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Original Article

The locomotor behaviour of subfossil Malagasy sloth-lemurs (Strepsirrhini: Indriidae) and koala-lemurs (Strepsirrhini: Megaladapidae): new insights from limb trabecular bone

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ABSTRACT

The locomotion of Malagasy Quaternary subfossil lemurs, including palaeopropithecines ('sloth-lemurs') and megaladapids ('koala-lemurs'), has been investigated on abundant postcranial remains. Proposed strategies include some that lack living primate parallels, such as sloth-like suspensory arboreality in palaeopropithecines, although the degree of suspensory behaviour in palaeopropithecines or locomotor diversity in koala-lemurs is poorly understood. Unlike the external morphology, internal bone structure in these taxa is largely unexplored. We compared the humeral and femoral trabecular architecture of sloth- and koala-lemurs with several extant mammals, studying spherical/hemispherical trabecular samples extracted from high-resolution scans. After defining locomotor categories from quantitative data, we tested links between trabecular parameters and locomotor modes through exploratory and multivariate analyses, accounting for body size and phylogeny. In extant mammals, only femoral trabecular traits, particularly the degree of anisotropy and bone volume fraction, were significantly associated with locomotion, distinguishing suspensory and bridging arboreal taxa from others. Using this model, we inferred suspensory adaptations in palaeopropithecines, especially *Palaeopropithecus*, confirming earlier reconstructions, but also in *Megaladapis edwardsi*, a striking result that would place it alongside extant orangutans as the largest mammals known to adopt such habits. This work highlights the potential of internal bone structure for reconstructing primate locomotor evolution.

Keywords: arboreal suspensory locomotion; cancellous bone; femur; humerus; Madagascar; *Megaladapis*; palaeopropithecines

INTRODUCTION

Studying the fauna of Madagascar offers a unique opportunity to address central questions in biology, owing to the exceptional biodiversity of the island and its distinctive geological and evolutionary history (e.g. Muldoon *et al.* 2009, Crowley 2010, Muldoon 2010). Lemurs, among the most iconic Malagasy organisms, are taxonomically diverse (representing ∼13% of living primates; Rowe 1996, Martin 2000) and ecologically varied (Martin 2000), particularly in their locomotor/postural behaviours. Among others, these include climbing and leaping, quadrupedalism (arboreal and terrestrial), vertical clinging, and terrestrial hopping (Walker 1974, 1979, Gebo 1987, Demes *et al.* 1996, Jungers *et al.* 2005, Furnell *et al.* 2015).

When humans first reached Madagascar (Muldoon 2010, see also Douglass *et al.* 2019; ∼2300 years ago), they encountered not only the modern primate community but also additional extinct lemur groups, i.e. palaeopropithecines ('sloth-lemurs'), archaeolemurines ('monkey-lemurs'), megaladapids ('koala-lemurs'), the

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daubentoniid *Daubentonia robusta* (Lamberton, 1934), and the lemurid *Pachylemur* Filhol, 1874. These species persisted for centuries alongside humans, with some surviving until ∼500 years ago (Crowley 2010). Their recent extinction led to the preservation of extensive skeletal material, which has been pivotal in reconstructing their biology, including body mass (e.g. Jungers *et al.* 2002, 2008), phylogenetic affinity (e.g. Yoder *et al.* 1999, Karanth *et al.* 2005, Kistler *et al.* 2015, Herrera and Dávalos 2016), and locomotor/positional behaviours (e.g. Godfrey *et al.* 1995, Jungers *et al.* 1997, Shapiro *et al.* 2005, see also below). Locomotor behaviours in particular were remarkably diverse, exhibiting a range of adaptations comparable to all the other primate clades (Walker 1974, Tattersall 1982, Godfrey *et al.* 1997, Jungers *et al.* 2002, 2005, Granatosky 2022).

Notably, within subfossil lemurs, sloth-lemurs and koala-lemurs share inferred ecological and physiological traits, i.e. slow arboreality, low metabolic rates, and dominance of rest in daily activity (Walker *et al.* 2008, Hogg *et al.* 2015, Godfrey *et al.* 2016, Alfieri *et al.* 2021, 2023). For instance, the radius of curvature of their semicircular canals (a proxy for locomotor agility, with the canals of cautious taxa shown to be smaller than those of agile taxa after accounting for body mass; Spoor *et al.* 2007) indicates that they were the least agile among subfossil lemurs (Walker *et al.* 2008). Such ecological traits, shared with tree-sloths and koalas, might be associated with convergent morphologies, such as low cortical bone compactness in limb diaphyses (Alfieri *et al.* 2021). However, other anatomical features suggest biomechanical divergence between sloth-lemurs and koala-lemurs, despite their broad ecological similarities (Alfieri 2022, Alfieri *et al.* 2023).

Sloth lemurs [*Palaeopropithecus* Grandidier, 1899, *Mesopropithecus* Standing, 1908, *Babakotia* Godfrey, Simons, Chatrath & Rakotosamimanana, 1990, and *Archaeoindris* Standing, 1908 (Simons *et al.* 1992, Jungers *et al.* 1997, Godfrey and Jungers 2003, Gommery *et al.* 2009)] ranged from ∼11 to ∼160 kg in body mass (Granatosky 2022), a range revised downwards to between ∼7 and ∼128 kg by more recent estimates (Thompson *et al.* 2025). Extant indriids are their closest living relatives (Tattersall 1973, Tattersall and Schwartz 1974, Karanth *et al.* 2005, Kistler *et al.* 2015, Herrera and Dávalos 2016). Although the locomotion of *Archaeoindris* remains debated owing to limited fossil evidence (e.g. Godfrey and Jungers 2002, Godfrey *et al.* 2016), abundant studies of postcranial axial and appendicular skeletal traits have suggested that *Palaeopropithecus*, *Mesopropithecus*, and *Babakotia* probably showed specialized suspensory adaptations based on below-branch quadrupedalism. This specialization was potentially more extreme in *Palaeopropithecus*, followed by *Babakotia*, which would have been intermediate, and finally by the least-specialized *Mesopropithecus* (Jungers 1980, Jungers *et al.* 1991, Shapiro *et al.* 1994, 2005, Godfrey *et al.* 1995, Wunderlich *et al.* 1996, Hamrick *et al.* 2000, Godfrey and Jungers 2003, Patel *et al.* 2013, Marchi *et al.* 2016, Granatosky 2018, 2020, 2022). Although there seems to be a certain consensus on the more extreme adaptations of *Palaeopropithecus*, the relative degree of specialization in suspensory behaviours of the other two taxa appears less clear. For instance, it was also proposed that *Babakotia* and *Mesopropithecus* (the smaller palaeopropithecines) were more similar to the two-toed sloth *Choloepus* Illiger, 1811, contrasting with *Palaeopropithecus*, which was instead inferred to resemble more the three-toed sloth *Bradypus* Linnaeus, 1758 (e.g. Marchi *et al.* 2016). Also, *Babakotia* and *Mesopropithecus* are not distinct for some potentially functional traits (i.e. within-limb proportions), hence they do not clearly reflect the expected different degree of suspensory adaptations mentioned above (Marchi *et al.* 2016). Accordingly, *Babakotia* and *Mesopropithecus* have been described overall as taxa with a more diverse locomotor repertoire, in comparison to *Palaeopropithecus* (Granatosky 2022).

Koala-lemurs, i.e. *Megaladapis* Major, 1893 spp. (Walker 1967, Tattersall 1975, Jungers 1977, 1980, Szalay and Delson 1979, Gebo 1986), include three species, with body mass ranging from the ∼45 kg of *Megaladapis madagascariensis* Forsyth Major, 1894 to the ∼85 kg of *Megaladapis edwardsi* Grandidier, 1899 and with the medium-sized *Megaladapis grandidieri* Standing, 1903 (∼75 kg) in between (Walker 1967, Tattersall 1975, Jungers 1978, 1977, Jungers *et al.* 2008). More recent estimates have revised these values downwards to ∼31.5, ∼65, and ∼56 kg, respectively (Thompson *et al.* 2025), thereby confirming the variation from the smallest *Megaladapis madagascariensis* to the largest *Megaladapis edwardsi*, with *Megaladapis grandidieri* in between. The phylogenetic position of *Megaladapis* spp. has been controversial, i.e. close to *Lepilemur* Geoffroy Saint-Hilaire, 1851 (Tattersall and Schwartz 1974, Godfrey *et al.* 2010), to Lemuridae (Karanth *et al.* 2005, Orlando *et al.* 2008, Kistler *et al.* 2015), or diverging early from all non-daubentoniid lemurs (Herrera and Dávalos 2016). Here, we will consider koala-lemurs as the sister taxon of Lemuridae, because this has been confirmed by more recent studies addressing nuclear DNA sequences (Upham *et al.* 2019, Marciniak *et al.* 2021). The locomotor behaviour of *Megaladapis* spp. has also been long debated (Godfrey and Jungers 2002). Although there is now wide consensus on their arboreality, with behaviours dominated by forelimb activity (but without being characterized by extreme suspensory adaptations, such as in palaeopropithecines, see above), which is supported by a high intermembral index, powerful hands and feet, and body proportions reminiscent of koalas (Jungers 1978, Wunderlich *et al.* 1996, Godfrey and Jungers 2002, Godfrey *et al.* 2016), some uncertainties remain regarding their specific postural and locomotor behaviours. A first traditional view holds that vertical climbing and clinging were the primary postures for all the *Megaladapis* taxa (Jungers 1977, 1978; agreeing with Carleton 1936). In this framework, the three species are considered merely as size and geographical variants, i.e. the largest *Megaladapis edwardsi* and the smallest *Megaladapis madagascariensis* representing the south-southwestern varieties, with the medium-sized *Megaladapis grandidieri* living in central Madagascar (Walker 1967, Tattersall 1975, Jungers 1977, 1978, Jungers *et al.* 2008). However, new fossil evidence has led to the recognition of two potential behaviourally distinct sublineages of koala-lemurs: the small to medium-sized and widely distributed *Megaladapis* (*Megaladapis madagascariensis* + *Megaladapis grandidieri*), characterized by vertical climbing combined with quadrupedal hanging and pedal suspension (Wunderlich *et al.* 1994, 1996, Jungers *et al.* 2002, 2008), and the large-sized and southern *Peloriadapis* Grandidier, 1899 (subgenus corresponding to *Megaladapis edwardsi*; Vuillame-Randriamanantena *et al.* 1992, Wunderlich *et al.* 1996), proposed as relatively more terrestrial compared with *Megaladapis madagascariensis* and *Megaladapis grandidieri* (Wunderlich *et al.* 1994, 1996, Jungers *et al.* 2002, 2008).

Most of the reconstructions of locomotion in subfossil lemurs have focused on bone external morphology (e.g. Godfrey *et al.*

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1995, Wunderlich *et al.* 1996, Marchi *et al.* 2016; although Marchi *et al.* also analysed diaphyseal cross-sectional properties). However, outer morphology, especially concerning joint anatomy, is potentially more genetically (thus, less functionally) driven than internal bone structure, i.e. the inner repartition of osseous tissue within skeletal elements (Rafferty and Ruff 1994, Lieberman *et al.* 2001). This is especially relevant for the long bones of the appendicular skeleton, which are well known for their ability to inform on locomotor behaviour (Dunn 2018). The external morphology of long bones mainly reflects the potential locomotor capabilities of an organism: what it could do theoretically, e.g. the maximum range of rotation allowed at a joint without causing disarticulation or injury. In contrast, the internal structure of long bones more closely reflects the realized niche, i.e. the behaviours the organism performs regularly. This applies to all levels of inner architecture, such as diaphyseal compact bone and epiphyseal trabecular structure. Particularly the latter has been shown (both experimentally, e.g. Biewener *et al.* 1996, Pontzer *et al.* 2006; and computationally, e.g. Huiskes *et al.* 2000, Keaveny *et al.* 2001) to adapt in response to biomechanical loadings (summarized by Kivell 2016). This characteristic highlights the potential of the trabecular structure of limb long bones to reflect the loading conditions to which they are subjected, which can, in turn, be linked to specific locomotor behaviours. Some studies have not found trabecular structural differences reflecting different locomotor habits (e.g. Carlson *et al.* 2008, Ryan and Walker 2010), which was explained by the fact that trabecular bone is also affected by non-functional aspects [e.g. systemic (Tsegai *et al.* 2018a), genetic (Ryan *et al.* 2017), ontogenetic (Macho *et al.* 2005), and hormonal (Khosla *et al.* 2006)]. However, many comparative analyses across several postcranial regions have shown that trabecular bone co-varies with locomotor behaviour (e.g. Fajardo and Müller 2001, Chang *et al.* 2008, Saparin *et al.* 2011, Ryan and Shaw 2012, Tsegai *et al.* 2013, Mielke *et al.* 2018, Georgiou *et al.* 2019, Arias-Martorell *et al.* 2021, Alfieri 2022, Alfieri *et al.* 2022), making the study of this anatomical level a common approach for inferring past locomotor habits in extinct primates (e.g. Ryan and Ketcham 2002a, Barak *et al.* 2013b, Kivell *et al.* 2018, Ryan *et al.* 2018). Despite its potential, the internal architecture of the long bones of the sloth-lemurs and koala-lemurs has not yet been analysed. Only recently, the trabecular structure of long bone epiphyses in palaeopropithecines and *Megaladapis* has been quantified, but primarily to investigate evolutionary patterns in slow arboreal mammals (Alfieri *et al.* 2023), rather than to infer their locomotor behaviour directly.

To fill this gap, in this study we examine humeral and femoral trabecular architecture in sloth-lemurs and koala-lemurs, comparing them with those of a sample of extant mammals, encompassing potential ecological analogues of subfossil lemurs, inferred sister taxa of sloth-lemurs and koala-lemurs, and other relevant groups (Fig. 1). Initially, we used quantitative behavioural data on extant taxa to classify them in locomotor categories; we then analysed their humeral and femoral trabecular structure with the aim of understanding which skeletal region and trabecular trait discriminate extant mammals according to their locomotion. Hence, we inferred the most likely locomotor behaviour for extinct lemurs, using both an exploratory approach (i.e. assessing morphospaces) and an analytical approach [i.e. running a phylogenetically informed discriminant function analysis (pDFA) on the most informative trabecular traits]. This protocol allowed us to understand whether trabecular bone supports previous hypotheses regarding: (i) the particularly derived suspensory adaptations of *Palaeopropithecus*; (ii) the relatively intermediate degree of suspensory specialization in *Mesopropithecus* and *Babakotia*; and (iii) potential locomotor differences across the small/medium-sized *Megaladapis madagascariensis* and *Megaladapis grandidieri*, and the large *Megaladapis edwardsi* (see above).

MATERIALS AND METHODS

Sample

Subfossil lemurs

We used high-resolution microcomputed tomography (μCT) data derived from humeri and femora of Malagasy subfossil lemurs collected in the Muséum national d'Histoire Naturelle (MNHN; Paris, France) and the Division of Fossil Primates, Duke Lemur

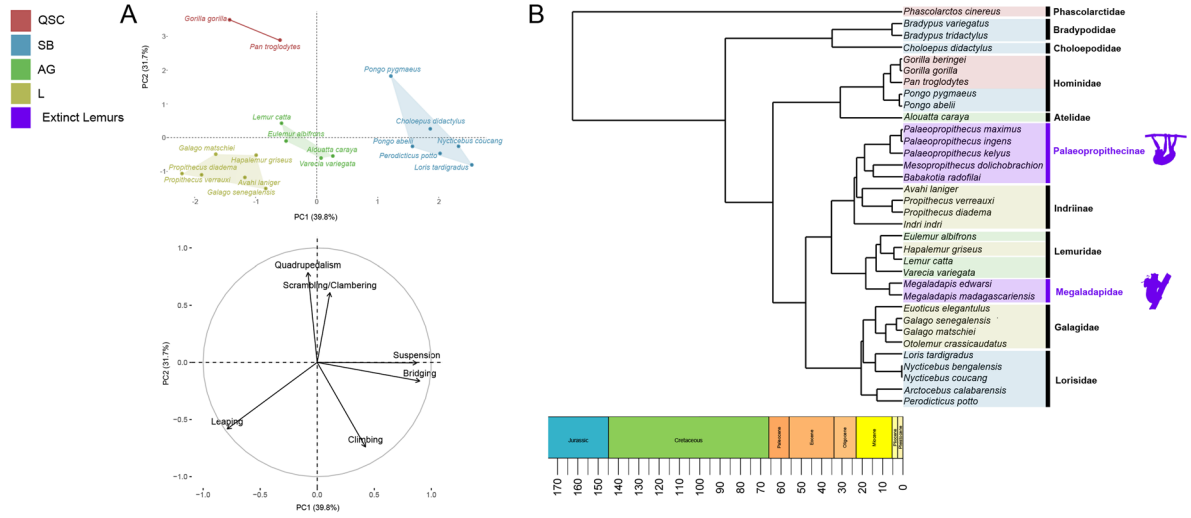

Figure 1. A, principal component analysis on quantitative locomotor data (top, scatterplot; bottom, variable loading plot). Identified locomotor categories are as follows: AG, arboreal generalist; L, leaping; QSC, quadrupedal/scrambling/clambering; and SB, suspensory/bridging. B, phylogenetic relationships between the studied species with locomotor categories mapped on the phylogeny.

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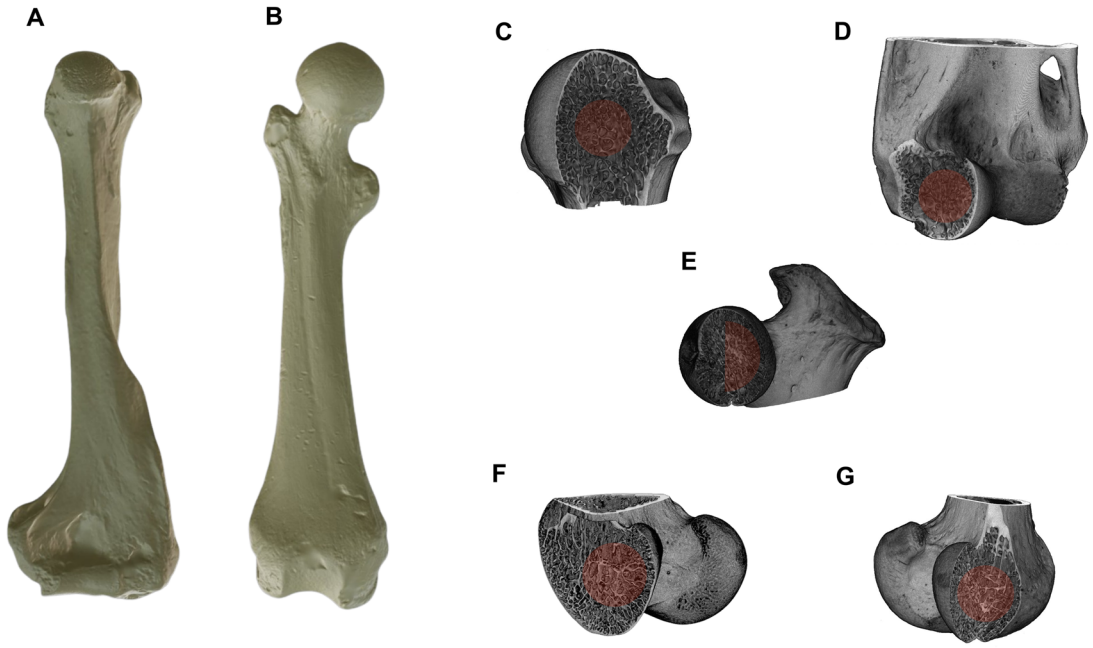

Figure 2. A, B, three-dimensional models of two subfossil lemur specimens studied in this work: A, humerus of *Megaladapis edwardsi* MNHN-MAD 7777; and B, femur of *Palaeopropithecus ingens* MNHM-MAD 8808. C–G, proximal (C) and distal (D) humeral epiphyses, in addition to proximal (E), distal lateral condyle (F), and distal medial condyle (G) femoral epiphyses, from which trabecular bone was studied. The extraction of spherical and hemispherical volumes of interest (highlighted in red) is shown. C–G refer to a humerus of *Perodicticus potto* (Müller, 1766) (NMW 32674) (C, D) and a femur of *Propithecus verreauxi* Grandidier, 1867 (AMNH 170474) (E–G). Images are not to scale.

Center (renamed as the Duke Lemur Center Museum of Natural History), Durham (NC, USA) (e.g. Fig. 2A, B). Details regarding acquisition can be found in the paper by Alfieri *et al.* (2023). The studied data are derived from specimens belonging to *Babakotia* sp. (one complete humerus and one distal humerus), *Palaeopropithecus* sp. (four complete humeri, one proximal humerus, one distal humerus, four complete femora, one proximal femur, and two distal femora), *Mesopropithecus dolichobrachion* (one complete humerus), and *Megaladapis* sp. (three complete humeri, one proximal humerus, one distal humerus, two complete femora, two proximal femora, and two distal femora). *Babakotia* sp. was assigned to *Babakotia radofilai*, the only species recognized within the genus, and *Palaeoprorithecus* sp. and *Megaladapis* sp. were assigned to known species within the two genera, following Alfieri *et al.* (2023) and as summarized in the Supporting Information (Appendix S1).

Extant primates

We built a comparative sample of extant mammal species (Table 1) by collecting µCT data from previous studies (Georgiou *et al.* 2018, 2019, Kivell *et al.* 2018, Ryan *et al.* 2018, Tsegai *et al.* 2018a,b, Arias-Martorell *et al.* 2021, Alfieri *et al.* 2022, 2023) and/or downloading data from MorphoSource (https://www.morphosource.org; Supporting Information, Tables S1 and S2). These data are derived from 55 humeri and 53 femora collected across several institutions (Supporting Information, Appendix S2). We studied adult specimens, as determined by full epiphyseal fusion, and selected epiphyses with preserved trabecular bone for the extant sample. For the subfossil lemur epiphyseal data, perfect preservation of trabeculae was not always possible; therefore, we either discarded these specimens or adopted procedures to analyse fragmented individuals (see below, section "Extraction of trabecular parameters"). Most of the studied extant mammals have been proposed as extant ecological analogues of extinct lemurs and/or were used in previous morphological comparative works of the studied subfossil species (e.g. Godfrey 1988, Godfrey *et al.* 1995, 2016, Wunderlich *et al.* 1996, Jungers *et al.* 1997, 2002, 2008, Hamrick *et al.* 2000, Shapiro *et al.* 2005, Walker *et al.* 2008, Granatosky *et al.* 2014, Boyer *et al.* 2015, Marchi *et al.* 2016, Amson and Nyakatura 2018, Granatosky 2022, Alfieri *et al.* 2021, 2023), i.e. tree-sloths (both three-toed sloths, Bradypodidae, and two-toed sloths, Choloepodidae), the koala (Phascolarctidae), lorisids (Lorisidae), and non-human great apes (Hominidae). We also included representatives from the two taxa inferred as the extant closest relatives of palaeopropithecines and *Megaladapis*, i.e. the subfamily Indriinae and the family Lemuridae, respectively (Baab *et al.* 2014, Herrera and Dávalos 2016, Upham *et al.* 2019, Marciniak *et al.* 2021, Fleagle *et al.* 2025). Also, we included the platyrrhine *Alouatta caraya* (Humboldt, 1812), as an example of a non-strepsirrhine primate adapted to an energy-saving slow arboreal lifestyle (Bicca-Marques and Calegaro-Marques 1998, Prates *et al.* 2018), an ecology that has been inferred for both palaeopropithecines and *Megaladapis* (Walker *et al.* 2008, Godfrey *et al.* 2016, Alfieri *et al.* 2021). Additonally, we included galagids, a strepsirrhine family that is not closely related to subfossil lemurs and whose members are specialized in vertical clinging and leaping (Walker 1979, Gebo 2011, Fleagle 2013), the most common and possibly ancestral behaviour in the strepsirrhine radiation (Boyer *et al.* 2017). By doing so, we were able to include a leaping group that is not closely related to extinct lemurs, contrary to Indriinae, which show leaping habits (see below, Results) but are also the extant sister taxon of palaeopropithecines (Fig. 1). All taxa

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Table 1. Taxa studied in this work, with the sample size for each analysed epiphyseal joint from which trabecular structure was quantified.

Taxon	Proximal humeri (*N*)	Distal humeri (*N*)	Proximal femora (*N*)	Femoral lateral condyles (*N*)	Femoral medial condyles (*N*)
Extant taxa					
Alouatta caraya	1	NA	1	NA	NA
Arctocebus calabarensis	1	1	1	1	1
Avahi laniger	3	3	3	3	3
Bradypus tridactylus	1	1	1	1	1
Bradypus variegatus	3	3	3	3	3
Choloepus didactylus	4	4	4	4	4
Eulemur albifrons	2	2	2	2	2
Euoticus elegantulus	1	1	1	1	1
Galago matschiei	1	1	1	1	1
Galago senegalensis	1	1	1	1	1
Gorilla beringei	NA	1	NA	NA	NA
Gorilla gorilla	1	1	1	1	1
Hapalemur griseus	2	2	2	2	2
Indri indri	3	3	3	3	3
Lemur catta	4 (1)	4	3	3	3
Loris tardigradus	1 (0)	1	1 (0)	1	1
Nycticebus bengalensis	1	1	1	1	1
Nycticebus coucang	3 (1)	3	3 (2)	3 (2)	3 (2)
Otolemur crassicaudatus	1 (0)	1 (0)	1	1	1
Pan troglodytes	1	1	2	1	1
Perodicticus potto	5	5	5 (4)	5 (4)	5
Phascolarctos cinereus	5 (2)	5	5 (2)	5	5
Pongo abelii	1	NA	1	NA	NA
Pongo pygmaeus	1	1	NA	1	1
Propithecus diadema	1	1	1	1	1
Propithecus verreauxi	2 (1)	2	2	2 (1)	2 (1)
Varecia variegata	1	1	1	1	1
Subfossil lemurs					
Babakotia radofilai	1	2	NA	NA	NA
Megaladapis edwardsi	2	2 (1)	2	2 (1)	2 (1)
Megaladapis madagascariensis	2	2	2	2 (1)	2 (1)
Mesopropithecus dolichobrachion	1	1 (0)	NA	NA	NA
Palaeopropithecus ingens	4	4	4 (3)	5 (4)	5 (2)
Palaeopropithecus kelyus	1	1	NA	NA	NA
Palaeopropithecus maximus	NA	NA	1 (0)	1	1

Abbreviations: *N*, number of specimens; NA, joints for which data were not available owing to fragmentary specimens. In cases where specimens were discarded because of poor trabecular bone preservation or an insufficient number of trabeculae (see the Materials and Methods; Supporting Information, Appendices S5–S7), the number of specimens ultimately used in the analyses is given in parentheses.

included in the sample were taxonomically categorized at the species level (Table 1; for more details, see Supporting Information, Tables S1 and S2).

Extant primates: locomotor diversity

For 62% of the extant species included here (Fig. 1), we were able to use data on the relative frequency (expressed in percentage) of locomotor behaviours collected by Granatosky (2018). In collecting these quantitative data, we largely followed the approach of Monclús-Gonzalo *et al.* (2023, 2025), i.e. we pooled the behaviours quantified by Granatosky (2018) in six broader locomotor categories: (i) leaping; (ii) quadrupedalism; (iii) climbing; (iv) suspension; (v) bridging; and (vi) scrambling/clambering. The description of the locomotor categories can be found in the paper by Monclús-Gonzalo *et al.* (2023). We transformed the frequency data through the arcsine square root, a common procedure when proportional ecological data are studied (Sokal and Rohlf 1995, Monclús-Gonzalo *et al.* 2023; Supporting Information, Table S3). For some species not listed by Granatosky (2018), we used quantitative data from closely related taxa (Supporting Information, Appendix S3). Given that we aimed to obtain quantitative data representative of species, in cases of multiple datasets for a single taxon reported by Granatosky (2018) we averaged the data for each behaviour, resulting in a single value per locomotor category per species. The behavioural dataset was used to run a principal component analysis (PCA; Supporting Information, Table S4), from which we visually identified, on the principal component (PC)1–PC2 biplot and variable loading plot, how taxa are divided into subgroups owing to their locomotor behaviours. These subgroups represented the discrete locomotor categories used to assign species for which quantitative locomotor data (*sensu* Granatosky 2018) were unavailable.

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Extraction of trabecular parameters

Most of the collected μCT data (i.e. all species except apes and *Alouatta caraya*) consisted of spherical volumes of interest (VOIs) of trabecular bone. These VOIs were extracted in previous studies (Alfieri *et al.* 2022, 2023) from proximal and distal humeral and femoral epiphyses after orienting the humeri and femora in standard anatomical positions, i.e. *x*-axis mediolaterally oriented, *y*-axis anteroposteriorly oriented, and *z*-axis proximodistally oriented (Supporting Information, Appendix S4). Each spherical VOI represents the largest sphere centred within the humeral head and capitulum, and within the femoral head, lateral condyle, and medial condyle (Fig. 2), such that only trabecular bone was included and cortical bone was entirely excluded. The femoral head VOIs were subsequently halved by removing the medial hemisphere (Fig. 2E). This modification was necessary because some taxa, including some of those newly analysed here [e.g. *Alouatta caraya* and *Gorilla gorilla* (Savage, 1847)], exhibit a pronounced fovea capitis on the medial side of the femoral head. Using a fully spherical VOI in these cases would have included a large empty space corresponding to the fovea capitis, thereby biasing trabecular measurements (Alfieri *et al.* 2022, 2023). As for the rest of the sample, VOIs were extracted using the same protocols. Ultimately, all the studied VOIs represent homologous regions. The VOIs were imported into ImageJ2 (Rueden *et al.* 2017) and segmented, isolating the trabecular bone fraction. For extant species, it generally corresponds to binarizing the μCT data, because only two fractions should be distinguished, i.e. trabecular bone from intertrabecular voids, to be assigned to foreground (i.e. one) and background (i.e. zero), respectively. Hence, for VOIs of almost all the extant species we used the automatic binarizing tool of ImageJ2 ('Threshold'), yielding a result that we considered satisfying by assessing, through a visual comparison, the respective non-binarized VOIs. For the other VOIs (the few from extant species and those from subfossil lemurs), we followed alternative procedures, based on manual cleaning and/or tools for automated recognition of non-osseous fractions (detailed in Supporting Information, Appendix S5). From binarized VOIs, we extracted trabecular parameters using BoneJ2 (ImageJ2 plugin; Domander *et al.* 2021), including degree of anisotropy (DA, unitless; averaged across three runs), mean trabecular thickness (Tb.Th, in millimetres), average branch length (Av.Br.Len, in millimetres), bone volume fraction (BV/TV, unitless), bone surface density (BS/TV, per millimetre), and connectivity density (Conn.D, per millimetre cubed). Because BoneJ2 assumes cubic VOIs, BV/TV, BS/TV, and Conn.D were corrected for spherical (or hemispherical, for the femoral head) VOIs using volume derived from VOI diameter. Connectivity was used as a proxy for the number of trabeculae to exclude VOIs with fewer than ~50 trabeculae (Mielke *et al.* 2018; see further details in Supporting Information, Appendix S6). Given our research focus on subfossil lemurs, we aimed to maximize their representation in our sample. Therefore, we included some of their VOIs even if they contained peripheral regions with broken or missing trabeculae. To do so, we gradually reduced the size of these VOIs until the biased regions were excluded. Notably, this approach requires applying the same scaling factor to all the other taxa to ensure consistency, i.e. studying anatomically homologous regions. However, reducing VOI sizes also decreases the number of trabeculae included. Thus, as justified in the Supporting Information (Appendix S7), for each epiphysis this procedure was balanced against the need to avoid under-representing some extant taxa owing to the discarding deriving from too low a number of trabeculae. Ultimately, the radii of the smallest analysed spheres (with the femoral head VOIs subsequently halved, see above) were as follows: proximal humerus = 0.74 mm [*Euoticus elegantulus* (LeConte, 1857)] (AMNH 241147), distal humerus = 0.74 mm (*Galago matschiei* Lorenz, 1917) (FMNH 148985), proximal femur = 0.89 mm [*Loris tardigradus* (Linnaeus, 1758)] (AMNH 269), femoral lateral condyle = 0.74 mm (*Loris tardigradus* AMNH 269), and femoral medial condyle = 0.75 mm [*Arctocebus calabarensis* (Smith, 1860)] (AMNH 212576).

Statistical analyses

Relationship between trabecular structure and locomotion: inferential tests

Owing to the high intercorrelation among trabecular parameters (e.g. Ryan and Shaw 2012), we analysed them collectively as multivariate datasets (i.e. five anatomically separated datasets were defined: proximal humerus, distal humerus, proximal femur, lateral condyle, and medial condyle) and through PCAs. PCA is commonly applied to datasets comprising intercorrelated variables (e.g. cranial measurements; Nishimura *et al.* 2019, Landi *et al.* 2021). We conducted a first set of PCAs on centred and scaled datasets including only trabecular parameters ('PCA_{TP}', hereafter). The resulting $PC_{TP}1$s–$PC_{TP}4$s (explaining the 93.4%–96.4% of the variance across the five datasets; Supporting Information, Tables S5–S9) were used to test for a relationship between trabecular structure and ecological categories while accounting for phylogenetic affinities among species. As a phylogeny, we used the time-calibrated tree deriving from the mammalian tree of Upham *et al.* (2019) adapted to our sample (Supporting Information, Appendix S8). We hence ran multivariate phylogenetic generalized least squares (mvPGLS) regressions ('mvgls' function, 'mvMORPH' package; Clavel *et al.* 2015) in R v.4.3.1 (R Core Team 2023) and phylogenetic MANCOVAs ('manova.gls' function, 'mvMORPH', Pillai's trace tests) (Table 2). Beyond locomotion and phylogeny, trabecular bone is also potentially affected by allometry. To account for this source of variation too, we included a body mass proxy (BMp) as covariate in mvPGLSs. As detailed in the Supporting Information (Appendix S9), as BMp we took the centroid size, deriving from the landmark coordinates from Alfieri *et al.* (2022, 2023), predicted from a linear regression of BMp against bone metric measurements for specimens lacking centroid size values. To establish whether, in mvPGLSs, we also needed to account for ecology–BMp interactions, we preliminarily tested for a relationship between BMp and locomotor categories (phylogenetic ANOVA, 'phylANOVA' function, 'phytools' package; Revell 2012).

Relationship between trabecular structure and locomotion: qualitative assessment

We conducted an additional set of PCAs on centred and scaled datasets including trabecular parameters and BMp ('PCA_{TP+BM}', hereafter). The BMp was included to visualize the effects of body size on trabecular structure and, in doing so, we could observe

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Table 2. Results from multivariate phylogenetic generalized least squares regressions and phylogenetic MANCOVAs testing the relationship between trabecular structure (quantified through $PC_{TP}1$–$PC_{TP}4$ at different anatomical regions) and locomotion, while accounting for body mass effects (for details, see the Materials and Methods).

Anatomical region (articulation)	Principal components	Proportion of variance (%)	Body mass *P*-value	Locomotion *P*-value
Proximal humerus (humeral head)	$PC_{TP}1$–$PC_{TP}4$	93.4	<.001	.21
Distal humerus (humeral capitulum)	$PC_{TP}1$–$PC_{TP}4$	95.6	<.001	.46
Proximal femur (femoral head)	$PC_{TP}1$–$PC_{TP}4$	95.4	<.001	.094
Distal femur (lateral condyle)	$PC_{TP}1$–$PC_{TP}4$	96.8	<.001	.024
Distal femur (medial condyle)	$PC_{TP}1$–$PC_{TP}4$	96.4	<.001	.019

locomotor patterns on biplots built with PC_{TP+BM}s that are not primarily driven by BMp. It could be detected by assessing how BMp contributes to PC_{TP+BM}s in the respective variable loading plots (i.e. through the length and direction of BMp vectors). Moreover, by this approach we avoided potential biases associated with univariate size correction (e.g. residuals), which may not fully remove size effects in multivariate analyses (e.g. Alfieri *et al.* 2025a). In PCA_{TP+BM}s, we also included data of subfossil lemurs to discuss their position on scatterplots. We built biplots with the first three PC_{TP+BM}s (Figs 3–7; Supporting Information, Tables S10–S14), and on them we observed the distribution of locomotion categories and which specific locomotor groups are discriminated by which specific trabecular properties. This included assessing whether subfossil lemurs occupy regions preferentially associated with certain extant taxa, thereby guiding our choice of relevant locomotor categories for further analysis (see Supporting Information, Appendix S10). When we identified a trend related to a single PC_{TP+BM} (i.e. locomotor categories, or combinations of them, are mainly discriminated along one PC_{TP+BM}), we tested for significance through univariate PGLS and ANOVA ('gls' function, 'NLME' package; Pinheiro *et al.* 2020). Additionally, we showed the univariate distribution of these single PC_{TP+BM}s through boxplots (Figs 5E, 6E, 7E). The contribution of trabecular traits and BMp to PC_{TP+BM}s was assessed through eigenvector loadings and correlation analyses (Pearson coefficients and coefficients of determination, R^2). To ascertain that the distribution of taxa on the PCA_{TP+BM} scatterplots was not primarily driven by the inclusion of BMp itself, we additionally generated scatterplots using the first three PC_{TP}s (i.e. from PCAs performed on datasets devoid of BMp; Supporting Information, Figs S1–S5).

Phylogenetic discriminant function analysis

Once a subset of trabecular traits from different anatomical levels was identified as the most effective at discriminating specific locomotor categories (Table 3), we compiled a single heterogeneous dataset to run a phylogenetic discriminant function analysis (pDFA). The pDFA preliminarily required a multivariate PGLS ('mvgls' function, 'MVMORPH') and phylogenetic MANOVA ('manova.gls' function, 'MVMORPH') on extant taxa to ensure that the selected traits captured significant locomotor variation. The multivariate PGLS fit was then used to run the pDFA model ('mvgls.dfa' function, 'MVMORPH'; discriminant function, DF1, Fig. 8; for summary statistics, see Supporting Information, Tables S15–S17). The pDFA model was then tested by predicting the known locomotor categories of extant taxa ('predict' R function). Owing to low sample size (all analyses being phylogenetically informed, the observations are represented not by single specimens but by taxa) that could overestimate the performance of the pDFA, we used a leave-one-out cross-validation, which involved the exclusion of one random observation from the training set, then using the pDFA model to predict the class of the excluded observation. This procedure was iterated until all the taxa were excluded once, but avoiding the repeated exclusion of the same taxon, and allowed us to compute the misclassification rate of the pDFA model. Finally, the pDFA model was applied to subfossil lemurs. To account for uncertainties in the classification of extinct taxa, we followed the approach of Monclús-Gonzalo *et al.* (2023) (see also Widrig *et al.* 2025), discouraging the use of posterior probabilities as a reliable proxy for classification uncertainties (e.g. owing to overfitting; Qiao *et al.* 2009), and instead using subsampling techniques. Hence, for the subfossil taxa, the locomotor assignment was iterated several times, each time subsampling the training set used to train the pDFA model, and counting the times the extinct species were assigned to each class. As a resampling technique, we used leave-one-out cross-validation.

RESULTS

The PC1–PC2 scatterplot and variable loading plot deriving from the PCA run on quantitative locomotor data revealed four locomotor groups (Fig. 1A): leaping (L), quadrupedal/scrambling/clambering (QSC), suspensory/bridging (SB) and arboreal generalists (AG). Accordingly, we framed, in these locomotor categories, the taxa for which quantitative data were not available, thus obtaining the final ecological categorization (Fig. 1B; see further details in Supporting Information, Appendix S11). The four categories were not significantly related to BMp (humerus, $P = .162$; femur, $P = .476$), implying that, in mvPGLS, the BMp–locomotion interaction effects should not be tested and that we could detect distinct effects of body mass and locomotion on trabecular data (Table 2).

Humeral trabecular structure

The humeral trabecular structure of the extant species was not correlated with locomotion. Indeed, from multivariate PGLSs and phylogenetic MANCOVAs, the humeral datasets were significantly correlated with BMp but not with locomotion (Table 2). Also, proximal and distal humerus PCA_{TP+BM} scatterplots and loading vectors showed that $PC1_{TP+BM}$s are primarily related to BMp and to a set of variables (i.e. Tb.Th, Conn.D., Av.Br.Len, and BS/TV). The strong body size effect of proximal and distal humeral $PC1_{TP+BM}$s was clear owing to the position of great apes and

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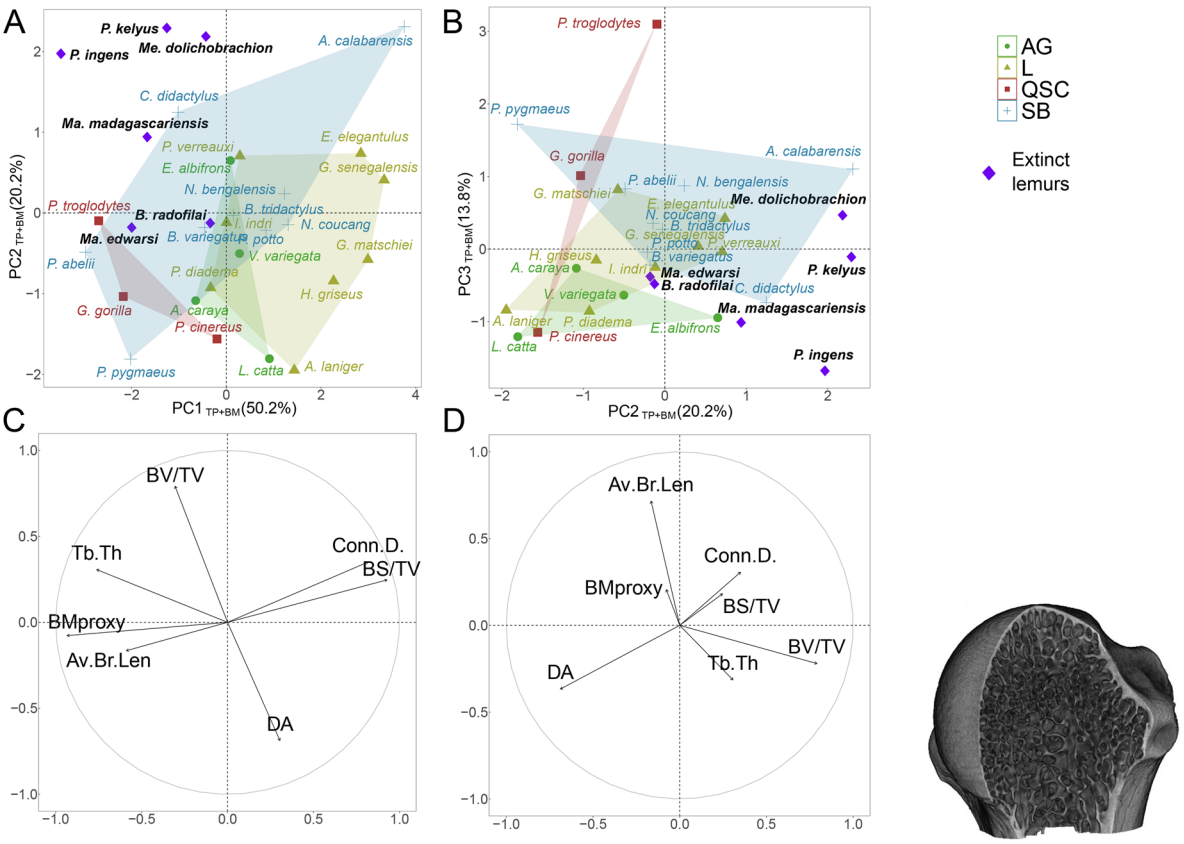

Figure 3. Proximal humerus results of principal component analyses (PCA) on centred and scaled datasets including trabecular parameters and body mass proxy (PCA_{TP+BM}). A, B, PC1–PC2 (A) and PC2–PC3 (B) scatterplots, with extant species grouped by locomotor category and subfossil lemur data shown with purple rhombi. C, D, PC1–PC2 (C) and PC2–PC3 (D) variable loading plots.

subfossil lemurs (i.e. the largest taxa) on one extreme of $PC1_{TP+BM}$ values with galagids and lorisids (i.e. the smallest taxa) instead lying on the other extreme (Figs 3A, 4A). In both the humeral epiphyses, correlation tests confirmed the strong BMp effects on $PC1_{TP+BM}$s, showing that Tb.Th, Conn.D., Av.Br.Len, and BS/TV contribute significantly to $PC1_{TP+BM}$s (Supporting Information, Table S18) and that these trabecular traits are related to BMp themselves (Supporting Information, Table S19). Both proximal and distal humeral DA and BV/TV, instead, arose as not significantly related to the respective $PC1_{TP+BM}$s (with the only exception of distal humeral $PC1_{TP+BM}$–BV/TV, but with $R^2 = .29$; Supporting Information, Table S18) and to body mass (Supporting Information, Table S19; Figs 3C, 4C).

Humeral proximal and distal $PC2_{TP+BM}$s and $PC3_{TP+BM}$s, instead, do not show any significant relationship with BMp (Figs 3B, 4B; Supporting Information, Table S18). Loading vectors suggest that the $PC2_{TP+BM}$s of both the proximal and distal humerus include information mainly related to DA and BV/TV (that do not contribute to PC1, see above; Figs 3D, 4D). It is confirmed by DA–$PC2_{TP+BM}$s and BV/TV–$PC2_{TP+BM}$s correlation tests, combined with the absence of significant correlation tests between any other trabecular variable and $PC2_{TP+BM}$s. Proximal and distal humeral $PC3_{TP+BM}$s contain information related to Av.Br.Len (precisely to its portion of variance not related to BMp, differently from the one driving PC1, see above), because this parameter yielded the longest vector oriented towards $PC3_{TP+BM}$s (Figs 3D, 4D) and showed a significant correlation with $PC3_{TP+BM}$s (Supporting Information, Table S18). Although a few other variables occasionally showed a significant correlation with $PC3_{TP+BM}$s too (DA in the proximal humerus, and Conn.D in the distal humerus), their low R^2 (.13 for DA and .20 for Conn.D; Supporting Information, Table S18) led us to consider their contribution to the respective $PC3_{TP+BM}$ as minor. The humeral $PC2_{TP+BM}$–$PC3_{TP+BM}$ scatterplots yielded a strong overlap of locomotor categories (especially clear for distal humeral data, with almost all the taxa clustering in the same region of the morphospace, i.e. positive $PC3_{TP+BM}$ scores and $PC2_{TP+BM}$ scores ranging between zero and one; Figs 3B, 4B). This, in addition to the non-significant relationship between PC1–PC4 and locomotion from multivariate PGLSs and phylogenetic MANCOVAs (Table 2), led us not to use humeral trabecular properties in the following steps of the analysis.

In the humeral $PC2_{TP+BM}$–$PC3_{TP+BM}$ morphospaces (in which allometric effects are minimized, see above), subfossil lemurs overall cluster in the same regions (i.e. positive $PC2_{TP+BM}$–negative $PC3_{TP+BM}$ scores for the proximal humerus, and positive $PC2_{TP+BM}$ scores for the distal humerus). In the range of variation of sloth-lemurs, *Palaeopropithecus* spp. tend to occupy the most peripheral position (with the exception of *Palaeopropithecus ingens* in the distal humerus), *Babakotia* lies the most closely to the other extant taxa, and *Mesopropithecus* (data available only for the proximal humerus) lies in another peripheral region of the morphospace (close to *Arctocebus calabarensis*; Figs 3B, 4B).

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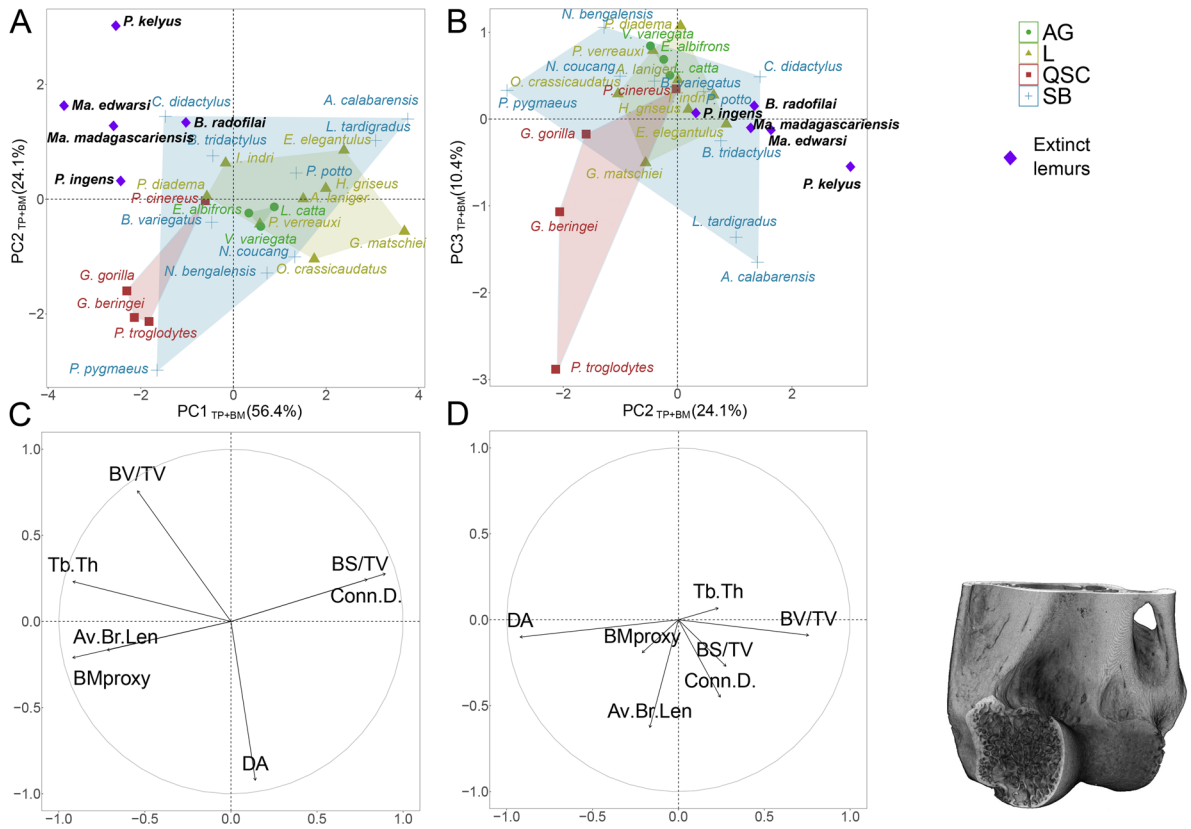

Figure 4. Distal humerus results of principal component analyses (PCA) on centred and scaled datasets including trabecular parameters and body mass proxy (PCA_{TP+BM}). A, B, PC1–PC2 (A) and PC2–PC3 (B) scatterplots, with extant species grouped by locomotor category and subfossil lemur data shown with purple rhombi. C, D, PC1–PC2 (C) and PC2–PC3 (D) variable loading plots.

Megaladapis spp. tend to lie close to *Babakotia*. Interestingly, in the humeral $PC2_{TP+BM}$–$PC3_{TP+BM}$ morphospaces, most subfossil lemurs tend to occupy distinct regions, i.e. they do not overlap with those of extant mammals. Indeed, in the proximal humerus, *Palaeopropithecus* spp., *Mesopropithecus dolichobrachion* Simons et al., 1995, and *Megaladapis madagascariensis* lie outside the convex hulls of extant mammal locomotor categories (Fig. 3B). In the distal humerus, a similar pattern is observed for *Palaeopropithecus kelyus* and *Megaladapis edwardsi*, whereas *Babakotia* and *Megaladapis madagascariensis* occupy peripheral positions within the SB area and trend towards *Palaeopropithecus kelyus* and *Megaladapis edwardsi* (Fig. 4B). Both the proximal and distal humeral outlying patterns of subfossil lemurs are mainly driven by high BV/TV (Figs 3D, 4D).

Femoral trabecular structure

Femoral data yielded patterns related to locomotor categories. Indeed, trabecular data from the lateral and medial condyles proved to be significantly related to locomotion, as shown by multivariate PGLSs and phylogenetic MANCOVAs (Table 2). These epiphyseal regions, such as the proximal femoral, are also significantly related to body mass (Table 2) but, given that locomotor and allometric effects are separated in PGLSs (see above), lateral and medial condyle size-corrected data are significantly related to locomotor categories. Although not reaching significance, proximal femoral data yielded a particularly low *P*-value for a relationship with locomotion (.09; Table 2).

The $PC1_{TP+BM}$s across three femoral datasets are explained by body mass and collect the allometric effects, as shown by the position of great apes/subfossil lemurs (i.e. the largest taxa) and galagids/lorisids (i.e. the smallest taxa) at the two extremes of $PC1_{TP+BM}$ scores (Figs 5A, 6A, 7A). This is also suggested by the directions of BMp loading vectors (Figs 5C, 6C, 7C), additionally indicating that $PC1_{TP+BM}$s are driven by a portion of variance of a subset of trabecular variables that are likely to include size effects themselves. Through correlation tests across the femoral datasets, we confirmed the significant relationship between $PC1_{TP+BM}$s and BMp, we identified the trabecular variables driving $PC1_{TP+BM}$s (i.e. Tb.Th., Conn.D., BS/TV, and Av.Br.Len; Supporting Information, Table S18), and we found that they drive $PC1_{TP+BM}$ through their relationships with BMp (Supporting Information, Table S19). In the proximal femur and in the medial condyle, a portion of BV/TV variance also is correlated with $PC1_{TP+BM}$ but with low strength (R^2_{prox} = .24, $R^2_{med.con}$ = .24; Supporting Information, Table S18). Likewise, BV/TV significantly but weakly relates to BMp in these two levels (R^2_{prox} = .21, $R^2_{med.con}$ = .23; Supporting Information, Table S19). DA makes a minor contribution to femoral $PC1_{TP+BM}$s, because it is not correlated or is weakly correlated with $PC1_{TP+BM}$s ($R^2_{lat.con}$ = .14; Supporting Information, Table S18) and is not correlated with BMp (Supporting Information, Table S19).

Femoral $PC2_{TP+BM}$s and $PC3_{TP+BM}$s do not include size effects, as suggested by BMp vectors in the loading plots (Figs 5D, 6D, 7D) and $PC2_{TP+BM}$s and $PC3_{TP+BM}$s not being correlated with BMp (Supporting Information, Table S18). Correlation tests

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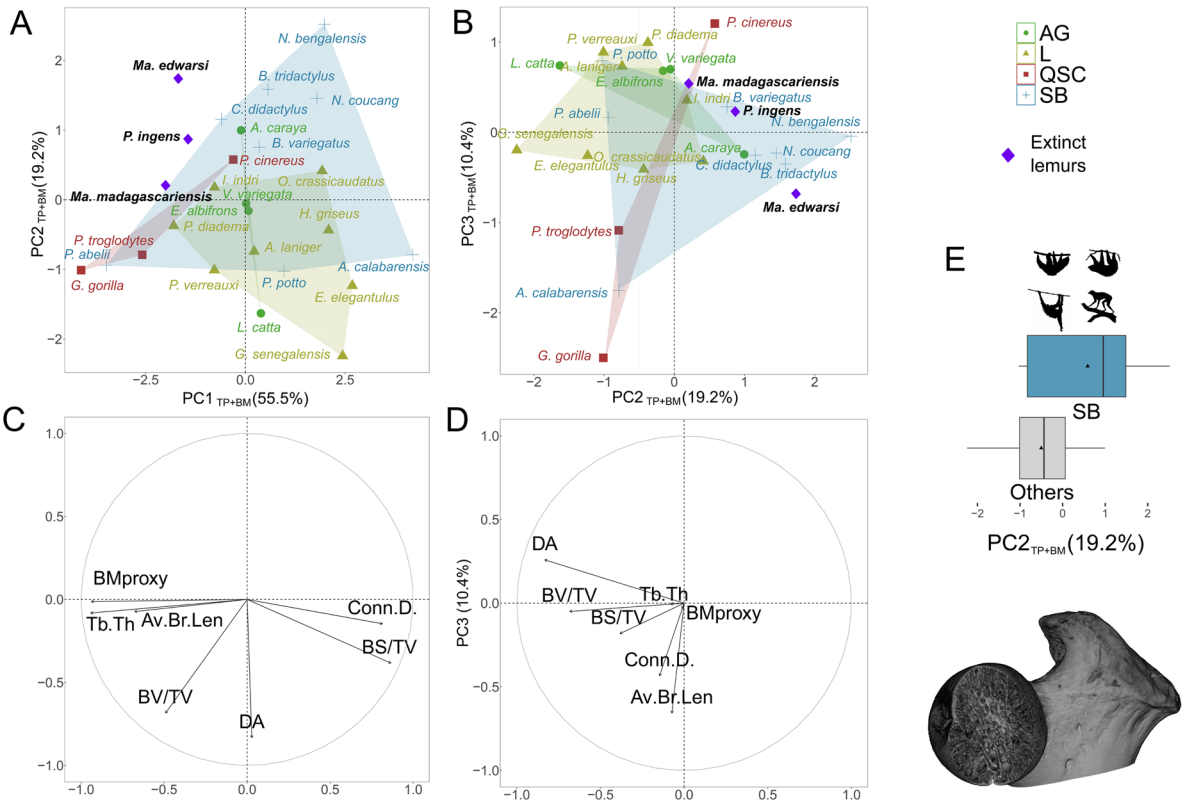

Figure 5. Proximal femur results of principal component analyses (PCA) on centred and scaled datasets including trabecular parameters and body mass proxy (PCA_{TP+BM}). A, B, PC1–PC2 (A) and PC2–PC3 (B) scatterplots, with extant species grouped by locomotor category and subfossil lemur data shown with purple rhombi. C, D, PC1–PC2 (C) and PC2–PC3 (D) variable loading plots. E, the univariate distribution of $PC2_{TP+BM}$, along which we identified the separation of suspensory/bridging (SB) from 'others', is shown through a boxplot.

show that proximal femoral $PC_{TP+BM}2$ is mainly driven by DA, especially ($R^2 = .69$), and BV/TV ($R^2 = .47$), and no other variables (Supporting Information, Table S18). Both DA and BV/TV contribute negatively to proximal femoral $PC2_{TP+BM}$, i.e. higher $PC2_{TP+BM}$ scores are yielded for lower DA and BV/TV (Fig. 5D; Table 3). Correlation tests also tell us that lateral and medial condyle $PC2_{TP+BM}$s are driven by BV/TV primarily, less strongly by Av.Br.Len, and not by other variables (no $P < .05$, with the only exception of DA in the medial condyle, $P = .02$, but with weak correlation, $R^2 = .19$; Supporting Information, Table S18). In the proximal femur, $PC3_{TP+BM}$ captures information on Av.Br.Len and, albeit weakly, on Conn.D ($R^2 = .18$), and no other variables (Fig. 5D; Supporting Information, Table S18). Correlation tests show that the lateral and medial condyle $PC3_{TP+BM}$s are mainly driven by DA and no other variables (Supporting Information, Table S18; Figs 6D, 7D). DA contributes negatively to lateral and medial condyles $PC3_{TP+BM}$s, i.e. lower DA is shown by taxa yielding higher $PC3_{TP+BM}$ scores (Figs 6D, 7D; Table 3).

On the femoral $PC2_{TP+BM}$–$PC3_{TP+BM}$ morphospaces, we visually identified a pattern of discrimination of 'SB' from all the other taxa ('others' hereafter) that possibly caused the significant relationship with locomotion arising from multivariate PGLSs and phylogenetic MANCOVAs for two femoral epiphyseal regions (Table 2). We focused on the discrimination between 'SB' and 'others', because in all the femoral anatomical levels, subfossil lemurs tended to lie in the morphospace areas occupied by 'SB', making this trend of interest for the focus of this work (Figs 5B, 6B, 7B). In the proximal femur, 'SB' tend to yield high $PC2_{TP+BM}$ scores (although *Perodicticus potto*, *Pongo abelii* Lesson, 1827, and *Arctocebus calabarensis* lie within 'others'; Fig. 5B). In the lateral and medial condyle, 'SB' yielded higher $PC3_{TP+BM}$ scores [with some exceptions: for the lateral condyle, the 'SB' *Pongo pygmaeus* (Linnaeus, 1760) lies within 'others', and *Pan troglodytes* (Blumenbach, 1775), belonging to 'others', instead lies within 'SB'; for the medial condyle, the position of a few taxa belonging to 'others', i.e. *Gorilla gorilla*, *Avahi laniger* (Gmelin, 1788), and *Pan troglodytes*, cause overlap with the 'SB' range; Figs 6B, 7B]. The $PC2_{TP+BM}$ pattern for the proximal femur and the $PC3_{TP+BM}$ patterns for lateral and medial condyles (Figs 5E, 6E, 7E) were all confirmed qualitatively through PGLSs and ANOVAs (Table 3).

All the patterns identified in the humeral and femoral PCA_{TP+BM} scatterplots outlined above are not driven primarily by the inclusion of BMp in the PCAs. Indeed, the distribution of locomotor groups, the positions of subfossil lemurs, and the variable loading plots remain largely unaltered in the PCA_{TP} scatterplots (cf. Figs 3–7 and Supporting Information, Figs S1–S5).

Phylogenetic discriminant function analysis

As detailed above, the discrimination between 'SB' and 'others' was the only pattern of interest yielded by trabecular structure. It was caused only by femoral traits and, specifically, by higher $PC2_{TP+BM}$ (primarily corresponding to lower BV/TV and DA) in the femoral head PCA_{TP+BM} (Fig. 5E) and by higher $PC3_{TP+BM}$

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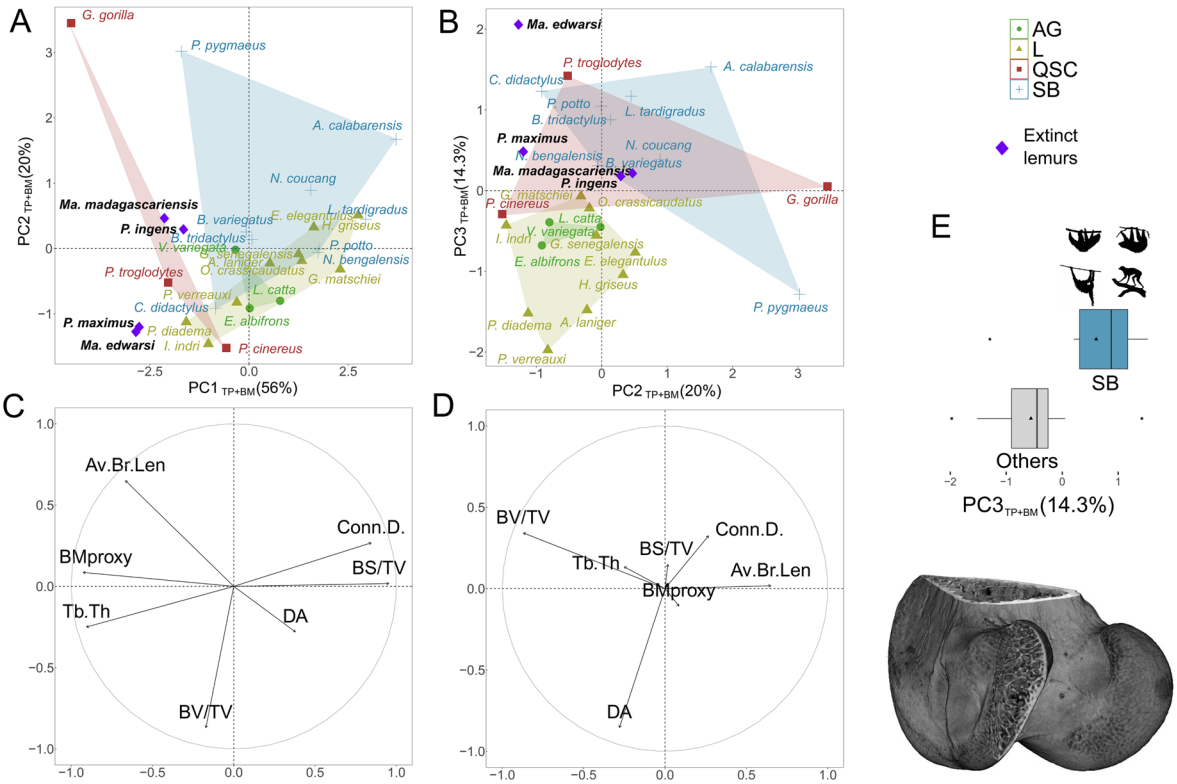

Figure 6. Lateral femoral condyle results of principal component analyses (PCA) on centred and scaled datasets including trabecular parameters and body mass proxy (PCA_{TP+BM}). A, B, PC1–PC2 (A) and PC2–PC3 (B) scatterplots, with extant species grouped by locomotor category and subfossil lemur data shown with purple rhombi. C, D, PC1–PC2 (C) and PC2–PC3 (D) variable loading plots. E, the univariate distribution of $PC3_{TP+BM}$, along which we identified the separation of suspensory/bridging (SB) from 'others', is shown through a boxplot.

(mainly corresponding to lower DA) in both the lateral and the medial condyle PCA_{TP+BM}s (Figs 6E, 7E). Hence, we took the trabecular traits primarily contributing to these femoral PC_{TP+BM}s (i.e. BV/TV_{prox}, DA_{prox}, $DA_{lat.con}$, and $DA_{med.con}$, identified as detailed above) and we built a multivariate heterogeneous dataset including only extant taxa (i.e. the training set), on which we trained a pDFA model that is, accordingly, potentially able to classify taxa in 'SB' or 'others'. The heterogeneous dataset confirmed the potential to discriminate 'SB' from 'others' (multivariate PGLS and phylogenetic MANOVA, $P = .002$), and the pDFA model trained on the training set yielded a misclassification rate of .14. We considered this value as sufficiently low (i.e. the model correctly predicted locomotion for 86% of the observations excluded during leave-one-out cross-validation). The pDFA generated a single discriminant function (i.e. DF1), because the model accounted for only two classes (i.e. 'SB' vs. 'others'). DF1 was positively correlated with all the variables on which the model was run (Supporting Information, Table S16) and, as shown with a boxplot, it neatly separated 'SB' (lower DF1, i.e. thus lower femoral BV/TV_{prox}, DA_{prox}, $DA_{lat.con}$, and $DA_{med.con}$) from 'others' (Fig. 8). The pDFA model, run on *Megaladapis madagascariensis*, *Megaladapis edwardsi*, and *Palaeopropithecus ingens* Grandidier, 1899 (the three subfossil lemur species for which we had data from the proximal femur, lateral condyle, and medial condyle), classified *Megaladapis edwardsi* and *Palaeopropithecus ingens* as 'SB' in 100% of the iterations, whereas *Megaladapis madagascariensis* was never classified as 'SB'.

DISCUSSION

Locomotor signal in extant mammal trabecular structure

When assessing the locomotor categories that we established mapped onto the phylogeny, it becomes evident that, although some clades are characterized by displaying a single locomotor category (e.g. all galagids are classified into the leaping category), the overall distribution reveals multiple independent acquisitions of the same (broadly defined) locomotor behaviour across distant lineages [e.g. SB in *Pongo* Lacépède, 1799, Bradypodidae, Choloepodidae, and Lorisidae; leaping in Galagidae, Indriinae, and *Hapalemur griseus* (Link, 1795); Fig. 1B]. This distribution supports the interpretation that any trabecular similarity among taxa sharing the same locomotor category in different regions of the phylogeny may be attributed to functional adaptations related to locomotor behaviours. Also, the relationship between trabecular structure and locomotion was tested through phylogenetically informed analyses (e.g. PGLS and pDFA) that account for shared phylogenetic history of the studied taxa. It ensures that the locomotion-related patterns that we found and discuss below are not attributable to phylogenetic affinity. We aimed not only to exclude phylogenetically driven patterns but potentially to observe them, in case they were dominant (i.e. by observing closely related taxa clustering in a region of the morphospace, such as subfossil lemurs more closely resembling other Malagasy strepsirrhines). This rationale was at the basis of our choice to use traditional PCAs instead of other techniques that erase phylogenetic trends (e.g. phylogenetic PCA; Polly *et al.* 2013), for qualitative assessments.

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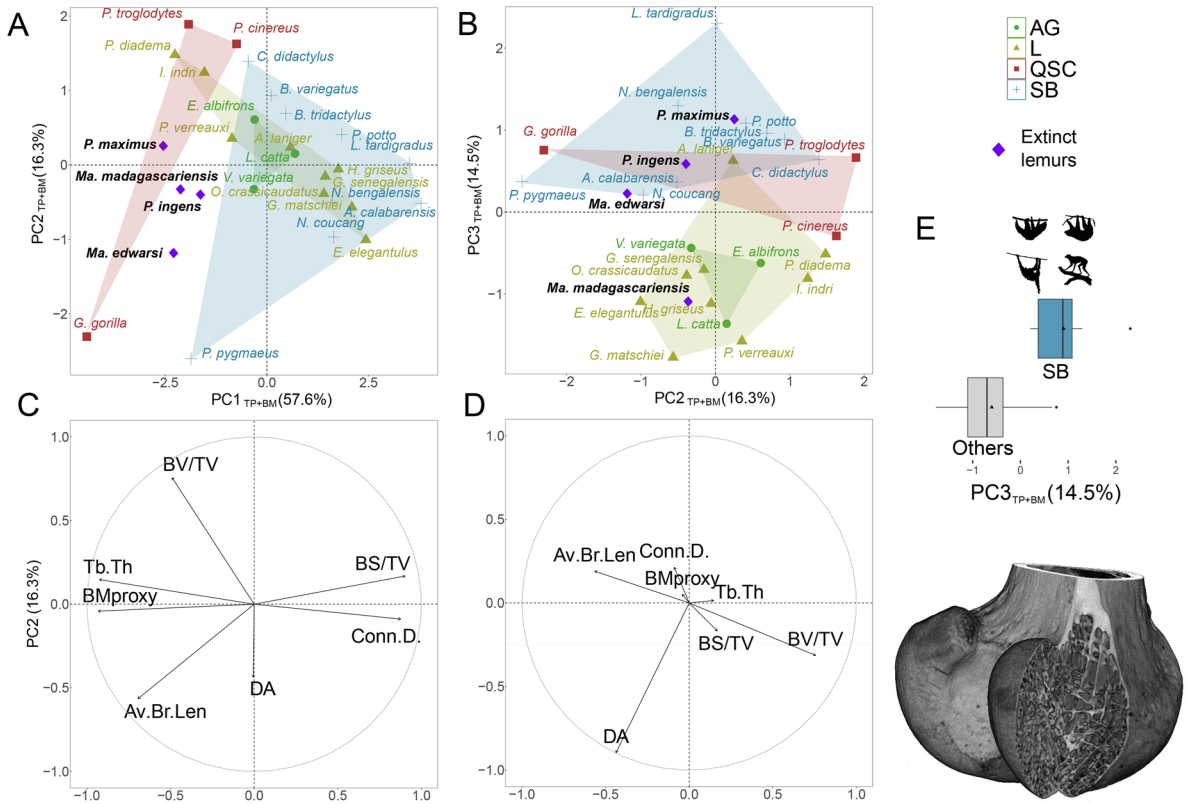

Figure 7. Medial femoral condyle results of principal component analyses (PCA) on centred and scaled datasets including trabecular parameters and body mass proxy (PCA_{TP+BM}). A, B, PC1–PC2 (A) and PC2–PC3 (B) scatterplots, with extant species grouped by locomotor category and subfossil lemur data shown with purple rhombi. C, D, PC1–PC2 (C) and PC2–PC3 (D) variable loading plots. E, the univariate distribution of $PC3_{TP+BM}$, along which we identified the separation of suspensory/bridging (SB) from 'others', is shown through a boxplot.

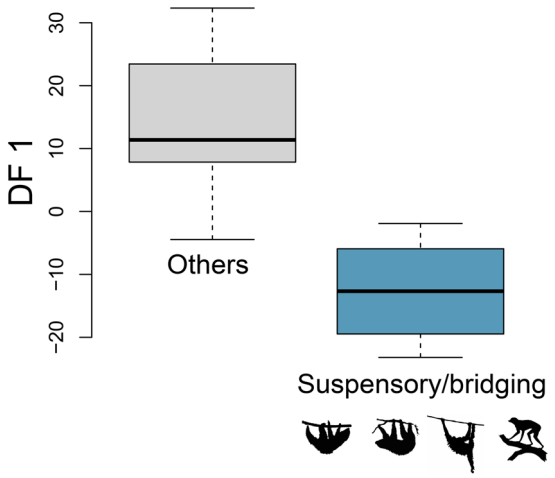

Figure 8. Distribution of discriminant function (DF1), deriving from a phylogenetic discriminant function analysis run on four predictor trabecular variables.

Regarding allometric effects, in both humeral and femoral PCAs they are mostly captured in $PC1_{TP+BM}$s (Figs 3C, 4C, 5C, 6C, 7C). Given that PC1 normally accumulates most of the variance in a PCA, a strong allometric effect on $PC1_{TP+BM}$s suggests that body mass is a major driving factor of trabecular bone in the sample studied. This was also evident from PGLSs (Table 2), and it is consistent with previous findings in mammals (Doube *et al.* 2011, Amson *et al.* 2017), especially primates (Ryan and Shaw 2013, Alfieri *et al.* 2025a), but also in other amniotes, both in broad amniote samples (e.g. Gônet *et al.* 2023) and in specific clades, such as birds (Doube *et al.* 2011, Alfieri *et al.* 2025b) and non-avian reptiles (Plasse *et al.* 2019). Investigation of detailed scaling patterns is outside the scope of this work, but it is interesting to note that, for instance, Conn.D and BS/TV positively co-vary in driving $PC1_{TP+BM}$s across all the studied regions (see the directions of loading vectors in Figs 3C, 4C, 5C, 6C, 7C), which is consistent with previous works (e.g. Gônet *et al.* 2023) and expected structural patterns (i.e. the higher Conn.D., the higher the number of trabeculae, and the greater the bone surface).

In all the PGLSs that we ran across the studied anatomical regions, effects of body mass were separated from locomotor ones. Hence, the effects of locomotion found in the PGLSs (Table 2) were already isolated from allometry. Also, all the locomotor patterns discussed below were derived from $PC2_{TP+BM}$s or $PC3_{TP+BM}$s and from two variables (BV/TV and DA) that largely did not include body mass effects. Indeed, no significant correlation with BMp was found for these parameters in the femoral datasets, with the only exceptions of BV/TV in the head and lateral condyle that were weakly correlated with BMp (Supporting Information, Table S19), and with BV/TV from lateral condyle that, importantly, was not used in the locomotor reconstructions. DA and/or BV/TV not being correlated to body mass aligns with many previous works (e.g. Cotter *et al.* 2009, Doube *et al.* 2011, Barak *et al.* 2013a, Fajardo *et al.* 2013, Rolvien *et al.* 2017, Kivell *et al.* 2018, Plasse

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Table 3. Results from phylogenetic generalized least squares regressions and phylogenetic ANOVAs testing the discrimination of 'SB' from 'others', run with the PC_{TP+BM}s (listed in the table, besides the explained portion of variance and by which traits they are mainly driven) that were previously identified as potentially yielding this locomotor information (for details, see the Materials and Methods).

Anatomical region (articulation)	Principal components	Proportion of variance (%)	Mainly related to	'SB'–'others' *P*-value
Proximal femur (femoral head)	$PC_{TP+BM}2$	19.18	BV/TV (inversely) DA (inversely)	.028
Distal femur (lateral condyle)	$PC_{TP+BM}3$	14.34	DA (inversely)	.001
Distal femur (medial condyle)	$PC_{TP+BM}3$	14.48	DA (inversely)	<.001

et al. 2019, Gônet *et al.* 2023) and indicates that the locomotion-related patterns we propose are independent of allometric effects. Moreover, the successful isolation of these two allometrically independent variables supports our choice to account for body mass effects by excluding PC1s (common practice in shape analyses; e.g. Somers 1989, Klingenberg 2022) instead of using other size-correction techniques, such as those based on regression residuals (which previously proved to not to exclude allometric effects fully from trabecular variables; e.g. Alfieri *et al.* 2025a). Concerning allometric effects, it is also important to note that, because VOIs represent the largest spheres or hemispheres containing only trabecular bone in each studied epiphysis, differences in VOI size reflect differences in epiphyseal joint size. As detailed in the Supporting Information (Appendix S9), epiphyseal metric measurements were used to predict the BMp for fragmentary specimens, which could not yield centroid size estimates because they were not analysed using three-dimensional geometric morphometrics by Alfieri *et al.* (2023). This prediction was possible owing to the strong correlation between values derived from epiphyseal metric measurements and BMp (Alfieri *et al.* 2023). Consequently, because VOI size depends on epiphyseal joint size and joint size is indirectly related to BMp, VOI size can reasonably be assumed to reflect differences in body mass. Differences in VOI size across the sample are therefore expected to have affected the results in a manner similar to body mass, with $PC1_{TP+BM}$s probably capturing most allometric effects, in addition to those associated with VOI size variation, and largely excluding these effects from $PC2\text{-}3_{TP+BM}$s, on which our functional inference is based.

The femoral trabecular structure yielded a relationship to locomotor behaviour, i.e. significant correlation between trabecular parameters of the femoral condyles and locomotor categories (Table 2, with proximal femoral trabecular properties yielding a *P*-value approaching significance). The $PC2_{TP+BM}$–$PC3_{TP+BM}$ morphospaces suggested that overall femoral trabecular structure is able to discriminate suspensory/bridging mammals (SB, i.e. lorisids, tree-sloths, and orangutans) from all the other extant mammals. Specifically, SB mammals are distinct for showing, on average, higher proximal femur $PC2_{TP+BM}$ scores (Fig. 5B), higher lateral condyle $PC3_{TP+BM}$ scores (Fig. 6B), and higher medial condyle $PC3_{TP+BM}$ scores (Fig. 7B). These patterns were confirmed quantitatively (see also Figs 5E, 6E, 7E) and, as indicated by loading vectors, are primarily driven by low BV/TV_{prox}, DA_{prox}, $DA_{lat.con}$, and $DA_{med.con}$ (Figs 5D, 6D, 7D; Table 3). Accordingly, when these four femoral trabecular parameters were analysed, they significantly discriminated SB from other taxa and, when used in a pDFA, yielded a DF that neatly discriminated SB from other mammals (Fig. 8) and that correctly classified them with a high success rate (i.e. 86%). Thus, multiple lines of evidence suggested that SB mammals differ from others by exhibiting lower bone volume (i.e. low BV/TV) in the proximal femur and a more isotropic trabecular structure (i.e. low DA) across all femoral levels. Proximal femur trabecular structure proved to be related to locomotor activities in many previous studies mostly focusing on the mammal, especially primate, femoral head (e.g. Fajardo and Müller 2001, MacLatchy and Müller 2002, Ryan and Ketcham 2002b, 2005, Ryan and Krovitz 2006, Saparin *et al.* 2011, Ryan and Shaw 2012, Mielke *et al.* 2018, Georgiou *et al.* 2019, 2020, Alfieri *et al.* 2022), aligning with our results.

Femoral low DA and BV/TV in SB mammals: functional interpretations

A functional interpretation for lower femoral DA and BV/TV in SB mammals compared with others is consistent with the fact that these two parameters can generally provide sufficient information on the biomechanical regime and, accordingly, on locomotor habits, because cumulatively they explain ≤98% of bone stiffness (through their contribution to Young's modulus; Stauber *et al.* 2006, Maquer *et al.* 2015).

As shown experimentally, trabecular orientation tends to follow loading directions (Biewener *et al.* 1996, Pontzer *et al.* 2006), which can, in turn, be informative on locomotor habits. DA captures the degree of preferential alignment of trabeculae, hence not the specific directions (e.g. in degrees of arc) of trabeculae but the extent to which they are uniformly oriented (as computed here, from DA = 0, i.e. highly multidirectional or fully isotropic structure, to DA = 1, highly directional or fully anisotropic structure; Harrigan and Mann 1984). Thus, DA is positively related to directional stereotypy of movements involved in locomotor activities, e.g. high DA is caused by fossoriality (Amson *et al.* 2017) and bipedalism (Ryan *et al.* 2018, Georgiou *et al.* 2019), whereas low DA derives from multidirectional locomotor repertoires. Arboreality represents a paradigmatic example of the latter condition, because moving in trees results in highly variable directions of biomechanical loadings (Carlson 2005, Demes *et al.* 2006). Our sample is represented by taxa that, to several extents, show arboreal habits (Fig. 1), hence the lower DA in both the proximal and distal femur of SB mammals possibly reflects their outstandingly broader mobility in the hip and knee joints (Ishida *et al.* 1992, Runestad 1997, Thorpe and Crompton 2005, Zihlman *et al.* 2011, Nyakatura 2012, Marshall *et al.* 2021, Youlatos *et al.* 2025), even in comparison to other arboreal taxa, whose joints are also expected to be relatively mobile. An exception is represented by leaping taxa that, although being fully arboreal, are characterized by a distinctive behaviour related to powerful leaps and take-offs that cause high directional stereotypy and, as expected, high DA

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(as found by Ryan and Ketcham 2002b, 2005). An extreme mobility in hip and knee joints, related to SB locomotion, has been reported, or derived from joint/muscle configuration, for orangutans (Thorpe and Crompton 2005, Zihlman *et al.* 2011), lorisids (Ishida *et al.* 1992, Runestad 1997, Youlatos *et al.* 2025), and tree-sloths (Nyakatura 2012, Marshall *et al.* 2021). Thus, SB taxa possibly occupy a positive extreme on the arboreal range of hindlimb joint mobility, and the consequent substantially multidirectional loadings acting on the hip and knee result in particularly isotropic trabeculae, i.e. low DA.

BV/TV measures the proportion of inner epiphysis occupied by ossified fraction and informs on trabecular bone compactness. Increased loadings are expected to unbalance bone modelling (*sensu* Barak 2020) in favour of bone deposition at the expense of bone reabsorption and resulting in a greater bone fraction, whereas the opposite is expected under decreased loading regimes (Pearson and Lieberman 2004). Within an epiphysis, it is reflected by BV/TV and, accordingly, a positive relationship between trabecular bone fraction and loadings has been found or hypothesized (e.g. Chang *et al.* 2008, Modlesky *et al.* 2008, Ryan and Shaw 2015). In this framework, the lower femoral BV/TV shown by SB taxa is possibly justified by particularly low hindlimb loadings related to arboreality based on SB. This condition has been consistently discussed for tree-sloths, owing to their outstandingly cautious lifestyle (e.g. Alfieri *et al.* 2021, 2022). Moreover, low hindlimb loadings have been proposed for lorisids, which in this regard are considered remarkable exceptions to primate hindlimb dominance (see above) (Ishida *et al.* 1990, Hanna *et al.* 2017, Yapuncich and Granatosky 2021). The same is likely to apply to orangutans, which, accordingly, show poorly robust hindlimb diaphyses (e.g. Ruff 1988). Based on these functional interpretations, we posit that low DA and BV/TV in the respective femoral epiphyses of subfossil lemurs are indicators of SB in these extinct taxa.

The locomotor behaviour of palaeopropithecines

We found strong confirmation for *Palaeopropithecus* as the most extremely suspensory sloth-lemur. Indeed, *Palaeopropithecus ingens* and/or *Palaeopropithecus maximus* always felt within the range that we interpreted as characterizing SB (i.e. higher femoral head PC2 scores and femoral condyles PC3 scores; Figs 5B, 6B, 7B). Furthermore, *Palaeopropithecus ingens*, the only sloth-lemur species for which we had data from all the studied femoral epiphyseal regions, was classified as SB in 100% of the iterations by the pDFA model. Thus, we add femoral trabecular structure to the growing list of anatomical traits (e.g. Jungers 1980, Jungers *et al.* 1991, Shapiro *et al.* 1994, 2005, Godfrey *et al.* 1995, Wunderlich *et al.* 1996, Hamrick *et al.* 2000, Godfrey and Jungers 2003, Patel *et al.* 2013, Marchi *et al.* 2016, Granatosky 2018, 2020, 2022) indicating that *Palaeopropithecus* spp. were large lemurs exhibiting highly specialized suspensory arboreality.

Previous works have proposed suspensory habits in *Babakotia* and *Mesopropithecus* too, but less extreme in comparison to *Palaeopropithecus* (Jungers *et al.* 1991, 2002, Simons *et al.* 1992, Godfrey *et al.* 1995, Hamrick *et al.* 2000, Godfrey and Jungers 2003, Shapiro *et al.* 2005, Marchi *et al.* 2016). Our results do not allow us to contribute to this view, owing to the availability/preservation of the specimens and the informative power that arose from the study of extant taxa, i.e. only femoral trabecular structure can be used for locomotor inference. Indeed, the fact that we had only humeral data for *Babakotia* and *Mesopropithecus* limits our inferential power on these smaller sloth-lemurs. Thus, we encourage further work to study femoral trabecular data on *Babakotia* and *Mesopropithecus* to test whether their DA and BV/TV are low enough to indicate suspensory/bridging habits for these two taxa too.

The locomotor behaviour of *Megaladapis* spp.

Despite early reconstructions not necessarily inferring an arboreal lifestyle for *Megaladapis*, with even an aquatic ecology having been suggested following the first fossil discoveries (summarized in Godfrey and Jungers 2002), in the last decades evidence from many postcranial skeletal traits indicates an arboreal lifestyle for koala-lemurs (Jungers 1978, Wunderlich *et al.* 1996, Godfrey and Jungers 2002, Godfrey *et al.* 2016). However, doubts remain concerning the type of arboreal behaviour that koala-lemurs engaged in across species. According to an earlier view, all the species belonging to the genus *Megaladapis* engaged in vertical climbing and clinging, Hence, in this framework, *Megaladapis* spp. would be represented by size and geographical variants (Carleton 1936, Jungers 1977, 1978). However, more recent inferences hypothesized the presence of two sublineages: *Megaladapis*, including the medium-small sized species *Megaladapis madagascariensis* and *Megaladapis grandidieri*, widely distributed in Madagascar, exhibiting more arboreal habits and mainly featuring vertical climbing (with additional potential behaviours, such as quadrupedal hanging and pedal suspension; Wunderlich *et al.* 1994, 1996, Jungers *et al.* 2002, 2008), and *Peloriadapis*, corresponding to *Megaladapis edwardsi* that, mainly owing to its large body size, has been proposed as relatively more terrestrial in comparison to other *Megaladapis* species (Wunderlich *et al.* 1994, 1996, Jungers *et al.* 2002, 2008). Our results did not yield the informative power allowing us to identify vertical climbing from femoral trabecular bone. This locomotor habit can be ascribed to the arboreal generalist (AG) and/or quadrupedalism/scrambling/clambering (QSC) within our categories [especially the latter, remarkably representing the koala *Phascolarctos cinereus* (Goldfuss, 1817)], but the trabecular data that we analysed did not reveal differences related to these locomotor styles. Instead, our results provide support for the existence of locomotor differences between small/medium and large koala-lemurs. Focusing on the femoral data, the smallest (*Megaladapis madagascariensis*) and the largest (*Megaladapis edwardsi*) koala-lemurs are distant in the femoral morphospaces, with *Megaladapis edwardsi* lying within the SB range of variation [i.e. higher $PC2_{TP+BM}$ scores in the head (Fig. 5B) and higher $PC3_{TP+BM}$ scores in the medial condyle, although close to the 'non-SB' range (Fig. 7B)] or even yielding the most extreme score in the direction interpreted as characterizing SB (i.e. extremely high $PC3_{TP+BM}$ score in the lateral condyle; Fig. 6B). In this regard, the results of pDFA for *Megaladapis madagascariensis* and *Megaladapis edwardsi* are striking. The smaller taxon *Megaladapis madagascariensis* was never classified as 'SB' across all the iterations, whereas the larger *Megaladapis edwardsi* was classified as SB in 100% of the iterations, mirroring *Palaeopropithecus* (see above). The remarkable aspect of this outcome mainly concerns the reconstruction of

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Megaladapis edwardsi as an extremely SB *Palaeopropithecus*-like taxon. This represents a new view that, to the best of our knowledge, has never been proposed before. In the traditional locomotor reconstruction of koala-lemurs, quadrupedal hanging and pedal suspension have been proposed in addition to the dominant vertical climbing (Wunderlich *et al.* 1994, 1996, Jungers *et al.* 2002, 2008), but this description did not refer to interspecific differences within *Megaladapis*, i.e. the wide arboreal repertoire was proposed for the entire genus. Here, instead, we highlight the intrageneric locomotor differences in *Megaladapis* but not aligning to the previously proposed relatively higher terrestriality of *Megaladapis edwardsi* (Wunderlich *et al.* 1994, 1996, Jungers *et al.* 2002, 2008). Here, the latter instead appears to be adapted substantially to SB arboreal habits; an adaptation that involves greater exploitation of trees, rather than reduced use. We are aware that this is a preliminary result, which should be confirmed by future work representing more *Megaladapis edwardsi* data and more directly testing this hypothesis (e.g. studying femoral diaphyseal cross-sections of koala-lemurs) and owing to the contradictory humeral results. However, *Megaladapis edwardsi* being a fully suspensory/bridging arboreal species is remarkable considering the reconstructed body mass for this taxon, ∼85 kg (Jungers *et al.* 2008), with more recent estimates suggesting an average of ∼65 kg but estimates for single specimens reaching up to ∼76 kg (Thompson *et al.* 2025). As of today, orangutans are the largest known extinct or extant mammals showing SB arboreal habits, with adult males of the largest orangutan species (i.e. Bornean orangutan *Pongo pygmaeus*) reaching 74 ± 9.78 kg (Rayadin and Spehar 2015); estimates that are consistent with older body mass estimates (e.g. 78 kg; Smith and Jungers 1997). Other paradigmatic arboreal SB mammals are characterized by smaller body mass (e.g. tree-sloths, 4–6 kg; Nowak 1999), even when other possibly extremely suspensory/bridging large-sized extinct lemurs are considered [*Palaeopropithecus* spp., ∼41–46 kg (Jungers *et al.* 2008); ∼30 kg (Thompson *et al.* 2025)]. Thus, the extreme SB adaptations of *Megaladapis edwardsi* would place it within the body size range of Bornean orangutans, making it one of the largest mammals capable of this behaviour, along with all the distinctive morphophysiological adaptations required to sustain such a specialized lifestyle (Granatosky 2022, Nyakatura *et al.* in press). *Archaeoindris* is another sloth-lemur (not studied in this work), and it is the largest reconstructed subfossil lemur [i.e. ∼161 kg (Jungers *et al.* 2008); ∼128 kg (Thompson *et al.* 2025)]. However, differently from other sloth-lemurs, such as *Palaeopropithecus*, its locomotion is still poorly understood owing to the few fragmented preserved postcranial elements for which locomotor inferences have been attempted: e.g. slow-moving arboreality, arboreal climbing and clinging, or ground sloth-like scansoriality (Godfrey and Jungers 2002, Godfrey *et al.* 2016). Retrieving and studying additional postcranial material of *Archaeoindris* might help to identify new instances of exceptionally large mammals with varying degrees of arboreal adaptation.

Final remarks

The absent locomotor signal in humeral trabecular bone, as revealed by multivariate inferential analyses (Table 2) and the fact that no visual distinctions between locomotor categories could be found in $PC2_{TP+BM}$–$PC3_{TP+BM}$ morphospaces (Figs 3B, 4B), contrasts with the femoral trabecular pattern and, in this way, aligns to previous evidence. A discrepant pattern between humeral and femoral anatomy, with the latter being more informative on locomotor habits, arose in the study by Ryan and Shaw (2012), agreeing with outcomes from primate diaphyseal principal moments of area (Carlson 2005). Also, Ryan and Walker (2010) highlighted different patterns between primate humeral and femoral trabecular bone. These interlimb trends were previously justified by the fact that in primates the vertical peak ground reaction forces to which hindlimbs are subjected are higher than those experienced by forelimbs (Scherf *et al.* 2013). This evidence is consistent with indications of higher hindlimb loadings provided by Ryan and Walker (2010) and has been built by studying different quadrupedal species from almost all primate subgroups (e.g. Kimura *et al.* 1979, Kimura 1985, 1992, Demes *et al.* 1994, Schmitt and Hanna 2004, Young 2012). Hence it can be considered a general primate condition ('hindlimb dominance') that is opposite to the one shown by other mammals (Larson 1998, Young 2012). If we consider that our extant mammal sample is largely composed of primates, hindlimb dominance might potentially explain the discrepant results between femoral and humeral trabecular structure. The composition of our sample might be related to another explanation for the absence of locomotor signal in humeral trabecular bone. Indeed, many studies that found an absent/weak locomotor signal in humeral trabecular structure (see above) focused on distantly related species, representing different phylogenetic subgroups (primates in the work by Ryan and Walker 2010, Ryan and Shaw 2012), in this regard mirroring our sample (Fig. 1). Hence, humeral trabecular structure might not co-vary strongly with locomotor behaviour when it is analysed across phylogenetically broad samples. This condition might not allow us to distinguish even highly divergent locomotor styles (e.g. see the strikingly similar humeral trabecular bone in bipeds and quadrumanous climbers in the study by Ryan and Shaw 2012). On the contrary, when restricted taxonomic contexts are analysed, broad-scale effects (e.g. phylogenetic, allometric) might be minimized, and functional aspects might be highlighted in forelimb trabecular structure. It would be consistent with the apparent locomotor signal found in humeral trabecular bone when restricted groups, e.g. hominids, were analysed (Scherf *et al.* 2013, Kivell *et al.* 2018), contrasting results from works focusing on distantly related taxa (Ryan and Walker 2010, Ryan and Shaw 2012). A similar explanation might justify the absence or limited locomotor signal in the trabecular structure of other skeletal regions, again in primates (e.g. distal fibula; Alfieri *et al.* 2025a) and even outside mammals [e.g. squamates, turtles, and crocodiles (Plasse *et al.* 2019); extant birds (Alfieri *et al.* 2025b); broad amniote sample (Reinecke and Angielczyk 2025)]. Future work on humeral vs. femoral trabecular structure of more extensive and diverse samples might help to elucidate the locomotor effects in taxonomically and phylogenetically broad contexts and how humeral/femoral patterns differ between primates and non-primates.

Apart from these considerations, it should be noted that in the proximal humeral $PC2_{TP+BP}$–$PC3_{TP+BP}$ biplot, *Pongo pygmaeus* occupies an outlying position in comparison to the other SB taxa, which tend to show higher $PC2_{TP+BP}$ scores (Fig. 3B). This suggests that the outlying proximal humeral results for this SB species alone

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might have prevented detection of significant locomotor effects from PGLSs ($P = .21$; Table 2). Remarkably, *Pongo pygmaeus* proximal humerus data come from a single specimen (i.e. *Pongo pygmaeus* ZSM 1907-609; Supporting Information, Table S1), whose patterns might not be representative of the species (a point that future studies might clarify). Thus, proximal humeral trabecular bone might have informed us about locomotion in a way similar to femoral trabecular traits if another individual or more individuals were chosen. Namely, SB would have been distinct compared with all the other taxa, through one single PC_{TP+BP} that is driven by low DA (similarly to femoral data) and by high BV/TV. The latter would represent the opposite pattern compared with the femoral one (i.e. low BV/TV in SB; see above). However, considering the strong loads experienced by the forelimbs in suspensory taxa, even in primates, where this may reverse the typical 'hindlimb dominance' characteristic of the group (Granatosky 2016), the humeral pattern could also be interpreted in functional terms (also considering that proximal humeral BV/TV has no relationship with BMp, see Results). In this framework, all subfossil lemurs would occupy the extreme peripheral range of the SB morphospace region. This would occur especially for *Palaeopropithecus* (both *Palaeopropithecus ingens* and *Palaeopropithecus kelyus*), whereas *Mesopropithecus* and *Babakotia* would occupy less distinctive regions. If more extreme positions in the SB region correspond to more extreme suspensory/bridging adaptations, then the humeral data results for subfossil lemurs would be consistent with previous locomotor reconstruction (Jungers *et al.* 1991, 2002, Simons *et al.* 1992, Godfrey *et al.* 1995, Hamrick *et al.* 2000, Godfrey and Jungers 2003, Shapiro *et al.* 2005, Marchi *et al.* 2016). Likewise, the more extreme position of *Megaladapis madagascariensis* compared with *Megaladapis edwardsi* would suggest more extreme suspensory/bridging arboreal habits in the former, small koala-lemur compared with the latter, large koala-lemur. However, this would partly contradict what we proposed based on femoral trabecular structure (see above). Future work investigating already available or newly unearthed postcranial material of subfossil lemurs is needed to clarify these puzzling patterns. It might be time to consider that the exceptional features of subfossil lemurs, such as their unusually large body mass relative to strepsirrhine standards, might make locomotor inference based solely on extant analogues limiting, as has been suggested for other peculiar mammalian groups (e.g. xenarthrans; Vizcaíno *et al.* 2018).

Finally, the single observations representing exceptions to the main patterns for femoral trabecular structure that we found (Figs 5B, 6B, 7B and above) should briefly be discussed. For instance, the chimpanzee *Pan troglodytes*, in this work categorized as QSC, often lies within the range interpreted as characterizing SB for femoral head (i.e. higher $PC2_{TP+BP}$ scores), lateral condyle (i.e. higher $PC3_{TP+BP}$ scores) and medial condyle (i.e. higher $PC3_{TP+BP}$ scores). The chimpanzee shows some SB in its locomotor repertoire (Supporting Information, Table S3; Granatosky 2018, Hunt 2022), which explains its position in the locomotor behaviour PCA, i.e. tending more, compared with *Gorilla gorilla*, to high PC1 scores, for which higher portions are occupied by SB (Fig. 1A). Also, the black howler *Alouatta caraya* (AG category, in this work) and the eastern woolly lemur *Avahi laniger* (L category, in this work) lie within the SB range of variation for proximal femoral and medial condyle data, respectively (Figs 5B, 6B, 7B), the latter also mirrored by *Gorilla gorilla* (QSC category, in this work). All these taxa, although assigned to other locomotor categories, rarely exhibit either bridging behaviour (*Alouatta caraya* and *Avahi laniger*) or suspensory behaviour (e.g. *Gorilla gorilla*), but not both, as is the case for *Pan troglodytes* (Supporting Information, Table S3), which, accordingly, lies within the SB range more often (see above). On the one hand, these patterns support the relationship between femoral trabecular properties and SB locomotion; on the other hand, they highlight again the common issue of locomotor discrete categories. In this work, we designed categories based on distribution on a PCA biplot, in turn deriving from locomotor quantitative data (Fig. 1A), because ultimately we needed discrete categories for the classification technique that we used, i.e. pDFA. However, assigning taxa to a single group inevitably obscures aspects of their locomotor diversity, such as the suspensory and/or bridging behaviours of African great apes. The latter are particularly difficult to categorize in broad mammalian contexts, because they display distinctive and nearly unique locomotor adaptations, such as knuckle-walking (Tarrega-Saunders *et al.* 2021), that resist classification into broad discrete categories. The complexity related to African great ape locomotor categorization is also reflected by the fact that their category in this work, i.e. QSC, often occupies wide morphospace regions, diagnostic of broad intra-category variability. Future works should aim to include quantitative behavioural data and analyse them as such, directly analysing the covariation between morphological and locomotor matrices.

CONCLUSION

In this work, we analysed the humeral and femoral trabecular structure of sloth- and koala-lemurs, addressing this aspect of their anatomy for the first time in a morphofunctional and comparative context, using a broad sample of extant mammals. We found that femoral trabecular structure distinguishes arboreal mammals that predominantly display suspensory and bridging behaviours, such as tree-sloths, lorisids, and orangutans. These taxa exhibit substantially more isotropic trabeculae and lower bone volume fraction; traits that can be interpreted functionally as adaptations to their specialized arboreal habits.

Accordingly, we found that the largest palaeopropithecine, *Palaeopropithecus*, was strongly adapted to a suspensory/bridging arboreal repertoire, aligning with previous reconstructions. However, incomplete or missing data prevented confirmation of previously reconstructed behaviours for other palaeopropithecines, namely *Babakotia* and *Mesopropithecus*. Regarding koala-lemurs, we could not provide a detailed reconstruction for the small *Megaladapis madagascariensis*, here only inferred as non-suspensory/bridging. Strikingly, however, we found that the largest species, *Megaladapis edwardsi*, was a specialized suspensory and bridging arboreal mammal. More studies are needed; nevertheless, our results provide evidence for one of the largest mammals ever known to show adaptations to an arboreal lifestyle characterized by the use of suspensory and bridging behaviour, alongside extant orangutans. These new insights substantiate the use of trabecular bone structure to clarify past locomotor habits

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and highlight the importance of studying or recovering additional postcranial elements from extinct primates.

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AUTHOR CONTRIBUTIONS

Fabio Alfieri (collection, processing, and analysis of µCT data; performing statistical analyses; drafting, writing, and editing of the manuscript; conceiving the study; designing the sample; planning statistical analysis steps; and interpreting results), Julia Arias-Martorell, Carla Argilés-Esturgó, and Damiano Marchi (conceiving the study; designing the sample; planning statistical analysis steps; interpreting results; and contributing to writing and editing of the manuscript).

SUPPLEMENTARY DATA

Supplementary data is available at *Zoological Journal of the Linnean Society* online.

CONFLICT OF INTEREST

None declared.

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DATA AVAILABILITY

Raw results and additional information on the studied specimens (Supporting Information, Tables S1 and S2, including MorphoSource ARK identified to download CT scan data), quantitative locomotor data on the studied species (Supporting Information, Table S3), summary statistics for all the PCAs (Supporting Information, Tables S4–S14), and additional methods and results (Supporting Information) can be downloaded from https://doi.org/10.6084/m9.figshare.30187675.v1.

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