Studio ver. 2023.12.1+402 (R Core Team 2023) following a modified version of a *ggplot2* code by Cedric Scherer (<https://z3tt.github.io/OutlierConf2021/>). The following packages were used: *tidyverse* (<https://www.tidyverse.org/packages/>; Wickham *et al.* 2019), *systemfonts* (<https://CRAN.R-project.org/package=systemfonts>), *ggtext* (<https://CRAN.R-project.org/package=ggtext>), *ggforce* (<https://CRAN.R-project.org/package=ggforce>), *ggplot2* (<https://ggplot2.tidyverse.org/>; Wick-

ham 2016), *xts* (<https://CRAN.R-project.org/package=xts>), *ggpp* (<https://CRAN.R-project.org/package=ggpp>), and *ggpmisc* (<https://CRAN.R-project.org/package=ggpmisc>). The standard major axis slope lines in Fig. 3 were created using the *stat\_ma\_line* function of *ggpmisc*. The scatterplots were further modified using Adobe Illustrator 27.0 (Adobe Inc.). This involved editing the shape and size of the data points, formatting the key, and adding the corresponding lineage silhouettes.

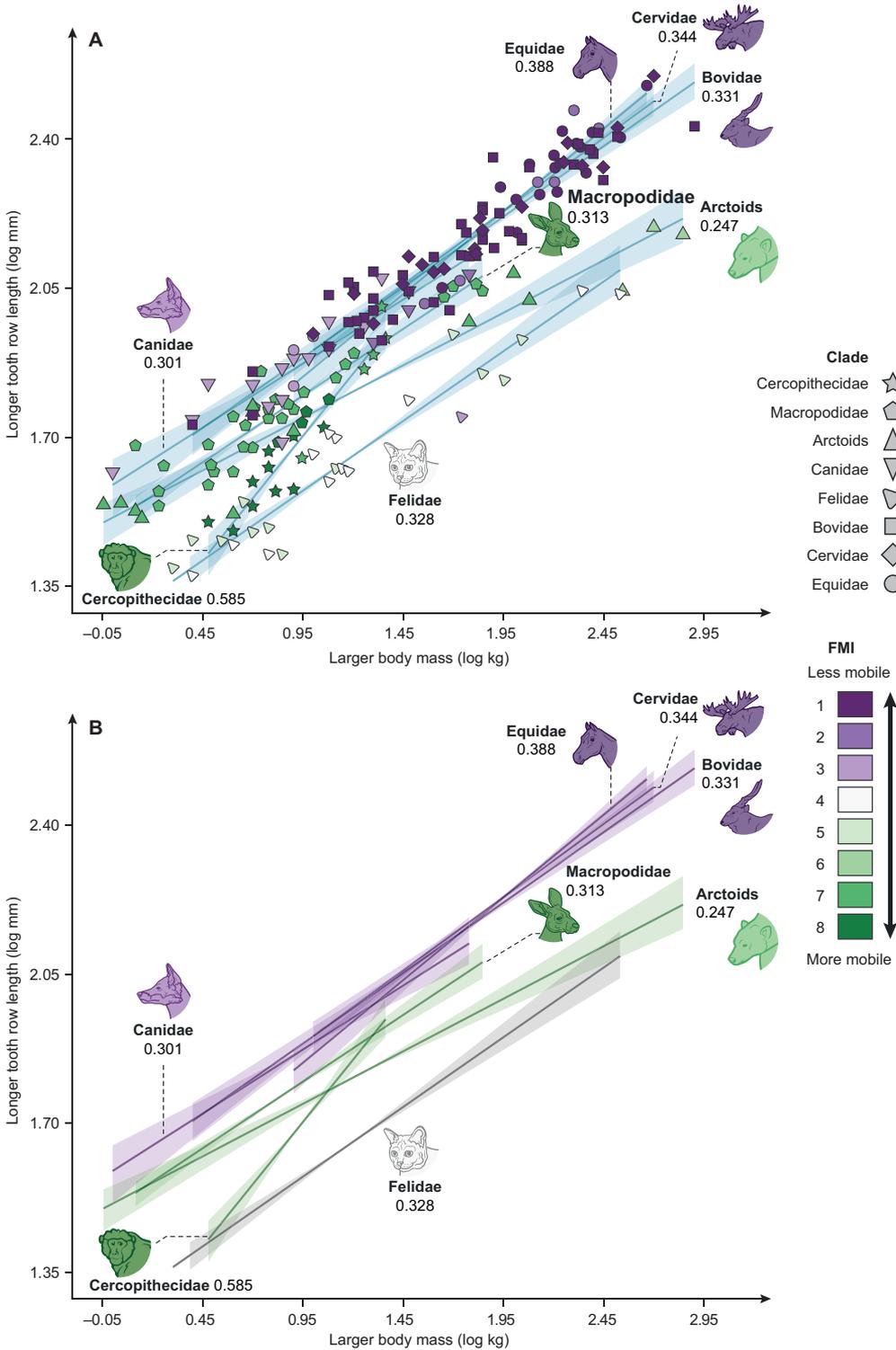
To test for a correlation between forelimb mobility index (FMI) and the relationship between size and facial length, we first calculated the average FMI for each family. Because the values for mean, median, and mode were nearly equivalent within each lineage, we treated the mean FMI values for each lineage as a continuous variable in the linear regression.

Felids were removed from this analysis. Their extremely short faces, combined with a relatively low FMI (which can be explained by their predatory lifestyle, see discussion below), render them anomalous, and the correlation non-significant with them present. We performed a linear regression of average FMI by the elevation of the best-fit line between tooth row length and body mass, using the  $y$ -intercept values from the standard major axis analyses of elevation, calculated for each family described above, and listed in Table 1.

## Results

The plot of facial length (log TRL) against body mass (log BM) is shown in Fig. 3. The face lengths of most taxa scale more or less with isometry, as would be expected following Radinsky (1985). A more detailed version of this plot, showing the regression lines for each individual taxon, can be seen in Appendix 3.

The three ungulate lineages have the highest elevations, being almost indistinguishable from each other at larger body masses; but at the smaller end of the scale, the equid regression line shows slightly lower elevation. Canids are very similar to the ungulates, but with a shift toward slightly smaller body sizes along the same allometric elevation that can be shown to be statisti-



**Fig. 3.** Results of standard major axis regressions of face length (tooth row length, TRL) and body mass (BM) by family (Arctoids = Ursidae + Ailuridae + Procyonidae). — **A:** All of the data points. — **B:** Emphasized differences in slopes. Figure by Science Graphic Design (sciencegraphicdesign.com). Heads by Hey Rabbit at the Noun Project (<https://thenounproject.com/heyrabbit/>), except for the bovid (the eland, *Taurotragus oryx*), drawn by NMM-G.

cally different from the ungulates (*see* Table 2). Felids, despite having only slightly higher FMI values than canids, have a very low elevation, with exceptionally short faces compared to the other mammals, even the primates.

Kangaroos have a middling elevation, with fairly long faces in comparison to the arctoid carnivores, which have similar FMI values. The arctoid carnivores commence with a similar elevation to the kangaroos, but larger arctoids (bears) have lower values, scaling with slight negative allometry. In contrast, the cercopithecoid primates commence with a relatively low elevation (similar to the felids), but then scale with positive allometry to catch up to the arctoid carnivores at larger body sizes.

Standardized major axis (SMA) analyses revealed that, among pairwise comparisons of

families, the slopes of the best-fit regression lines of log-transformed tooth row length (TRL) and log-transformed body size were significantly different between cercopithecids and all other families, but were otherwise only significantly different only between arctoids and equids, and arctoids and cervids (Table 3). Pairwise comparisons of best-fit line elevations ( $y$ -intercepts), fitted to a common slope = 0.3182–0.3549: we found significant differences between nearly all families, except between arctoids and macropodids; arctoids and cercopithecids; and pairwise comparison combinations of bovids, cervids, equids, and canids with each other (*see* Table 1). Among the families for which significant differences in elevation were not found, we made pairwise comparisons for shifts along allometry (i.e. extensions of allometry into larger

**Table 1.** Results of SMA pairwise comparisons of differences in elevation ( $y$ -intercept) between lineages; degrees of freedom (df) = 1. Columns “Elevation 1” and “Elevation 2” refer to the slope of the best-fit line for the taxa in that row in columns “Lineage 1” and “Lineage 2”, respectively.  $P$  values were adjusted using the Šidák correction, and those indicating significant results are set in boldface.

Lineage 1	Lineage 2	$p$	Likelihood ratio	Elevation 1	Elevation 2
Arctoids	Bovidae	< <b>0.001</b>	36.89	1.4386	1.6148
Arctoids	Canidae	< <b>0.001</b>	30.60	1.4938	1.6263
Arctoids	Cercopithecidae	> 0.99	1.60	1.4773	1.4354
Arctoids	Cervidae	< <b>0.001</b>	38.05	1.4354	1.6255
Arctoids	Equidae	<b>0.004</b>	14.52	1.3797	1.5421
Arctoids	Felidae	< <b>0.001</b>	30.11	1.4515	1.3009
Arctoids	Macropodidae	0.37	5.79	1.4665	1.5254
Bovidae	Canidae	> 0.99	0.87	1.5832	1.5639
Bovidae	Cercopithecidae	< <b>0.001</b>	43.76	1.5358	1.3626
Bovidae	Cervidae	> 0.99	0.61	1.5631	1.5736
Bovidae	Equidae	> 0.99	0.28	1.5311	1.5390
Bovidae	Felidae	< <b>0.001</b>	353.57	1.5755	1.2611
Bovidae	Macropodidae	< <b>0.001</b>	30.60	1.5852	1.4915
Canidae	Cercopithecidae	< <b>0.001</b>	31.34	1.4120	1.2442
Canidae	Cervidae	> 0.99	1.02	1.5552	1.5792
Canidae	Equidae	> 0.99	0.10	1.5206	1.5117
Canidae	Felidae	< <b>0.001</b>	232.85	1.5678	1.2712
Canidae	Macropodidae	< <b>0.001</b>	19.65	1.5787	1.5032
Cercopithecidae	Cervidae	< <b>0.001</b>	29.53	1.3414	1.5015
Cercopithecidae	Equidae	<b>0.022</b>	11.28	1.2986	1.4051
Cercopithecidae	Felidae	< <b>0.001</b>	27.99	1.3583	1.2280
Cercopithecidae	Macropodidae	< <b>0.001</b>	20.43	1.3699	1.4735
Cervidae	Equidae	> 0.99	0.01	1.5191	1.5178
Cervidae	Felidae	< <b>0.001</b>	308.04	1.5753	1.2536
Cervidae	Macropodidae	< <b>0.001</b>	26.07	1.5868	1.4865
Equidae	Felidae	< <b>0.001</b>	206.17	1.5335	1.2270
Equidae	Macropodidae	<b>0.027</b>	10.86	1.5439	1.4666
Felidae	Macropodidae	< <b>0.001</b>	199.93	1.2714	1.4940

or smaller size ranges) and found significant differences between canids and equids; canids and cervids; and canids and bovids (Table 2). Details of all the SMA analyses can be found in Appendix 4.

For the forelimb mobility index, with felids excluded (*see* discussion below), we found a correlation between family-average FMI and elevation (i.e.  $y$ -intercept values of the allometric regression lines; Appendix 4). Excluding felids:  $\text{Int} \sim \text{FI}$ , slope =  $-0.0274$ , intercept =  $1.5839$ ,  $\text{df} = 5$ ,  $R^2 = 0.8314$ ,  $p = 0.0027$ . Figure 4 shows the regression line excluding felids. If the felids are included the results are not significant, and the effect size is reduced:  $\text{Int} \sim \text{FI}$ , slope =  $-0.0254$ , intercept =  $1.6027$ ,  $\text{df} = 6$ ,  $R^2 = 0.3402$ ,  $p = 0.0754$ .

## Discussion

The high elevation of the regression lines of the ungulates is reflected in their low FMI values. The slightly lower elevation at the lower end of the equid regression line is explained by the inclusion of the small hyracotheres (FMI = 3) that retained a foot pad and were in a number of ways less cursorially adapted than later equids. The basal anchitheres, despite their lack of the more derived equid spring foot, do not appear to show any difference in face length compared to the equine equids, as also noted by Radinsky (1984). Among bovids, grazers have been noted to have longer faces than browsers and mixed feeders (Spencer 1995), but in our study all ungulates have long faces in comparison to other mammals, even if there might be some variation

**Table 2.** Results of SMA pairwise comparisons of shifts along allometries between lineages; degrees of freedom ( $\text{df}$ ) = 1. Columns “Shift 1” and “Shift 2” refer to the slope of the best-fit line for the taxa in that row in columns “Lineage 1” and “Lineage 2”, respectively.  $P$  values were adjusted using the Šidák correction, and those indicating significant results are set in boldface.

Lineage 1	Lineage 2	$p$	Likelihood ratio	Shift 1	Shift 2
Arctoids	Bovidae	0.17	7.34	2.1867	2.6466
Arctoids	Canidae	> 0.99	0.00	2.1315	2.1354
Arctoids	Cercopithecidae	> 0.99	1.51	2.1480	1.9445
Arctoids	Cervidae	<b>0.034</b>	10.41	2.1899	2.7660
Arctoids	Equidae	<b>0.003</b>	14.93	2.2455	2.9769
Arctoids	Felidae	> 0.99	1.02	2.1738	1.9946
Arctoids	Macropodidae	> 0.99	0.95	2.1587	2.0010
Bovidae	Canidae	< <b>0.001</b>	33.20	2.6782	2.1978
Bovidae	Cercopithecidae	< <b>0.001</b>	62.99	2.7256	2.0174
Bovidae	Cervidae	> 0.99	1.67	2.6983	2.8178
Bovidae	Equidae	0.11	8.20	2.7303	2.9800
Bovidae	Felidae	< <b>0.001</b>	43.84	2.6859	2.0344
Bovidae	Macropodidae	< <b>0.001</b>	79.49	2.6762	2.0349
Canidae	Cercopithecidae	0.81	3.61	2.3497	2.1357
Canidae	Cervidae	< <b>0.001</b>	36.03	2.2065	2.8123
Canidae	Equidae	< <b>0.001</b>	59.29	2.2411	3.0073
Canidae	Felidae	0.95	2.67	2.1939	2.0243
Canidae	Macropodidae	0.7	4.14	2.1830	2.0232
Cercopithecidae	Cervidae	< <b>0.001</b>	60.89	2.0385	2.8899
Cercopithecidae	Equidae	< <b>0.001</b>	91.76	2.0813	3.1139
Cercopithecidae	Felidae	> 0.99	0.17	2.0217	2.0675
Cercopithecidae	Macropodidae	> 0.99	0.25	2.0101	2.0530
Cervidae	Equidae	> 0.99	1.51	2.8724	3.0013
Cervidae	Felidae	< <b>0.001</b>	46.60	2.8162	2.0419
Cervidae	Macropodidae	< <b>0.001</b>	70.90	2.8046	2.0400
Equidae	Felidae	< <b>0.001</b>	68.27	2.9855	2.0685
Equidae	Macropodidae	< <b>0.001</b>	111.83	2.9751	2.0599
Felidae	Macropodidae	> 0.99	0.01	2.0241	2.0325

around the individual regression lines related to diet (which we did not investigate).

The high elevation of the canid regression line, and the relatively long face of canids, reflects the fact that canids lack the ability to use their forelimbs to capture their prey. Canids, unlike felids (with the exception of the cheetah), cannot grapple their prey, and must rely on pouncing or hunting in groups. While the family cat can fish food out of the garbage with its forepaws, the family dog must rely on sticking its head into the bin.

Although a powerful bite at the front of the jaw bestowed by a shorter face with greater mechanical advantage would no doubt be useful for their prey capture, canids remain reliant on a long face for food prehension (but see earlier comments about the relatively shorter face of the

hunting dog, *Lycaon pictus*). This is of course why humans breed dogs with very short faces for fighting, as the resultant high mechanical advantage will enable a strong grip, while dogs used for hunting retain longer faces.

Felids are shown here to have exceptionally short faces, even shorter than those of the primates considered. This must relate to their reliance on a powerful bite at the anterior end of the jaw for dispatching prey and, as noted, they can still use their forelimbs for a good deal of food manipulation, including grasping and subduing prey. Felids (FMI = 4–5, with the exception of the cheetah) have a greater degree of cursorial adaptations to more nimble arctoid carnivores, such as raccoons (FMI = 7), with a digitigrade foot posture, elongated and compressed metacarpals, and the reduction of manual digit 1 to a dew

**Table 3.** Pairwise SMA pairwise comparisons of allometric slope between lineages; degrees of freedom (df) = 1. Columns “Slope 1” and “Slope 2” refer to the slope of the best-fit line for the taxa in that row in columns “Lineage 1” and “Lineage 2”, respectively. *P* values were adjusted using the Šidák correction, and those indicating significant results are set in boldface.

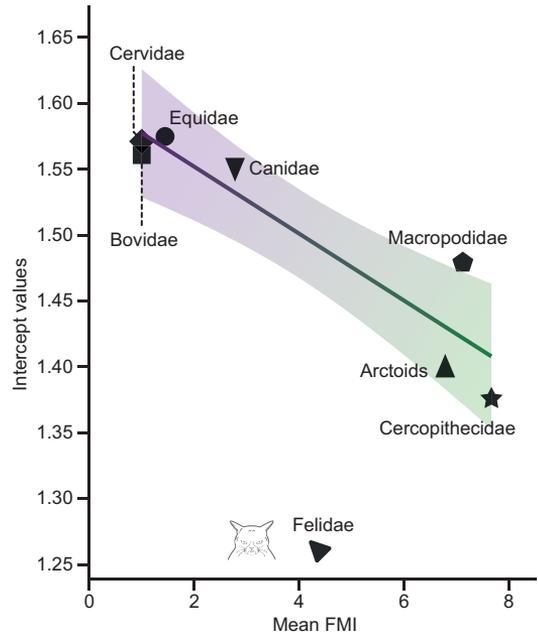
Lineage 1	Lineage 2	<i>p</i>	Likelihood ratio	Slope 1	Slope 2
Arctoids	Bovidae	0.084	8.74	0.2468	0.3310
Arctoids	Canidae	0.99	2.12	0.2468	0.3005
Arctoids	Cercopithecidae	< <b>0.001</b>	28.51	0.2468	0.5848
Arctoids	Cervidae	<b>0.045</b>	9.93	0.2468	0.3440
Arctoids	Equidae	<b>0.002</b>	15.92	0.2468	0.3883
Arctoids	Felidae	0.15	7.63	0.2468	0.3275
Arctoids	Macropodidae	0.42	5.46	0.2468	0.3131
Bovidae	Canidae	> 0.99	0.61	0.3310	0.3005
Bovidae	Cercopithecidae	< <b>0.001</b>	18.70	0.3310	0.5848
Bovidae	Cervidae	> 0.99	0.23	0.3310	0.3440
Bovidae	Equidae	0.71	4.09	0.3310	0.3883
Bovidae	Felidae	> 0.99	0.02	0.3310	0.3275
Bovidae	Macropodidae	> 0.99	0.44	0.3310	0.3131
Canidae	Cercopithecidae	<b>0.001</b>	16.86	0.3005	0.5848
Canidae	Cervidae	> 0.99	1.12	0.3005	0.3440
Canidae	Equidae	0.75	3.90	0.3005	0.3883
Canidae	Felidae	> 0.99	0.46	0.3005	0.3275
Canidae	Macropodidae	> 0.99	0.10	0.3005	0.3131
Cercopithecidae	Cervidae	<b>0.001</b>	16.68	0.5848	0.3440
Cercopithecidae	Equidae	<b>0.017</b>	11.75	0.5848	0.3883
Cercopithecidae	Felidae	< <b>0.001</b>	18.68	0.5848	0.3275
Cercopithecidae	Macropodidae	< <b>0.001</b>	20.31	0.5848	0.3131
Cervidae	Equidae	0.99	2.06	0.3440	0.3883
Cervidae	Felidae	> 0.99	0.33	0.3440	0.3275
Cervidae	Macropodidae	> 0.99	1.12	0.3440	0.3131
Equidae	Felidae	0.73	3.97	0.3883	0.3275
Equidae	Macropodidae	0.35	5.91	0.3883	0.3131
Felidae	Macropodidae	> 0.99	0.26	0.3275	0.3131

claw. These cursorial morphologies reflect their ambush hunting style; as active predators they need to be able to have a degree of sustained locomotion, if not to the extent seen in canids.

While felids are unique among extant predatory mammals in their extremely short faces, a parallel may have been seen in some extinct marsupial cat-like predators, such as the thylacoleonids (“marsupial lions”) of Australia. These predators evidenced more mobile forelimbs than felids (see Figueirido *et al.* 2016, Wells & Nichol 1997). Although a decent size range of thylacoleonids exists (from house cat size to puma size), all fairly short faced, we did not have access to the appropriate humeral data to include them. Likewise, the thylacinids (“marsupial wolves”) would be interesting to study; they had long, canid-like snouts but more mobile forelimbs (see Figueirido & Janis 2011, Janis & Figueirido 2014).

Arctoid carnivores, especially procyonids and ailurids, are able to use their forelimbs in feeding to a considerable extent, and they have shorter faces than canids, but as they are not usually active predators, they do not require the high mechanical advantage of a very short face seen in the felids. The reason for the negative allometric slope of the line (although not significantly different from most other regression lines) is perhaps related to the fact that the relatively small-sized procyonids include more insects in their diets than do bears; thus, they tend to have somewhat longer and more pointy snouts (i.e. higher TRL values; e.g. the ringtail, *Bassariscus astutus*) than do bears.

The cercopithecoid primates differ from the other taxa here in having a regression line that is of low elevation but with a slope of positive allometry. This may be because the largest forms are all baboons (genera *Papio* and *Theropithecus*), highly terrestrial primates with long faces and a greater degree of limb modification for terrestrial life (e.g. digitigrade forelimbs; Patel 2009). It is possible that our data on the cercopithecids is biased by the fact that males tend to have larger gapes than females for canine display (Hylander 2013), and in at least one species (*Macaca fascicularis*, Terhune *et al.* 2015) this large gape is facilitated by relatively longer jaws in the males. We have noted the sex of the primates we measured in Appendix 2 and in the



**Fig. 4.** Correlation between forelimb mobility index (FMI) and elevation of the regression slope (intercept values) of tooth row length (TRL).  $\text{Int} \sim \text{FI}$ , slope = 0.02540, intercept = 1.3741,  $df = 5$ ,  $R^2 = 0.8314$ ,  $p = 0.0027$ . Image of cat from Nicky Knicky, The Noun Project. Figure by Science Graphic Design (science-graphicdesign.com).

figure in Appendix 3. Most of the smaller species are of unknown sex, and our *M. fascicularis* is a female, but most of the larger species are males.

Macropodids have hands that are relatively unspecialized, but they have less shoulder mobility than seen in primates (Janis *et al.* 2020). Extant kangaroos (Macropodidae, Macropodinae) have relatively long faces, which may reflect the fact that, while they are capable of using their hands for grasping food, this is not usually seen during foraging in kangaroos except in the tree-kangaroos, which also have relatively short faces for a kangaroo (Mitchell *et al.* 2018). However, among the extinct sthenurine kangaroos (Macropodidae, Sthenurinae) many species had very short faces — but these kangaroos also had highly mobile forelimbs and grasping hands, and likely used their forelimbs for high-level browsing (see Mitchell *et al.* 2024, Richardson *et al.* 2024).

There are other large herbivorous mammals that have (or had) short faces, and these also use

(or used) their forelimbs for feeding. Great apes are a prime example. Elephants have very short faces, and highly immobile forelimbs, but they are able to use their trunk for food prehension and ingestion. Extant sloths have short faces; they are not very large mammals, but there was a wide range of sizes among extinct ground sloths that appear to have had shorter faces than ungulates of similar size. This would be an interesting group to further investigate.

Some extinct carnivorans might be interesting to investigate. For example, Richardson (2021) found that the extinct borophagine canids, which have shorter metapodials and a greater degree of forelimb mobility than the extant canine canines (Figueirido *et al.* 2015), also have shorter faces than extant canids (but statistical significance of the regression lines was not investigated). Hyaenids would also be interesting to consider. Many extinct species were smaller and with more canid-like long faces than most of the extant ones, but some were much larger and short-faced like most extant species. Their limb morphology also appears to have been more canid-like than felid-like, especially in the distal humerus (Andersson 2004). However, we did not have access to the relevant data for the fossil species to include them in this study.

Note that Iwaniuk *et al.* (2000) found that, in carnivorans, their forelimb dexterity index (derived from observed behaviour) was significantly negatively correlated with diet, in that carnivorans with more meat in their diet had less dextrous forelimbs. They ascribed this to the need for forelimbs modified for support to a greater extent in carnivorans that had to chase after their prey, despite the probable utility of dextrous forelimbs in prey capture. This accords with our hypothesis here.

Mitchell *et al.* (2024) propose a reason for why larger mammals might have longer faces in general, in their notion of “facial gracilisation”. Although they are referring to within-lineage trends, not among-lineage trends as we do here, this proposal deserves some attention. Longer skulls also tend to be more gracile, i.e. more lightly built. Bone is metabolically expensive to produce, a robust skull will be heavier than a gracile one, and larger animals may not

have the necessity to produce absolutely greater bite forces than their smaller relatives as food mechanical properties remain constant. Thus, larger animals may be able to have more gracile skulls without sacrificing performance, and this would save energy in both ontogeny (growing the skull) and day-to-day biology (the cost of transporting a heavy head). This might explain some intraspecific scaling, especially the long faces of ungulates which tend to be large mammals. However, we do not think that this hypothesis applies to our observations here. Within any size range, ungulates have longer faces than other mammals, and the face length of canids (which have a completely different diet, but a forelimb mobility index almost as low as that of ungulates) have similar absolute face lengths.

## Conclusion

We show here that ungulates (at least cursorial ungulates — we did not examine other lineages such as rhinos, due to a paucity of species and body size range) have relatively longer faces than other large (> 10 kg) mammals, across a wide range of body sizes, although canids have faces that are almost as relatively long as those of ungulates. We propose that relatively long faces in mammals relate to the utility of a long snout to aid in food prehension, placing the incisors (used for cropping or seizing prey) at a distance from the molars and so allowing for a greater reach, although this is then at the expense of the mechanical advantage of the bite force at the front of the jaw. This longer reach is important for mammals that cannot use, or have limited use of, their forelimbs to aid in feeding, and we show here that facial length can be correlated with the degree of forelimb mobility. The wider gape potentially afforded by a longer face may be of utility to canids in grasping prey, but in ungulates their gape is limited by their cranial design and musculature. Across the range of mammals studied, the long-faced ungulates have the least degree of forelimb mobility, with long-faced canids being somewhat similar, and short-faced primates the greatest degree of mobility. However, felids (with an intermediate degree of forelimb mobility) have the shortest faces,

likely because of their need for a high mechanical advantage at the canines for their predatory lifestyle.

We consider our investigation to be a novel approach, with a novel explanation, for the reason why, among larger mammals, herbivorous forms have relatively longer faces than carnivores. The exceptions (e.g. long-faced canids, extinct shorter-faced kangaroos) are easily explained within the framework of a consideration of the degree of forelimb mobility. And, in conclusion, to answer the old joke: why *does* the horse have a long face? Because, no matter what its height, it doesn't have any hands.

## Acknowledgements

We thank the curators at several museums for providing access to specimens in their care, for photographs by the first author. Mark Omura and Judy Chupasko at the Museum of Comparative Zoology, Harvard University, USA; Eileen Westwig, Ross McPhee (Mammalogy), Judy Galkin and Jin Meng (Vertebrate Paleontology) at the American Museum of Natural History, New York, USA; David Stemmer (South Australian Museum, Adelaide, Australia). Funds to the first author from the Bushnell Foundation (Brown University) aided in the photographing of specimens in museum collections. Thanks to Emily Green at Science Graphic Design for drawing the bones in Figure 2, and to comments from two reviewers that helped to improve the manuscript.

## References

- Andersson, K. 2004: Elbow-joint morphology as a guide to forearm function and foraging behaviour in mammalian carnivores. — *Zoological Journal of the Linnean Society* 142: 91–104.
- Benoit, M. H. 2010: What's the difference? A multiphasic allometric analysis of fossil and living lions. — In: Goswami, A. & Frisca, A. (eds.), *Carnivorous evolution*: 165–188. Cambridge University Press, <https://doi.org/10.1017/CBO9781139193436.007>.
- Bicknevicus, A. R., Van Valkenburgh, B. & Walker, J. 1996: Incisor size and shape: implications for feeding behaviors in saber-toothed “cats”. — *Journal of Vertebrate Paleontology* 16: 510–531.
- Biewener, A. A. 2005: Biomechanical consequences of scaling. — *Journal of Experimental Biology* 208: 1665–1676, <https://doi.org/10.1242/jeb.10520>.
- Bishop, A. 1964: The use of the hands in lower primates. — In: Buettner-Janusch, J. (ed.), *Evolutionary and genetic biology of primates*: 122–225. Academic Press, New York.
- Cantalapiedra, J. L., Prado, J. L., Hernández Fernández, M. & Alberdi, M. T. 2017: Decoupled ecomorphological evolution and diversification in Neogene-Quaternary horses. — *Science* 355, 627–630, <https://doi.org/10.1126/science.aag1772>.
- Cardini, A. 2019: Craniofacial allometry is a rule in evolutionary radiations of placentals. — *Evolutionary Biology* 46: 239–248, <https://doi.org/10.1007/s11692-019-09477-7>.
- Cardini, A. & Polly, P. D. 2013: Larger mammals have longer faces because of size-related constraints on skull form. — *Nature Communications* 4: 1–7, <https://doi.org/10.1038/ncomms3458>.
- Cardini, A., Polly, D., Dawson, R. & Milne, N. 2015: Why the long face? Kangaroos and wallabies follow the same ‘rule’ of cranial evolutionary allometry (CREA) as placentals. — *Evolutionary Biology* 42: 169–176, <https://doi.org/10.1007/s11692-015-9308-9>.
- Evans, K. M., Bernt, M. J., Kolmann, M. A., Ford, K. L. & Albert, J. S. 2019: Why the long face? Static allometry in the sexually dimorphic phenotypes of Neotropical electric fishes. — *Zoological Journal of the Linnean Society* 186: 633–649, <https://doi.org/10.1093/zoolinnean/zly076>.
- Dick, T. J. M. & Clemente, C. J. 2017: Where have all the giants gone? How animals deal with the problem of size. — *PLoS Biology* 15, e2000473, <https://doi.org/10.1371/journal.pbio.2000473>.
- Emerson, S. B. & Bramble, D. M. 1993: Scaling, allometry, and skull design. — In: Hanken, J. & Hall, B. K. (eds.), *The skull*, vol. 3: *Functional and evolutionary mechanisms*: 384–421. University of Chicago Press, Chicago.
- Figueirido, B. & Janis, C. M. 2011: The predatory behaviour of the thylacine: Tasmanian tiger or marsupial wolf? — *Biology Letters* 7: 937–940, <https://doi.org/10.1098/rsbl.2011.0364>.
- Figueirido, B., Martín-Serra, A. & Janis, C. M. 2016: Ecomorphological determinations in the absence of living analogues: the predatory behavior of the marsupial lion (*Thylacoleo carnifex*) as revealed by elbow joint morphology. — *Paleobiology* 42: 508–531, <https://doi.org/10.1017/pab.2015.55>.
- Figueirido, B., Martín-Serra, A., Tseng, J. Z. & Janis, C. M. 2015: Habitat changes and changing predatory habits in North American fossil canids. — *Nature Communications* 6: 7976, <https://doi.org/10.1038/ncomms5976>.
- Gill, P. G., Purnell, M. A., Crumpton, N., Robson Brown, K., Gostling, N. J., Stamptononi, M. & Rayfield, E. J. 2014: Dietary specializations and diversity in feeding ecology of the earliest stem mammals. — *Nature* 512: 303–307, <https://doi.org/10.1038/nature13622>.
- Heck, L., Sanchez-Villagra, M. R. & Stange, M. 2019: Why the long face? Comparative shape analysis of miniature, pony, and other horse skulls reveals changes in ontogenetic growth. — *PeerJ* 7, e7678, <https://doi.org/10.7717/peerj/7678>.
- Herring, S. W. 1974: Adaptations for gape in the hippopotamus and its relatives. — *Forma et Functio* 8: 85–100.
- Herring, S. W. & Herring, S. E. 1974: The superficial masseter and gape in mammals. — *The American Naturalist*

- 108: 561–576.
- Hylander, W. L. 2013: The functional significance of canine reduction in early hominins. — *American Journal of Physical Anthropology* 150: 247–259, <https://doi.org/10.1002/ajpa.22195>.
- Iwaniuk, A. N. 1996: *An analysis of skilled forelimb movements in members of the Macropodoidea*. — B.Sc. (Honours) thesis, Monash University, Monash, Australia.
- Iwaniuk, A. N., Whishaw, I. & Nelson, J. E. 1998: Reaching, grasping and manipulation of food objects by two tree kangaroo species, *Dendrolagus lumholtzi* and *Dendrolagus matschiei*. — *Australian Journal of Zoology* 46: 235–248.
- Iwaniuk, A. N., Pellis, S. N. & Whishaw, I. Q. 1999: Brain size is not correlated with forelimb dexterity: a comparative test of the principle of proper mass. — *Brain, Behavior and Evolution* 54: 167–180.
- Iwaniuk, A. N., Pellis, S. N. & Whishaw, I. Q. 2000: The relative importance of body size, phylogeny, and diet in the evolution of forelimb dexterity in fissiped carnivores (Carnivora). — *Canadian Journal of Zoology* 78: 1110–1125.
- Janis, C. M. 1990: Correlation of cranial and dental variables with body size in ungulates and macropodoids. — In: Damuth, J. & MacFadden, B. J. (eds.), *Body size in mammalian paleobiology: estimation and biological implications*: 255–300. Cambridge University Press, New York.
- Janis, C. M. 2023: Asymmetry of evolutionary patterns between New World and Old World equids and among New World equine tribes. — In: Casanovas-Vilar, I., Janis, C. M., van den Hoek Ostende, L. W. & Saarinen, J. J. (eds.), *Evolution of Cenozoic land mammal faunas and ecosystems — 25 years of the NOW database of fossil mammals*: 143–164. Springer, New York.
- Janis, C. M. & Bernor, R. L. 2019: The evolution of equid monodactyly: a review including a new hypothesis. — *Frontiers in Ecology and Evolution* 7, 119, <https://doi.org/10.3389/fevo.2019.00119>.
- Janis, C. M. & Figueirido, B. 2014: Forelimb anatomy and the discrimination of predatory strategies in mammalian carnivores: the behavior of the thylacine as a case study. — *Journal of Morphology* 275: 1321–1338, <https://doi.org/10.1002/jmor.20303>.
- Janis, C. M. & Martín-Serra, A. 2020: Postcranial elements of small mammals as indicators of locomotion and habitat. — *PeerJ* 8, e9634, <https://doi.org/10.7717/peerj.9634>.
- Janis, C. M., Gordon, I. & Illius, A. 1994: Modelling equid/ruminant competition in the fossil record. — *Historical Biology* 8: 15–29.
- Janis, C. M., Napoli, J. G., Billingham, C. & Martín-Serra, A. 2020: Proximal humerus morphology indicates divergent patterns of locomotion in extinct giant kangaroos. — *Journal of Mammalian Evolution* 27: 627–647, <https://doi.org/10.1007/s10914-019-09494-5>.
- Jones, B., Martín-Serra, A., Rayfield, E. J. & Janis, C. M. 2022: Distal humeral morphology indicates locomotory divergence in extinct giant kangaroos. — *Journal of Mammalian Evolution* 29: 27–41, <https://doi.org/10.1007/s10914-021-09576-3>.
- Kubo, T., Sakamoto, M., Meade, A. & Venditti, V. 2019: Transitions between foot postures are associated with elevated rates of body size evolution in mammals. — *Proceedings of the National Academy of Sciences of the United States of America* 116: 2618–2623, <https://doi.org/10.1073/pnas.1814329116>.
- Laird, M. F., Polvadore, T. A., Hirschhorn, G. A., McKinney, J. C., Ross, C. F., Taylor, A. B., Terhune, C. E. & Iriarte-Diaz, J. 2024: Tradeoffs between bite force and gape in *Eulemur* and *Varecia*. — *Journal of Morphology* 285, e21699, <https://doi.org/10.1002/jmor.21699>.
- MacFadden, B. J. 1986: Fossil horses from ‘Eohippus’ (*Hyracotherium*) to *Equus*: scaling, Cope’s Law, and the evolution of body size. — *Paleobiology* 12: 355–369.
- Maynard Smith, J. & Savage, R. J. G. 1959: The mechanics of mammalian jaws. — *The School Science Review* 141: 289–301.
- Mitchell, D. R., Sherratt, M. & Weisbecker, V. 2024: Facing the facts: adaptive trade-offs along body size ranges determine mammalian craniofacial scaling. — *Biological Reviews* 99: 498–524, <https://doi.org/10.1101/2023.09.28.560051>.
- Mitchell, D. R., Sherratt, E., Ledogar, J. A. & Wroe, S. 2018: The biomechanics of foraging determines face length among kangaroos and their relatives. — *Proceedings of the Royal Society of London B* 285, 21080845, <https://doi.org/10.1098/rspb.2018.0845>.
- Morales-García, N. M., Gill, P. G., Janis, C. M. & Rayfield, E. J. 2021: Jaw shape and mechanical advantage are indicative of diet in Mesozoic mammals. — *Communications Biology* 4, 242, <https://doi.org/10.1038/s42003-021-01757-3>.
- Pancirolli, E., Janis, C., Stockdale, M. & Martín-Serra, A. 2017: Correlates between calcaneal morphology and locomotion in extant and extinct carnivorous mammals. — *Journal of Morphology* 278: 1333–1353, <https://doi.org/10.1002/jmor.20716>.
- Patel, B. A. 2009: Not so fast: Speed effects on forelimb kinematics in cercopithecine monkeys and implications for digitigrade postures in primates. — *American Journal of Biological Anthropology* 140: 92–112, <https://doi.org/10.1002/ajpa.21039>.
- Polly, P. D. 2007: Limbs in mammalian evolution. — In: Hall, B. K. (ed.), *Fins into limbs: evolution, development, and transformation*: 245–268. University of Chicago Press, Chicago.
- R Core Team 2023: *R: a language and environment for statistical computing*. — R Foundation for Statistical Computing, <https://www.R-project.org/>
- RStudio Team 2023: *RStudio: integrated development environment for R*. — RStudio, Inc., <http://www.rstudio.com/>; now Posit Software, PBC formerly RStudio, PBC, <https://posit.co/>.
- Radinsky, L. B. 1984: Ontogeny and phylogeny in horse skull evolution. — *Evolution* 38: 1–15.
- Radinsky, L. B. 1985: Approaches in morphology: a search for patterns. — *Annual Review of Ecology and Systematics* 16: 1–14.
- Richardson, W. 2021: *Investigating correlations between body size, face length and forelimb mobility in mammals*.

- M.Sc. thesis, University of Bristol, Bristol, UK.
- Richardson, W., Morales-García, N. M., Singh, S., Damuth, J. & Janis, C. M. 2024: Why the short face? The face lengths of sthenurine kangaroos scale with negative allometry. — *Journal of Vertebrate Paleontology*, <https://doi.org/10.1080/02724634.2024.2336145>.
- Scapino, R. P. 1972: Adaptive radiation of mammalian jaws. — In: Schumacher, G. H. (ed.), *Morphology of the maxilla-mandibular apparatus*: 33–39. VEB Georg Thieme, Leipzig.
- Shoemaker, L. & Clauset, A. 2014: Body mass evolution and diversification within horses (family Equidae). — *Ecology Letters* 7: 211–220, <https://doi.org/10.1111/ele.12221>.
- Silva, M. & Downing, J. A. 1995: *CRC handbook of mammalian body masses*. — CRC Press, Boca Raton.
- Slater, G. J. & Van Valkenburgh, B. 2009: Allometry and performance: the evolution of skull form and function in felids. — *Journal of Evolutionary Biology* 22: 2278–2287, <https://doi.org/10.1111/j.1420-9101.2009.01845.x>.
- Slater, G. J., Dumont, E. R. & Van Valkenburgh, B. 2009: Implications of predatory specialization for cranial form and function in canids. — *Journal of Zoology* 278: 181–188, <https://doi.org/10.1111/j.1469-7998.2009.00567.x>.
- Spencer, L. M. 1995: Morphological correlates of dietary resource partitioning in the African Bovidae. — *Journal of Mammalogy* 76: 448–471.
- Taskinen, S. & Warton, D. I. 2011: Robust estimation and inference for bivariate line-fitting in allometry. — *Biometrical Journal* 53: 652–672, <https://doi.org/10.1002/bimj.201000018>.
- Terhune, C. E., Hylander W. L., Vinyard, C. J. & Taylor, A. B. 2015. Jaw architecture and mandibular morphology influence maximum jaw gapes in the sexually dimorphic *Macaca fascicularis*. — *Journal of Human Evolution* 82: 145–158, <https://doi.org/10.1016/j.jhevol.2015.02.006>.
- Warton, D. I., Duursma, R. A., Falster, D. S. & Taskinen, S. 2012: Smatr 3 — an R package for estimation and inference about allometric lines. — *Methods in Ecology and Evolution* 3: 257–259, <https://doi.org/10.1111/j.2041-210X.2011.00143.x>.
- Warton, D. I., Wright, I. J., Falster, D. S. & Westoby, M. 2006: Bivariate line-fitting methods for allometry. — *Biological Reviews* 81: 259–291, <https://doi.org/10.1017/S1464793106007007>.
- Wells, R. T. & Nichol, B. 1977: On the manus and pes of *Thylacoleo carnifex* Owen (Marsupialia). — *Transactions of the Royal Society of South Australia* 101: 139–146.
- Wickham, H. 2016: *ggplot2: elegant graphics for data analysis*. — Springer-Verlag New York.
- Wickham, H., Averick, M., Bryan, J., Chang, W., McGowan, L. D., François, R., Grolemond, G., Hayes, A., Henry, L., Hester, J., Kuhn, M., Pedersen, T. L., Miller, E., Bache, S. M., Müller, K., Ooms, J., Robinson, D., Seidel, D. P., Spinu, V., Takahashi, K., Vaughan, D., Wilke, C., Woo, K. & Yutani, H. 2019: Welcome to the tidyverse. — *Journal of Open Source Software* 4, 1686, <https://doi.org/10.21105/joss.01686>.
- Whishaw, I. Q., Sarna, J. R. & Pellis, S. M. 1998: Rodent-typical and species-specific limb use in eating: evidence for specialized paw use from a comparative analysis of ten species. — *Behavioural Brain Research* 96: 79–91.
- Wood, A. R., Behej, R. M., Manz, C. L., Begun, D. L. & Gingerich, P. D. 2011: Postcranial functional morphology of *Hyracotherium* (Equidae, Perissodactyla) and locomotion in the earliest horses. — *Journal of Mammalian Evolution* 18: 1–32, <https://doi.org/10.1007/s10914-010-9145>.

**Appendix 1.** Taxa with the tooth row length (TRL) and body mass used in paper; sex given after the species name (in parentheses) for cercopithecids only: F = female, M = male, U = unknown. † before the genus name = genus extinct, ‡ before the species name = species extinct but other species in the genus extant.

Species	Family	Subfamily	Specimen	TRL (mm)	Body mass (kg)
<i>Aepyceros melampus</i>	Bovidae	Antilopinae	MCZ 8203	159	55
<i>Alcelaphus buselaphus</i>	Bovidae	Antilopinae	MCZ 13675	221	170
<i>Capra sibirica</i>	Bovidae	Antilopinae	MCZ 25354	139	80
<i>Cephalophus callipygus</i>	Bovidae	Antilopinae	MSUM 34351	123	20
<i>Cephalophus dorsalis</i>	Bovidae	Antilopinae	MSUM 34344	108	12
<i>Cephalophus leucogaster</i>	Bovidae	Antilopinae	MSUM 34347	113	16
<i>Cephalophus niger</i>	Bovidae	Antilopinae	MSUM 15248	88	17
<i>Cephalophus nigrifrons</i>	Bovidae	Antilopinae	MSUM 34353	116	15
<i>Cephalophus silvicultor</i>	Bovidae	Antilopinae	MSUM 34523	174	70
<i>Cephalophus zebra</i>	Bovidae	Antilopinae	UMMZ 176798	96	18
<i>Connochaetes taurinus</i>	Bovidae	Antilopinae	MCZ 13677	232	250
<i>Damaliscus lunatus</i>	Bovidae	Antilopinae	UMMZ 124070	216	120
<i>Damaliscus pygargus</i>	Bovidae	Antilopinae	MCZ 34497	171	70
<i>Eudorcas thomsonii</i>	Bovidae	Antilopinae	MCZ 21225	110	30

*continued*

## Appendix 1. Continued.

Species	Family	Subfamily	Specimen	TRL (mm)	Body mass (kg)
<i>Gazella dorcas</i>	Bovidae	Antilopinae	UMMZ 161037	94	17
<i>Gazella gazella</i>	Bovidae	Antilopinae	MSUM 4596	95	25
<i>Gazella subgutturosa</i>	Bovidae	Antilopinae	UMMZ 170470	104	40
<i>Hippotragus equinus</i>	Bovidae	Antilopinae	MCZ 1531	260	265
<i>Kobus defassa</i>	Bovidae	Antilopinae	MCZ 5089	237	240
<i>Kobus kob</i>	Bovidae	Antilopinae	MSUM 2721	145	110
<i>Kobus leche</i>	Bovidae	Antilopinae	MCZ 51752	147	110
<i>Litocranius walleri</i>	Bovidae	Antilopinae	ZFMK_MAM_1936.0055	100	48
<i>Madoqua kirkii</i>	Bovidae	Antilopinae	MCZ 8073	56	5
<i>Naemorhedus goral</i>	Bovidae	Antilopinae	MCZ 34501	120	28
<i>Nanger dama</i>	Bovidae	Antilopinae	UMMZ	134	65
<i>Nanger granti</i>	Bovidae	Antilopinae	UMMZ 163805	134	55
<i>Neotragus batesi</i>	Bovidae	Antilopinae	UMMZ 39516	54	2.5
<i>Oreamnos americanus</i>	Bovidae	Antilopinae	UMMZ 60546	146	70
<i>Oreotragus oreotragus</i>	Bovidae	Antilopinae	MCZ 8086	93	15
<i>Oryx beisa</i>	Bovidae	Antilopinae	UMMZ 124570	228	79
<i>Oryx dammah</i>	Bovidae	Antilopinae	UMMZ 170468	219	200
<i>Ourebia ourebi</i>	Bovidae	Antilopinae	MCZ 5011	99	20
<i>Ovibos moschatus</i>	Bovidae	Antilopinae	UMMZ 112377	255	330
<i>Ovis canadensis</i>	Bovidae	Antilopinae	UMMZ 102446	153	95
<i>Philantomba monticola</i>	Bovidae	Antilopinae	MSUM 34339	72	5
<i>Raphicerus campestris</i>	Bovidae	Antilopinae	MCZ 23070	82	12
<i>Redunca arundinum</i>	Bovidae	Antilopinae	MSUM3969	152	58
<i>Rupicapra rupicapra</i>	Bovidae	Antilopinae	MCZ 29676	133	40
<i>Sylvicapra grimmia</i>	Bovidae	Antilopinae	MCZ 42715	85	22
<i>Boselaphus tragocamelus</i>	Bovidae	Bovidae	AMNH 21511	245	210
<i>Taurotragus derbianus</i>	Bovidae	Bovidae	FMNH 63858	269	800
<i>Tetracerus quadricornis</i>	Bovidae	Bovidae	NHM 56.9.22.11	106	20
<i>Tragelaphus imberbis</i>	Bovidae	Bovidae	MCZ 23999	168	85
<i>Tragelaphus scriptus</i>	Bovidae	Bovidae	MCZ 31972	133	60
<i>Tragelaphus strepsiceros</i>	Bovidae	Bovidae	MCZ 13675	201	280
<i>Alces alces</i>	Cervidae	Capreolinae	MCZ 1736	354	500
<i>Blastocerus dichotomus</i>	Cervidae	Capreolinae	MCZ 35553	174	110
<i>Capreolus capreolus</i>	Cervidae	Capreolinae	MCZ 8315	115	28
<i>Hippocamelus bisulcus</i>	Cervidae	Capreolinae	MCZ 15315	154	70
<i>Hydropotes inermis</i>	Cervidae	Capreolinae	CAS:MAMM 9676	109	16
<i>Mazama americana</i>	Cervidae	Capreolinae	MCZ 20007	122	40
<i>Mazama gouazoubira</i>	Cervidae	Capreolinae	ZIN RAS O.2359	93	20
<i>Odocoileus virginianus</i>	Cervidae	Capreolinae	MCZ 1674	164	68
<i>Ozotoceras bezoarticus</i>	Cervidae	Capreolinae	MCZ 29058	127	35
<i>Pudu puda</i>	Cervidae	Capreolinae	MCZ 6029	88	10
<i>Rangifer tarandus</i>	Cervidae	Capreolinae	MCZ 21956	216	280
<i>Axis porcinus</i>	Cervidae	Cervinae	MCZ 1816	125	45
<i>Cervus elaphus</i>	Cervidae	Cervinae	MCZ 30231	267	330
<i>Cervus nippon</i>	Cervidae	Cervinae	DKY 0143	139	64
<i>Dama dama</i>	Cervidae	Cervinae	HMG NH.0.419	135	65
<i>Elaphurus davidianus</i>	Cervidae	Cervinae	MCZ 8733	246	186
<i>Muntiacus muntjac</i>	Cervidae	Cervinae	MCZ 35918	133	30
<i>Rucervus duvaucelli</i>	Cervidae	Cervinae	AMNH 54496	222	178
<i>Rusa unicolor</i>	Cervidae	Cervinae	MCZ 35924	218	220
† <i>Hyracotherium</i> sp. <sup>1</sup>	Equidae	Hyracotheriinae	AM 55986	80	8 <sup>a</sup>
† <i>Hyracotherium vasacciense</i> <sup>2</sup>	Equidae	Hyracotheriinae	AM 4832	87	10 <sup>a</sup>
† <i>Orohippus pumilis</i> <sup>3</sup>	Equidae	Hyracotheriinae	AM11625	66	8 <sup>a</sup>

continued

## Appendix 1. Continued.

Species	Family	Subfamily	Specimen	TRL (mm)	Body mass (kg)
† <i>Anchitherium clarencei</i>	Equidae	Anchitheriinae	AMNH 22684	199	132 <sup>b</sup>
† <i>Archaeohippus penultimus</i>	Equidae	Anchitheriinae	FAM61659	112	44 <sup>c</sup>
† <i>Desmatippus</i> sp.	Equidae	Anchitheriinae	F:AM 11818	186	135 <sup>b</sup>
† <i>Meshippus bairdii</i>	Equidae	Anchitheriinae	F:AM 74001	103	36 <sup>c</sup>
† <i>Miohippus obiquidens</i>	Equidae	Anchitheriinae	F:AM116328	117	54 <sup>d</sup>
† <i>Hypohippus equinus</i>	Equidae	Anchitheriinae	YPM-PU 11623	294	200 <sup>e</sup>
† <i>Kalobatippus agatensis</i>	Equidae	Anchitheriinae	F:AM 83200	199	160 <sup>e</sup>
† <i>Megahippus matthewi</i>	Equidae	Anchitheriinae	F:AM 60700	266	266 <sup>b</sup>
† <i>Parahippus leonensis</i>	Equidae	Anchitheriinae	AM 39578	152	70 <sup>c</sup>
† <i>Calippus martini</i>	Equidae	Equinae	F:AM 114159	219	120 <sup>f</sup>
† <i>Cormohipparion occidentale</i>	Equidae	Equinae	F:AM 119074	215	161 <sup>g</sup>
<i>Equus asinus</i>	Equidae	Equinae	AMNH 20410	189	165 <sup>h</sup>
<i>Equus grevyi</i>	Equidae	Equinae	AMNH 82036	254	341 <sup>h</sup>
<i>Equus hemionus</i>	Equidae	Equinae	AMNH 57212	209	230 <sup>h</sup>
<i>Equus zebra</i>	Equidae	Equinae	AMNH 82319	235	247 <sup>h</sup>
† <i>Dinohippus leidyana</i>	Equidae	Equinae	AM 17224	262	175 <sup>g</sup>
† <i>Hippidion neogaenum</i>	Equidae	Equinae	AM 11872	336	462 <sup>g</sup>
† <i>Merychippus primus</i>	Equidae	Equinae	F:AM 111119	152	104 <sup>g</sup>
† <i>Merychippus sejunctus</i>	Equidae	Equinae	F:AM 111119	194	86 <sup>b</sup>
† <i>Nannippus lenticularis</i>	Equidae	Equinae	AM 127969	230	159 <sup>f</sup>
† <i>Neohipparion coloradense</i>	Equidae	Equinae	F:AM 69503	261	247 <sup>g</sup>
† <i>Pliohippus pernix</i>	Equidae	Equinae	F:AM 60800	241	215 <sup>g</sup>
† <i>Protohippus simus</i>	Equidae	Equinae	F:AM 60353	245	206 <sup>g</sup>
† <i>Pseudohipparion retrusum</i>	Equidae	Equinae	F:AM 50005	181	103 <sup>g</sup>
<i>Canis aureus</i>	Canidae	Caninae	UMMZ 101191	77	9.5
<i>Canis latrans</i>	Canidae	Caninae	UMMZ 82499	91	18
<i>Canis lupus</i>	Canidae	Caninae	UMMZ 60914	121	60
<i>Canis mesomelas</i>	Canidae	Caninae	UMMZ 163807	77	8
<i>Canis rufus</i>	Canidae	Caninae	UMMZ 111222	111	30
<i>Cerdocyon thous</i>	Canidae	Caninae	UMMZ 126121	73	7
<i>Chrysocyon brachyurus</i>	Canidae	Caninae	UMMZ 170489	119	22
<i>Cuon alpinus</i>	Canidae	Caninae	IOZ 26747	84	20
<i>Lycalopex culpaeus</i>	Canidae	Caninae	UMMZ 157157	94	12
<i>Lycalopex griseus</i>	Canidae	Caninae	UMMZ 165626	67	3
<i>Lycalopex gymnocercus</i>	Canidae	Caninae	UMMZ 124458	67	5
<i>Lycaon pictus</i>	Canidae	Caninae	FMNH 33478	100	30
<i>Nyctereutes procyonoides</i>	Canidae	Caninae	UMMZ 115808	49	7
<i>Speothos venaticus</i>	Canidae	Caninae	UMMZ 115805	59	6
<i>Urocyon cinereoargenteus</i>	Canidae	Caninae	UMMZ 123396	61	7
<i>Vulpes velox</i>	Canidae	Caninae	UMMZ 88064	55	2.5
<i>Vulpes vulpes</i>	Canidae	Caninae	UMMZ 57756	81	12
<i>Vulpes zerda</i>	Canidae	Caninae	UMMZ 159320	42	1
<i>Acinonyx jubatus</i>	Felidae	Felinae	UMMZ 114800	56	55
<i>Caracal caracal</i>	Felidae	Felinae	UMMZ 166222	42	15
<i>Felis catus</i>	Felidae	Felinae	UMMZ 88418	30	5
<i>Felis chaus</i>	Felidae	Felinae	UMMZ 122370	39	12
<i>Felis manul</i>	Felidae	Felinae	UMMZ 177415	28	4
<i>Felis margarita</i>	Felidae	Felinae	UMMZ 118429	24	2.5
<i>Felis silvestris</i>	Felidae	Felinae	UMMZ 24293	35	4.5
<i>Leopardus geoffroyi</i>	Felidae	Felinae	UMMZ 146504	31	6
<i>Leopardus guigna</i>	Felidae	Felinae	MSUM 2116	29	2.5
<i>Leopardus pardalis</i>	Felidae	Felinae	UMMZ 79533	42	13
<i>Leopardus tigrinus</i>	Felidae	Felinae	UMMZ 64041	25	2

continued

## Appendix 1. Continued.

Species	Family	Subfamily	Specimen	TRL (mm)	Body mass (kg)
<i>Leopardus weidii</i>	Felidae	Felinae	UMMZ 126123	29	3.5
<i>Leptailurus serval</i>	Felidae	Felinae	FMNH 18862	42	14
<i>Lynx canadensis</i>	Felidae	Felinae	UMMZ 98131	51	12
<i>Lynx lynx</i>	Felidae	Felinae	MSUM 3483	61	30
<i>Lynx rufus</i>	Felidae	Felinae	UMMZ 173510	50	13
<i>Panthera leo</i>	Felidae	Felinae	UMMZ 114804	111	220
<i>Panthera onca</i>	Felidae	Felinae	UMMZ 76743	85	110
<i>Panthera pardus</i>	Felidae	Felinae	BM Aa1819	87	50
<i>Panthera tigris</i>	Felidae	Felinae	UMMZ 167640	109	340
<i>Prionailurus bengalensis</i>	Felidae	Felinae	UMMZ 161319	27	6
<i>Prionailurus viverrinus</i>	Felidae	Felinae	MSUM 37636	46	10
<i>Puma concolor</i>	Felidae	Felinae	UMMZ 56590	68	90
<i>Puma yagouaroundi</i>	Felidae	Felinae	UMMZ 146505	27	7
<i>Uncia uncia</i>	Felidae	Felinae	UMMZ 157859	71	70
<i>Helarctos melayanus</i>	Ursidae	Ursinae	FMNH 54316	94	60
<i>Melursus ursinus</i>	Ursidae	Ursinae	BM Ab4169	122	100
<i>Ursus americanus</i>	Ursidae	Ursinae	UMMZ 60907	110	350
<i>Ursus arctos</i>	Ursidae	Ursinae	BM Aa4034	156	500
<i>Ursus maritimus</i>	Ursidae	Ursinae	UMMZ 100779	150	700
<i>Ursus thibetanus</i>	Ursidae	Ursinae	BM Ab4150	105	120
<i>Ailurus fulgens</i>	Ailuridae	Aliurinae	NHMUK 22.9.1.38	57	5
<i>Bassaricyon gabbii</i>	Procyonidae	Procyoninae	UMMZ 112322	34	1.3
<i>Bassaricyon neblina</i>	Procyonidae	Procyoninae	FMNH 88476	32	1.4
<i>Bassariscus astutus</i>	Procyonidae	Procyoninae	UMMZ 63902	35	1.1
<i>Bassariscus sumichrasti</i>	Procyonidae	Procyoninae	UMMZ 114646	35	0.9
<i>Potos flavus</i>	Procyonidae	Procyoninae	UMMZ 114645	33	4
<i>Procyon cancrivorus</i>	Procyonidae	Procyoninae	UMMZ 146502	59	5
<i>Procyon lotor</i>	Procyonidae	Procyoninae	UMMZ 98905	52	8
<i>Cercopithecus cephus</i> (U)	Cercopithecidae	Cercopithecinae	UMMZ 39508	30	4
<i>Cercopithecus dryas</i> (M)	Cercopithecidae	Cercopithecinae	YP MAM 16890	32	3
<i>Cercopithecus mitis</i> (M)	Cercopithecidae	Cercopithecinae	AMNH 36386	40	5
<i>Cercopithecus mona</i> (U)	Cercopithecidae	Cercopithecinae	UMMZ 85350	35	5
<i>Cercopithecus neglectus</i> (U)	Cercopithecidae	Cercopithecinae	MSUM 29074	47	6
<i>Chlorocebus sabaues</i> (U)	Cercopithecidae	Cercopithecinae	BM Ag1153	38	6.5
<i>Erythrocebus patas</i> (F)	Cercopithecidae	Cercopithecinae	DKY 2683	45	8.8
<i>Lophocebus albigena</i> (M)	Cercopithecidae	Cercopithecinae	FMNH 27537	51	8
<i>Macaca fascicularis</i> (F)	Cercopithecidae	Cercopithecinae	UMMZ 161311	43	6
<i>Macaca fuscata</i> (M)	Cercopithecidae	Cercopithecinae	DKY 0639	53	11
<i>Macaca mulatta</i> (M)	Cercopithecidae	Cercopithecinae	FMNH 99669	38	8
<i>Papio anubis</i> (M)	Cercopithecidae	Cercopithecinae	FMNH 27277	102	22
<i>Papio cynocephalus</i> (U)	Cercopithecidae	Cercopithecinae	BM Aa4353	86	23
<i>Papio hamadryas</i> (M)	Cercopithecidae	Cercopithecinae	DKY 1075	79	20
<i>Theropithecus gelada</i> (M)	Cercopithecidae	Cercopithecinae	AMNH 60568	73	18
<i>Lagostrophus fasciatus</i>	Macropodidae	Lagostrophinae	AMNH 197003	35	1.7
<i>Dendrolagus dorianus</i>	Macropodidae	Macropodinae	NHM 1939.2938	54	8.8
<i>Dendrolagus goodfellowi</i>	Macropodidae	Macropodinae	NHM 1950.1429	49	6.7
<i>Dendrolagus inustus</i>	Macropodidae	Macropodinae	NHM 1939.4152	62	12
<i>Dendrolagus mayri</i>	Macropodidae	Macropodinae	NHM 1939.2931	58	9.3
<i>Dorcopsis hageni</i>	Macropodidae	Macropodinae	NHM 1922.2.2.63	72	5.5
<i>Dorcopsis muelleri</i>	Macropodidae	Macropodinae	NHM 1946.691	64	9
<i>Dorcopsulus vanheurni</i>	Macropodidae	Macropodinae	NHM 1922.2.264	43	1.8
<i>Dorcopsulus maclaeyi</i>	Macropodidae	Macropodinae	AMNH 104086	42	4
<i>Lagorchestes hirsutus</i>	Macropodidae	Macropodinae	NHM 1906.10.5.18	37	1.7

continued

## Appendix 1. Continued.

Species	Family	Subfamily	Specimen	TRL (mm)	Body mass (kg)
<i>Lagorchestes conspicillatus</i>	Macropodidae	Macropodinae	AMNH 196976	43	3.1
<i>Lagorchestes †leporides</i> <sup>4</sup>	Macropodinae	Macropodinae	NHM 1841.1128	39	3
<i>Macropus fuliginosus</i>	Macropodidae	Macropodinae	AMNH 107371	113	50
<i>Macropus giganteus</i>	Macropodidae	Macropodinae	NHM 1846.3.17.13	115	65
<i>Notamacropus agilis</i>	Macropodidae	Macropodinae	NHM 1841.1130	79	16
<i>Notamacropus eugenii</i>	Macropodidae	Macropodinae	AMNH 197524	58	6
<i>Notamacropus †greyi</i> <sup>a</sup>	Macropodidae	Macropodinae	AMNH 197114	69	13
<i>Notamacropus irma</i>	Macropodidae	Macropodinae	WAM M15830	58	8
<i>Onychogalea fraenata</i>	Macropodidae	Macropodinae	NHM 1897.4.12.1	47	5
<i>Onychogalea unguifera</i>	Macropodidae	Macropodinae	NHM 1923.1.5.19	60	7.5
<i>Osphranter robustus</i>	Macropodidae	Macropodinae	NHM 1922.12.29.9	107	45
<i>Osphranter rufus</i>	Macropodidae	Macropodinae	NHM 5.4.1.5	111	70
<i>Petrogale burbidgei</i>	Macropodidae	Macropodinae	NHM 1925.12.3.1	48	1.3
<i>Petrogale brachyotis</i>	Macropodidae	Macropodinae	AMNH 106256	48	4.5
<i>Petrogale godmani</i>	Macropodidae	Macropodinae	NHM 1928.10.1.4	56	7
<i>Petrogale herberti</i>	Macropodidae	Macropodinae	AMNH 65217	56	6
<i>Petrogale lateralis</i>	Macropodidae	Macropodinae	NHM 1866.4.23.1	53	4.6
<i>Petrogale wilkinsi</i>	Macropodidae	Macropodinae	AMNH 65127	48	3
<i>Setonix brachyurus</i>	Macropodidae	Macropodinae	NHM 1844.2.15.3	42	3.2
<i>Thylogale brunii</i>	Macropodidae	Macropodinae	NHM 1841.1155	56	4
<i>Thylogale billardeirii</i>	Macropodidae	Macropodinae	NHM 44.7.2.1	62	6.5
<i>Thylogale stigmatica</i>	Macropodidae	Macropodinae	MV C17342	59	5.1
<i>Wallabia bicolor</i>	Macropodidae	Macropodinae	NHM 1846.4.25.14	74	15

<sup>1</sup>a little smaller than *Hyracotherium vasacciense*, <sup>2</sup>same size as *Hyracotherium grangeri*, <sup>3</sup>same size as *Hyracotherium* sp., <sup>4</sup>recently extinct macropodid.

Body mass from AnimalDiversity.org except for <sup>a</sup>Wood *et al.* 2011, <sup>b</sup>Shoemaker & Clauset 2014, <sup>c</sup>Janis 1990, <sup>d</sup>MacFadden 1986, <sup>e</sup>Janis *et al.* 1994, <sup>f</sup>Cantalapiedra *et al.* 2017, <sup>g</sup>Janis 2023, <sup>h</sup>Silva & Downing 1995.

Museum abbreviations: AMNH = American Museum of Natural History (New York, USA); BM = Bristol Museum (Bristol, UK); CAS = California Academy of Sciences (San Francisco, USA); DKY = Dokkyo Medical University (Mibu, Japan); F:AM = Frick collection, American Museum of Natural History; FMNH = Field Museum of Natural History (Chicago, USA); HMG NH = Horniman Museum and Gardens (London, UK); IOZ = Institute of Zoology, Chinese Academy of Sciences (Beijing, China); MCZ = Museum of Comparative Zoology, Harvard University (Cambridge, UK); MSUM = Michigan State University Museum (East Lansing, USA); NHMUK - Natural History Museum (London, UK); MV = Museum Victoria (Melbourne, Australia); UMMZ = University of Michigan Museum of Zoology (Ann Arbor, USA); YPM MAM = Yale Peabody Museum, Department of Mammalogy, Yale University (New Haven, USA); YPM-PU = Yale Peabody Museum, Princeton collections (Paleontology), Yale University (New Haven, USA); WAM = Western Australian Museum (Perth, Australia); ZFMK-MAM = Zoological Research Museum Alexander Koenig (Bonn, Germany); ZIN-RA = Zoological Institute of the Russian Academy of Sciences (St. Petersburg, Russia).

**Appendix 2.** Taxa designations of forelimb mobility (FMI) and corresponding anatomy. **LOCOMOTION:** A = arboreal, C = cursorial, C/S = mainly cursorial but can occasionally climb (felids only), HC = highly cursorial, S = scansorial, T = terrestrial (large, never/rarely climb), T (Aq) = terrestrial (semiaquatic) (polar bear only, not highly modified for swimming). Note that most macropodids could be considered as cursorial or highly cursorial, but only when hopping bipedally; the quadrupedal gait using the forelimbs is considered here. **FOOT POSTURE:** Ung = unguligrade, SemiUng = SemiUnguligrade (with foot pad), Dig = Digitigrade, SemiDig = Semidigitigrade (primates only, digitigrade forelimbs only), Pla = Plantigrade; note that all macropodids have highly specialized hindlimbs, and hop with a digitigrade stance, only forelimbs considered here. **METACARPALS:** Number = number of digits; 3R = lateral and medial metapodials reduced, 4R = first metacarpal greatly reduced; First letter = compression of metacarpals; F = fused, HC = highly compressed, MC = moderately compressed, C = compressed, NC = not compressed; Second letter = elongation of metacarpals; EE = extremely elongated, VHE = very highly elongated, HE = highly elongated, E = elongated, ME = moderately elongated, NE = not elongated. **SHOULDER MOBILITY** (from proximal humeral head shape and observed behaviour): NA/A = no ability for abduction/adduction, LA/A = little ability for abduction/adduction, SA/A = some ability for abduction/adduction, MA/A = moderate ability for abduction/adduction, HA/A = high ability for abduction/adduction. **ELBOW MOBILITY** (from proximal humeral articular surface shape and observed behaviour, plus information from Figueirido *et al.* 2016); NS = no ability for supination, LS = little ability for supination, MS = moderate ability for supination, GS = good ability for supination. Locomotor categories from a diversity of sources, including Figueirido *et al.* 2016, Janis *et al.* 2020, Jones & Janis 2022, Iwaniuk *et al.* 2000. Foot posture and metapodial anatomy categories from observations of museum specimens by CMJ. Shoulder mobility categories from Janis *et al.* 2020 (for ungulates, from observations of bones by CMJ). Elbow mobility categories from Figueirido *et al.* 2016, Jones & Janis 2022 (for ungulates, from observations of bones by CMJ). † before the genus name = genus extinct, ‡ before the species name = species extinct but other species in the genus extant.

Species	Family	FMI	Locomotion	Foot posture	Metacarpals	Shoulder mobility	Elbow mobility
<i>Aepyceros melampus</i>	Bovidae	1	HC	Ung	2, F, EE	NA/A	NS
<i>Aicelaphus buselaphus</i>	Bovidae	1	HC	Ung	2, F, EE	NA/A	NS
<i>Capra sibirica</i>	Bovidae	1	HC	Ung	2, F, EE	NA/A	NS
<i>Cephalophus callipygus</i>	Bovidae	1	HC	Ung	2, F, EE	NA/A	NS
<i>Cephalophus dorsalis</i>	Bovidae	1	HC	Ung	2, F, EE	NA/A	NS
<i>Cephalophus leucogaster</i>	Bovidae	1	HC	Ung	2, F, EE	NA/A	NS
<i>Cephalophus niger</i>	Bovidae	1	HC	Ung	2, F, EE	NA/A	NS
<i>Cephalophus nigrifrons</i>	Bovidae	1	HC	Ung	2, F, EE	NA/A	NS
<i>Cephalophus silvicultor</i>	Bovidae	1	HC	Ung	2, F, EE	NA/A	NS
<i>Cephalophus zebra</i>	Bovidae	1	HC	Ung	2, F, EE	NA/A	NS
<i>Connochaetes taurinus</i>	Bovidae	1	HC	Ung	2, F, EE	NA/A	NS
<i>Damaliscus lunatus</i>	Bovidae	1	HC	Ung	2, F, EE	NA/A	NS
<i>Damaliscus pygargus</i>	Bovidae	1	HC	Ung	2, F, EE	NA/A	NS
<i>Eudorcas thomsonii</i>	Bovidae	1	HC	Ung	2, F, EE	NA/A	NS
<i>Gazella dorcas</i>	Bovidae	1	HC	Ung	2, F, EE	NA/A	NS
<i>Gazella gazella</i>	Bovidae	1	HC	Ung	2, F, EE	NA/A	NS
<i>Gazella subgutturosa</i>	Bovidae	1	HC	Ung	2, F, EE	NA/A	NS
<i>Hippotragus equinus</i>	Bovidae	1	HC	Ung	2, F, EE	NA/A	NS
<i>Kobus defassa</i>	Bovidae	1	HC	Ung	2, F, EE	NA/A	NS
<i>Kobus kob</i>	Bovidae	1	HC	Ung	2, F, EE	NA/A	NS
<i>Kobus leche</i>	Bovidae	1	HC	Ung	2, F, EE	NA/A	NS
<i>Litocranius walleri</i>	Bovidae	1	HC	Ung	2, F, EE	NA/A	NS
<i>Madoqua kirkii</i>	Bovidae	1	HC	Ung	2, F, EE	NA/A	NS
<i>Naemorhedus goral</i>	Bovidae	1	HC	Ung	2, F, EE	NA/A	NS
<i>Nanger dama</i>	Bovidae	1	HC	Ung	2, F, EE	NA/A	NS
<i>Nanger granti</i>	Bovidae	1	HC	Ung	2, F, EE	NA/A	NS
<i>Neotragus batesi</i>	Bovidae	1	HC	Ung	2, F, EE	NA/A	NS
<i>Oreamnos americanus</i>	Bovidae	1	HC	Ung	2, F, EE	NA/A	NS
<i>Oreotragus oreotragus</i>	Bovidae	1	HC	Ung	2, F, EE	NA/A	NS
<i>Oryx beisa</i>	Bovidae	1	HC	Ung	2, F, EE	NA/A	NS
<i>Oryx dammah</i>	Bovidae	1	HC	Ung	2, F, EE	NA/A	NS
<i>Ourebia ourebi</i>	Bovidae	1	HC	Ung	2, F, EE	NA/A	NS
<i>Ovibos moschatus</i>	Bovidae	1	HC	Ung	2, F, EE	NA/A	NS

continued

## Appendix 2. Continued.

Species	Family	FMI	Locomotion	Foot posture	Metacarpals	Shoulder mobility	Elbow mobility
<i>Ovis canadensis</i>	Bovidae	1	HC	Ung	2, F, EE	NA/A	NS
<i>Philantomba monticola</i>	Bovidae	1	HC	Ung	2, F, EE	NA/A	NS
<i>Raphicerus campestris</i>	Bovidae	1	HC	Ung	2, F, EE	NA/A	NS
<i>Redunca arundinum</i>	Bovidae	1	HC	Ung	2, F, EE	NA/A	NS
<i>Rupicapra rupicapra</i>	Bovidae	1	HC	Ung	2, F, EE	NA/A	NS
<i>Sylvicapra grimmia</i>	Bovidae	1	HC	Ung	2, F, EE	NA/A	NS
<i>Boselaphus tragocamelus</i>	Bovidae	1	HC	Ung	2, F, EE	NA/A	NS
<i>Taurotragus derbianus</i>	Bovidae	1	HC	Ung	2, F, EE	NA/A	NS
<i>Tetracerus quadricornis</i>	Bovidae	1	HC	Ung	2, F, EE	NA/A	NS
<i>Tragelaphus imberbis</i>	Bovidae	1	HC	Ung	2, F, EE	NA/A	NS
<i>Tragelaphus scriptus</i>	Bovidae	1	HC	Ung	2, F, EE	NA/A	NS
<i>Tragelaphus strepsiceros</i>	Bovidae	1	HC	Ung	2, F, EE	NA/A	NS
<i>Alces alces</i>	Cervidae	1	HC	Ung	2, F, EE	NA/A	NS
<i>Blastocerus dichotomus</i>	Cervidae	1	HC	Ung	2, F, EE	NA/A	NS
<i>Capreolus capreolus</i>	Cervidae	1	HC	Ung	2, F, EE	NA/A	NS
<i>Hippocamelus bisulcus</i>	Cervidae	1	HC	Ung	2, F, EE	NA/A	NS
<i>Hydropotes inermis</i>	Cervidae	1	HC	Ung	2, F, EE	NA/A	NS
<i>Mazama americana</i>	Cervidae	1	HC	Ung	2, F, EE	NA/A	NS
<i>Mazama gouazoubira</i>	Cervidae	1	HC	Ung	2, F, EE	NA/A	NS
<i>Odocoileus virginianus</i>	Cervidae	1	HC	Ung	2, F, EE	NA/A	NS
<i>Ozotoceras bezoarticus</i>	Cervidae	1	HC	Ung	2, F, EE	NA/A	NS
<i>Pudu puda</i>	Cervidae	1	HC	Ung	2, F, EE	NA/A	NS
<i>Rangifer tarandus</i>	Cervidae	1	HC	Ung	2, F, EE	NA/A	NS
<i>Axis porcinus</i>	Cervidae	1	HC	Ung	2, F, EE	NA/A	NS
<i>Cervus elaphus</i>	Cervidae	1	HC	Ung	2, F, EE	NA/A	NS
<i>Cervus nippon</i>	Cervidae	1	HC	Ung	2, F, EE	NA/A	NS
<i>Dama dama</i>	Cervidae	1	HC	Ung	2, F, EE	NA/A	NS
<i>Elaphurus davidianus</i>	Cervidae	1	HC	Ung	2, F, EE	NA/A	NS
<i>Muntiacus muntjac</i>	Cervidae	1	HC	Ung	2, F, EE	NA/A	NS
<i>Rucervus duvaucelli</i>	Cervidae	1	HC	Ung	2, F, EE	NA/A	NS
<i>Rusa unicolor</i>	Cervidae	1	HC	Ung	2, F, EE	NA/A	NS
† <i>Hyracotherium</i> sp.	Equidae	3	C	SubUng	4, C, HE	LA/A	LS
† <i>Hyracotherium vasacciense</i>	Equidae	3	C	SubUng	4, C, HE	LA/A	LS
† <i>Orohippus pumilis</i>	Equidae	3	C	SubUng	4, C, HE	LA/A	LS
† <i>Anchitherium clarencei</i>	Equidae	2	HC	Ung	3R, HC, EE	NA/A	NS
† <i>Archaeohippus penultimus</i>	Equidae	1	HC	Ung	3R, HC, EE	NA/A	NS
† <i>Desmatippus</i> sp.	Equidae	1	HC	Ung	3R, HC, EE	NA/A	NS
† <i>Mesohippus bairdii</i>	Equidae	2	HC	SubUng	3R, HC, EE	NA/A	NS
† <i>Miohippus obliquens</i>	Equidae	2	HC	SubUng	3R, HC, EE	NA/A	NS
† <i>Hypohippus equinus</i>	Equidae	2	HC	SubUng	3R, HC, EE	NA/A	NS
† <i>Kalobatippus agatensis</i>	Equidae	2	HC	SubUng	3R, HC, EE	NA/A	NS
† <i>Megahippus matthewi</i>	Equidae	2	HC	SubUng	3R, HC, EE	NA/A	NS
† <i>Parahippus leonensis</i>	Equidae	1	HC	Ung	3R, HC, EE	NA/A	NS
† <i>Calippus martini</i>	Equidae	1	HC	Ung	3R, HC, EE	NA/A	NS
† <i>Cormohipparion occidentale</i>	Equidae	1	HC	Ung	3R, HC, EE	NA/A	NS
<i>Equus asinus</i>	Equidae	1	HC	Ung	1, -, EE	NA/A	NS
<i>Equus grevyi</i>	Equidae	1	HC	Ung	1, -, EE	NA/A	NS
<i>Equus hemionus</i>	Equidae	1	HC	Ung	1, -, EE	NA/A	NS
<i>Equus zebra</i>	Equidae	1	HC	Ung	1, -, EE	NA/A	NS
† <i>Dinohippus leidyianus</i>	Equidae	1	HC	Ung	1, -, EE	NA/A	NS
† <i>Hippidion neogaenum</i>	Equidae	1	HC	Ung	1, -, EE	NA/A	NS
† <i>Merychippus primus</i>	Equidae	1	HC	Ung	3R, HC, EE	NA/A	NS
† <i>Merychippus sejunctus</i>	Equidae	1	HC	Ung	3R, HC, EE	NA/A	NS
† <i>Nannippus lenticularis</i>	Equidae	1	HC	Ung	3R, HC, EE	NA/A	NS

continued

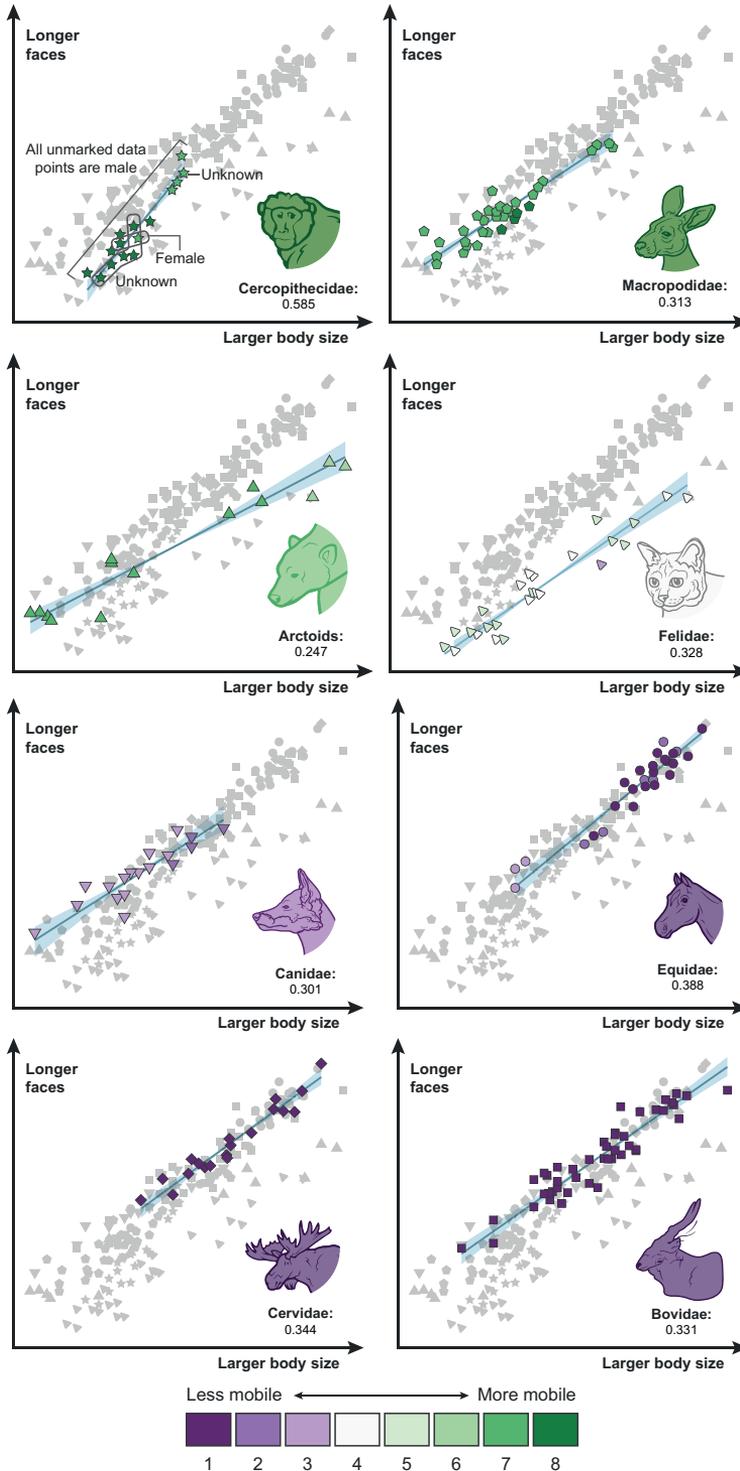
## Appendix 2. Continued.

Species	Family	FMI	Locomotion	Foot posture	Metacarpals	Shoulder mobility	Elbow mobility
† <i>Neohipparion coloradense</i>	Equidae	1	HC	Ung	3R, HC, EE	NA/A	NS
† <i>Pliohippus pernix</i>	Equidae	1	HC	Ung	3R, HC, EE	NA/A	NS
† <i>Protohippus simus</i>	Equidae	1	HC	Ung	3R, HC, EE	NA/A	NS
† <i>Pseudohipparion retrusum</i>	Equidae	1	HC	Ung	3R, HC, EE	NA/A	NS
<i>Canis aureus</i>	Canidae	3	C	Dig	4R, HC, HE	LA/A	LS
<i>Canis latrans</i>	Canidae	3	C	Dig	4R, HC, VHE	LA/A	LS
<i>Canis lupus</i>	Canidae	2	HC	Dig	4R, HC, VHE	LA/A	LS
<i>Canis mesomelas</i>	Canidae	3	C	Dig	4R, HC, HE	LA/A	LS
<i>Canis rufus</i>	Canidae	2	HC	Dig	4R, HC, VHE	LA/A	LS
<i>Cerdocyon thous</i>	Canidae	3	C	Dig	4R, HC, HE	LA/A	LS
<i>Chrysocyon brachyurus</i>	Canidae	3	C	Dig	4R, HC, VHE	LA/A	LS
<i>Cuon alpinus</i>	Canidae	2	HC	Dig	4R, HC, VHE	LA/A	LS
<i>Lycalopex culpaeus</i>	Canidae	3	C	Dig	4R, HC, HE	LA/A	LS
<i>Lycalopex griseus</i>	Canidae	3	C	Dig	4R, HC, HE	LA/A	LS
<i>Lycalopex gymnocercus</i>	Canidae	3	C	Dig	4R, HC, HE	LA/A	LS
<i>Lycan pictus</i>	Canidae	2	HC	Dig	4R, HC, VHE	LA/A	LS
<i>Nyctereutes procyonoides</i>	Canidae	3	C	Dig	4R, HC, HE	LA/A	LS
<i>Speothos venaticus</i>	Canidae	3	C	Dig	4R, HC, HE	LA/A	LS
<i>Urocyon cinereoargenteus</i>	Canidae	3	C	Dig	4R, HC, HE	LA/A	LS
<i>Vulpes velox</i>	Canidae	3	C	Dig	4R, HC, HE	LA/A	LS
<i>Vulpes vulpes</i>	Canidae	3	C	Dig	4R, HC, HE	LA/A	LS
<i>Vulpes zerda</i>	Canidae	3	C	Dig	4R, HC, HE	LA/A	LS
<i>Acinonyx jubatus</i>	Felidae	3	HC	Dig	4R, HC, HE	LA/A	MS
<i>Caracal caracal</i>	Felidae	4	C/S	Dig	4R, HC, E	SA/A	MS
<i>Felis catus</i>	Felidae	5	S	Dig	4R, HC, E	SA/A	MS
<i>Felis chaus</i>	Felidae	4	C/S	Dig	4R, HC, E	SA/A	MS
<i>Felis manul</i>	Felidae	4	C/S	Dig	4R, HC, E	SA/A	MS
<i>Felis margarita</i>	Felidae	4	C/S	Dig	4R, HC, E	SA/A	MS
<i>Felis silvestris</i>	Felidae	5	S	Dig	4R, C, E	SA/A	MS
<i>Leopardus geoffroyi</i>	Felidae	5	S	Dig	4R, C, E	SA/A	MS
<i>Leopardus guigna</i>	Felidae	5	S	Dig	4R, C, E	SA/A	MS
<i>Leopardus pardalis</i>	Felidae	5	S	Dig	4R, C, E	SA/A	MS
<i>Leopardus tigrinus</i>	Felidae	5	S	Dig	4R, C, E	SA/A	MS
<i>Leopardus weidii</i>	Felidae	5	S	Dig	4R, C, E	SA/A	MS
<i>Leptailurus serval</i>	Felidae	4	C/S	Dig	4R, HC, E	SA/A	MS
<i>Lynx canadensis</i>	Felidae	4	C/S	Dig	4R, HC, E	SA/A	MS
<i>Lynx lynx</i>	Felidae	4	C/S	Dig	4R, HC, E	SA/A	MS
<i>Lynx rufus</i>	Felidae	4	C/S	Dig	4R, HC, E	SA/A	MS
<i>Panthera leo</i>	Felidae	4	C/S	Dig	4R, HC, E	SA/A	MS
<i>Panthera onca</i>	Felidae	5	S	Dig	4, C, E	SA/A	MS
<i>Panthera pardus</i>	Felidae	5	S	Dig	4, C, E	SA/A	MS
<i>Panthera tigris</i>	Felidae	4	C/S	Dig	4, HC, E	SA/A	MS
<i>Prionailurus bengalensis</i>	Felidae	4	C/S	Dig	4, HC, E	SA/A	MS
<i>Prionailurus viverrinus</i>	Felidae	4	C/S	Dig	4, HC, E	SA/A	MS
<i>Puma concolor</i>	Felidae	4	C/S	Dig	4, HC, E	SA/A	MS
<i>Puma yagouaroundi</i>	Felidae	5	S	Dig	4, C, E	SA/A	MS
<i>Uncia uncia</i>	Felidae	5	S	Dig	4, C, E	SA/A	MS
<i>Helarctos melayanus</i>	Ursidae	7	S	Plan	5, MC, NE	MA/A	GS
<i>Melursus ursinus</i>	Ursidae	7	S	Plan	5, MC, NE	MA/A	GS
<i>Ursus americanus</i>	Ursidae	6	S	Plan	5, MC, NE	MA/A	GS
<i>Ursus arctos</i>	Ursidae	6	T	Plan	5, MC, NE	MA/A	MS
<i>Ursus maritimus</i>	Ursidae	6	T (Aq)	Plan	5, MC, NE	MA/A	MS
<i>Ursus thibetanus</i>	Ursidae	7	S	Plan	5, MC, NE	MA/A	GS
<i>Ailurus fulgens</i>	Ailuridae	7	A	Plan	5, NC, NE	MA/A	GS

continued

## Appendix 2. Continued.

Species	Family	FMI	Locomotion	Foot posture	Metacarpals	Shoulder mobility	Elbow mobility
<i>Bassaricyon gabpii</i>	Procyonidae	7	A	Plan	5, NC, NE	MA/A	GS
<i>Bassaricyon neblina</i>	Procyonidae	7	A	Plan	5, NC, NE	MA/A	GS
<i>Bassariscus astutus</i>	Procyonidae	7	S	Plan	5, NC, NE	MA/A	GS
<i>Bassariscus sumichrasti</i>	Procyonidae	7	S	Plan	5, NC, NE	MA/A	GS
<i>Potos flavus</i>	Procyonidae	7	A	Plan	5, NC, NE	MA/A	GS
<i>Procyon cancrivorus</i>	Procyonidae	7	S	Plan	5, NC, NE	MA/A	GS
<i>Procyon lotor</i>	Procyonidae	7	S	Plan	5, NC, NE	MA/A	GS
<i>Cercopithecus cephus</i>	Cercopithecidae	8	A	Plan	5, NC, NE	HA/A	GS
<i>Cercopithecus dryas</i>	Cercopithecidae	8	A	Plan	5, NC, NE	HA/A	GS
<i>Cercopithecus mitis</i>	Cercopithecidae	8	A	Plan	5, NC, NE	HA/A	GS
<i>Cercopithecus mona</i>	Cercopithecidae	8	A	Plan	5, NC, NE	HA/A	GS
<i>Cercopithecus neglectus</i>	Cercopithecidae	8	A	Plan	5, NC, NE	HA/A	GS
<i>Chlorocebus sabaesus</i>	Cercopithecidae	8	A	Plan	5, NC, NE	HA/A	GS
<i>Erythrocebus patas</i>	Cercopithecidae	7	T	SemiDig	5, MC, ME	HA/A	GS
<i>Lophocebus albigena</i>	Cercopithecidae	8	A	Plan	5, NC, NE	HA/A	GS
<i>Macaca fascicularis</i>	Cercopithecidae	8	A	Plan	5, NC, NE	HA/A	GS
<i>Macaca fuscata</i>	Cercopithecidae	8	A	Plan	5, NC, NE	HA/A	GS
<i>Macaca mulatta</i>	Cercopithecidae	8	A	Plan	5, NC, NE	HA/A	GS
<i>Papio anubis</i>	Cercopithecidae	7	T	SemiDig	5, MC, ME	HA/A	GS
<i>Papio cynocephalus</i>	Cercopithecidae	7	T	SemiDig	5, MC, ME	HA/A	GS
<i>Papio hamadryas</i>	Cercopithecidae	7	T	SemiDig	5, MC, ME	HA/A	GS
<i>Theropithecus gelada</i>	Cercopithecidae	7	T	SemiDig	5, MC, ME	HA/A	GS
<i>Lagostrophus fasciatus</i>	Macropodidae	7	T	Plan	5, NC, NE	MA/A	GS
<i>Dendrolagus dorianus</i>	Macropodidae	8	A	Plan	5, NC, NE	HA/A	GS
<i>Dendrolagus goodfellowi</i>	Macropodidae	8	A	Plan	5, NC, NE	HA/A	GS
<i>Dendrolagus inustus</i>	Macropodidae	8	A	Plan	5, NC, NE	HA/A	GS
<i>Dendrolagus mayri</i>	Macropodidae	8	A	Plan	5, NC, NE	HA/A	GS
<i>Dorcopsis hageni</i>	Macropodidae	7	T	Plan	5, NC, NE	MA/A	GS
<i>Dorcopsis muelleri</i>	Macropodidae	7	T	Plan	5, NC, NE	MA/A	GS
<i>Dorcopsulus vanheurni</i>	Macropodidae	7	T	Plan	5, NC, NE	MA/A	GS
<i>Dorcopsulus maclaeyi</i>	Macropodidae	7	T	Plan	5, NC, NE	MA/A	GS
<i>Lagorchestes hirsutus</i>	Macropodidae	7	T	Plan	5, NC, NE	MA/A	GS
<i>Lagorchestes conspicillatus</i>	Macropodidae	7	T	Plan	5, NC, NE	MA/A	GS
<i>Lagorchestes leporides</i>	Macropodinae	7	T	Plan	5, NC, NE	MA/A	GS
<i>Macropus fuliginosus</i>	Macropodidae	7	T	Plan	5, NC, NE	MA/A	GS
<i>Macropus giganteus</i>	Macropodidae	7	T	Plan	5, NC, NE	MA/A	GS
<i>Notamacropus agilis</i>	Macropodidae	7	T	Plan	5, NC, NE	MA/A	GS
<i>Notamacropus eugenii</i>	Macropodidae	7	T	Plan	5, NC, NE	MA/A	GS
<i>Notamacropus greyi</i>	Macropodidae	7	T	Plan	5, NC, NE	MA/A	GS
<i>Notamacropus irma</i>	Macropodidae	7	T	Plan	5, NC, NE	MA/A	GS
<i>Onychogalea fraenata</i>	Macropodidae	7	T	Plan	5, NC, NE	MA/A	GS
<i>Onychogalea unguifera</i>	Macropodidae	7	T	Plan	5, NC, NE	MA/A	GS
<i>Osphranter robustus</i>	Macropodidae	7	T	Plan	5, NC, NE	MA/A	GS
<i>Osphranter rufus</i>	Macropodidae	7	T	Plan	5, NC, NE	MA/A	GS
<i>Petrogale burbidgei</i>	Macropodidae	7	T	Plan	5, NC, NE	MA/A	GS
<i>Petrogale brachyotis</i>	Macropodidae	7	T	Plan	5, NC, NE	MA/A	GS
<i>Petrogale godmani</i>	Macropodidae	7	T	Plan	5, NC, NE	MA/A	GS
<i>Petrogale herberti</i>	Macropodidae	7	T	Plan	5, NC, NE	MA/A	GS
<i>Petrogale lateralis</i>	Macropodidae	7	T	Plan	5, NC, NE	MA/A	GS
<i>Petrogale wilkinsi</i>	Macropodidae	7	T	Plan	5, NC, NE	MA/A	GS
<i>Setonix brachyurus</i>	Macropodidae	7	T	Plan	5, NC, NE	MA/A	GS
<i>Thylogale brunii</i>	Macropodidae	7	T	Plan	5, NC, NE	MA/A	GS
<i>Thylogale billardeirii</i>	Macropodidae	7	T	Plan	5, NC, NE	MA/A	GS
<i>Thylogale stigmatica</i>	Macropodidae	7	T	Plan	5, NC, NE	MA/A	GS
<i>Wallabia bicolor</i>	Macropodidae	7	T	Plan	5, NC, NE	MA/A	GS



**Appendix 3.** Results of standard major axis regressions of face length (tooth row length, TRL (mm)) and body mass (BM, kg) shown for the individual lineages. Both variables were log-transformed. Blue shading represents 95% confidence intervals. Heads by Hey Rabbit at the Noun Project (<https://thenounproject.com/heyrabbit/>), except for the bovid (the eland, *Taurotragus oryx*), drawn by NMM-G. (Arctoids = Ursidae + Ailuridae + Procyonidae). Figure by Science Graphic Design ([sciencegraphicdesign.com](http://sciencegraphicdesign.com))

**Appendix 4.** Results of standard major axis regressions (SMA) of (log-transformed) body mass and tooth row length for family groups. — **A:** Regressions by slope. — **B:** Regressions by elevation (with fixed, common slope). — **C:** Regression by elevational shift (shifts along allometries, common slope).

Lineage	<i>n</i>	<i>R</i> <sup>2</sup>	<i>p</i>	Slope (95%CI)	Intercept (95%CI)
<b>A</b> Arctoids	14	0.9389	< 0.001	0.2468 (0.2114–0.2882)	1.5111 (1.4497–1.5724)
Bovidae	45	0.8834	< 0.001	0.3310 (0.2981–0.3676)	1.5729 (1.5114–1.6344)
Canidae	18	0.8089	< 0.001	0.3005 (0.2389–0.3781)	1.5877 (1.5134–1.6620)
Cercopithecidae	15	0.9064	< 0.001	0.5848 (0.4874–0.7018)	1.1476 (1.0440–1.2513)
Cervidae	19	0.9401	< 0.001	0.3440 (0.3036–0.3898)	1.5603 (1.4782–1.6424)
Equidae	27	0.9193	< 0.001	0.3883 (0.3455–0.4364)	1.4733 (1.3789–1.5677)
Felidae	25	0.9165	< 0.001	0.3275 (0.2892–0.3709)	1.2634 (1.2093–1.3176)
Macropodidae	33	0.8733	< 0.001	0.3131 (0.2750–0.3566)	1.5004 (1.4617–1.5390)
<b>B</b> Arctoids	14	0.9389	< 0.001	0.3360 (0.3182–0.3549)	1.4022 (1.3253–1.4791)
Bovidae	45	0.8834	< 0.001	0.3360 (0.3182–0.3549)	1.5646 (1.5305–1.5987)
Canidae	18	0.8089	< 0.001	0.3360 (0.3182–0.3549)	1.5532 (1.5161–1.5902)
Cercopithecidae	15	0.9064	< 0.001	0.3360 (0.3182–0.3549)	1.3784 (1.3294–1.4274)
Cervidae	19	0.9401	< 0.001	0.3360 (0.3182–0.3549)	1.5752 (1.5370–1.6134)
Equidae	27	0.9193	< 0.001	0.3360 (0.3182–0.3549)	1.5793 (1.5380–1.6206)
Felidae	25	0.9165	< 0.001	0.3360 (0.3182–0.3549)	1.2535 (1.2208–1.2863)
Macropodidae	33	0.8733	< 0.001	0.3360 (0.3182–0.3549)	1.4812 (1.4576–1.5049)
<b>C</b> Arctoids	14	0.9389	< 0.001	0.3360 (0.3182–0.3549)	1.4022 (1.4497–1.5724)
Bovidae	45	0.8834	< 0.001	0.3360 (0.3182–0.3549)	1.5646 (1.5114–1.6344)
Canidae	18	0.8089	< 0.001	0.3360 (0.3182–0.3549)	1.5532 (1.5134–1.6620)
Cercopithecidae	15	0.9064	< 0.001	0.3360 (0.3182–0.3549)	1.3784 (1.0440–1.2513)
Cervidae	19	0.9401	< 0.001	0.3360 (0.3182–0.3549)	1.5752 (1.4782–1.6424)
Equidae	27	0.9193	< 0.001	0.3360 (0.3182–0.3549)	1.5793 (1.3789–1.5677)
Felidae	25	0.9165	< 0.001	0.3360 (0.3182–0.3549)	1.2535 (1.2093–1.3176)
Macropodidae	33	0.8733	< 0.001	0.3360 (0.3182–0.3549)	1.4812 (1.4617–1.5390)